Vegetation response to control of invasive alien European rabbits (*Oryctolagus cuniculatus*) on South African offshore islands: insights from Robben Island

By

Thabisisani Ndhlovu

Submitted in fulfilment of the academic requirements for the degree of
Doctor of Philosophy in Ecological Sciences

School of Life Sciences
College of Agriculture, Engineering and Science
University of KwaZulu-Natal
Pietermaritzburg
November 2023

GENERAL ABSTRACT

The European rabbit (*Oryctolagus cuniculus*), a small mammal native to the Iberian Peninsula, exemplifies the catastrophic effects of introducing invasive alien species to new environments. Released on uninhabited islands as a food source for early world explorers, these rabbits have established populations on over 800 islands worldwide, posing significant threats to biodiversity and human livelihoods. European rabbits have been introduced to some of the more than 33 offshore islands that occur along the southern African coast, 24 of which are part of South African territory. While the impact of invasive European rabbits on global ecosystems has been extensively studied, research on their effects on southern African offshore islands is comparatively sparse. A handful of studies have assessed rabbit herbivory’s impact on the vegetation of some South African offshore islands, but the vegetation’s response to rabbit control remains largely unexplored. Given that European rabbits are classified as a Category 1b invasive species under South Africa's National Environment Management: Biodiversity Act 10 of 2004, understanding how offshore island vegetation might respond to rabbit control is crucial, especially considering the islands' long history of rabbit occupation and highly degraded ecosystems.

This thesis examined an attempt to restore degraded vegetation on Robben Island, South Africa, through the control of invasive European rabbits. The aim was to understand the impact of rabbit control on the island's vegetation, particularly the potential effects of their removal. Changes in plant species cover were monitored at nine sites, including strand (n=3), eucalyptus (n=3), and inland dune (n=3), on the south-eastern part of Robben Island over four years (2010-2013). Vegetation monitoring followed an attempt to eradicate European rabbits from the island between 2008 and 2009. Robben Island, the largest and most environmentally degraded of South Africa's offshore islands, has a long history of rabbit occupation dating back to 1654. It is the only South African offshore island where there has been a deliberate and sustained effort to eradicate European rabbits. While South African offshore islands vary in geology, size, distance offshore, and climatic conditions, insights into vegetation dynamics on Robben Island following rabbit control could provide valuable understanding of potential vegetation responses on other invaded South African offshore islands.

The thesis addressed these specific questions:

Question 1: How did vegetation composition change following rabbit control on Robben Island and what ecological factors and vegetation processes underlay the observed changes? The thesis hypothesised that vegetation on Robben Island would revert to its original composition following rabbit control, with the re-establishment of late-successional perennial grasses, succulents, herbs, and an increase in woody shrubs. However, findings were contrary to this expectation in that instead of secondary succession towards the original composition, changes in plant species were solely driven by increases in early successional species, including the woody shrub *Tetragonia fruticosa* and grasses *Ehrharta longiflora*, *Cynodon dactylon*, and *Ehrharta villosa*. Secondly, there was no change in vegetation composition at eucalyptus sites due to subdued responses of *Phyllobolus canaliculatus*, *Oxalis pes-caprae* and *T. fruticosa* to rabbit control. These observations suggest a shift to an alternative stable degraded state rather than successional processes. Prolonged rabbit grazing has driven the island's vegetation beyond a critical ecological threshold, eliminating competitive late successional species and preventing them from driving successional change post-rabbit control. This results in an arrested succession state dominated by herbivory-resilient, early successional species. The vegetation composition at eucalyptus sites remained unchanged most likely because of the inhibitory effects of the alien trees on understory vegetation dynamics.

Question 2: How did vegetation species diversity change following rabbit control on Robben Island and what ecological factors and vegetation processes underlay the observed changes? The study hypothesised that rabbit control on Robben Island would boost species diversity by allowing suppressed palatable plant species to re-establish. It was further expected that residual non-rabbit herbivory would prevent these recovering species from dominating the vegetation and displacing less competitive species, leading to greater diversity. Findings showed that contrary to expectations, rabbit control led to a decrease in species diversity across strand and inland dune sites, while it remained unchanged at eucalyptus sites. The decline in diversity was due to the loss of seven plant species (*Anagallis arvensis*, *Euphorbia peplus*, *Hypochaeris glabra*, *Wahlenbergia androsacea*, *Emex australis*, *Ornithoglossum viride* and *Trachyandra* sp.), offset by the emergence of one species (*Cynodon dactylon*) at strand sites. In addition, species evenness declined across strand and inland dune sites following rabbit control. Before rabbit control, species cover at these sites was dominated by four species (*Conicosia pugioniformis*, *Oncosiphon suffruticosum*, *E. peplus,* and *A. arvensis*) and six species (*O. viride*, *E. australis*, *Trachyandra* sp., *O. suffruticosum*, *C. pugioniformis,* and *Bromus diandrus*) respectively, but after control, it was dominated by *T. fruticosa* and *E. longiflora* at strand and *T. fruticosa* and *E. villosa* at inland dune sites at each site. The changes in species diversity were attributed to the long-term effects of rabbit herbivory on the island's vegetation. Prolonged rabbit herbivory depleted palatable plant species, leaving a community dominated by unpalatable and less palatable species. The release of vegetation from rabbit herbivory allowed the fewer, more competitive, palatable species to outcompete the more numerous, less competitive, unpalatable, and less palatable species. This led to a decrease in their abundance and a decline in species diversity. Eucalyptus sites showed no change in diversity likely due to the inhibitory effects of the alien *Eucalyptus* trees on understory vegetation dynamics.

Question 3: How did vegetation grazing capacity change following rabbit control on Robben Island, and what ecological factors and vegetation processes underlay the observed changes? An increase in grazing capacity on Robben Island, following the control of invasive European rabbits, was anticipated based on the premise that the removal of these herbivores would alleviate the pressure on the island's vegetation, allowing for the recovery and re-establishment of palatable plant species previously suppressed by rabbit grazing. Results confirmed this as the control of rabbit herbivory led to an anticipated increase in grazing capacity across strand and inland dune sites on Robben Island. This increase was driven by the recovery and re-establishment of palatable forage species, such as *T. fruticosa*, *E.* villosa, *E. longiflora*, and *Avena fatua*. Being selective herbivores, rabbits preferentially browse and graze on these palatable plants. When rabbit herbivory was reduced, these palatable plants were able to recover, leading to an increase in grazing capacity. However, grazing capacity remained unchanged at eucalyptus sites following rabbit control, due to the subdued responses of *T. fruticosa*, *E. longiflora*, *O. pes-caprae*, and *P. canaliculatus* to rabbit control. The lack of change in grazing capacity at sites under *Eucalyptus* plantations was likely because of the inhibitory effects of the alien trees on understory vegetation dynamics.

Question 4: What insights do the results provide into the potential response of vegetation on other South African offshore islands? The research posited that studying vegetation dynamics on Robben Island could offer valuable insights into how vegetation on other invaded offshore islands (Dassen,

Jutten, Schaapen, Seal, and Vondeling Islands) might respond to rabbit control. Although the available data limited the precision of the predictions, the theoretical framework developed in the thesis provided a valuable starting point for understanding the potential consequences of rabbit control on these islands. Findings from the thesis revealed a promising outlook for vegetation recovery post-rabbit control on invaded islands. Across the islands, an initial resurgence of early successional, palatable species like *T. fruticosa* and *Ehrharta* spp. is anticipated. In the long term, recolonisation by late successional species and increased vegetation diversity are expected, particularly on islands closer to the mainland where dispersal is facilitated. This shift towards a more complex and resilient vegetation structure signifies a potential return to a functional island ecosystem. However, the specific trajectory and pace of these changes will depend on various island-specific ecological factors and necessitate ongoing monitoring and adaptive management. With more comprehensive data, this thesis's predictions could be further refined, leading to enhanced optimisation of restoration intervention effectiveness.

PREFACE

The data described in this thesis were collected on Robben Island, the Republic of South Africa, from October 2010 to December 2013. The analysis and writing up of the data was carried out between March 2021 and November 2023 while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Dr Zivanai Tsvuura. This thesis, submitted for the degree of Doctor of Philosophy in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

Signed: [redacted]
Thabisisani Ndhlovu
December 2023

I certify that the above statement is correct, and as the candidate's supervisor, I have approved this thesis for submission.

Signe [redacted]…
Dr Zivanai Tsvuura
Supervisor
December 2023

COLLEGE OF AGRICULTURE, ENGINEERING AND SCIENCE

DECLARATION 1 – PLAGIARISM

I, Thabisisani Ndhlovu, declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs, or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
    a) Their words have been re-written, but the general information attributed to them has been referenced.
    b) Where their exact words have been used, then their writing has been placed in italics and inside quotation marks and referenced.
5. This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.

Signed: [redacted]

Thabisisani Ndhlovu

December 2023

COLLEGE OF AGRICULTURE, ENGINEERING AND SCIENCE

DECLARATION 2 – PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Publication: Published in *African Journal of Range and Forage Science*

Grazing capacity change on a small Mediterranean-type South African offshore island following the control of invasive alien European rabbits (*Oryctolagus cuniculus*).

DOI:10.2989/10220119.2022.2125577

Thabisisani Ndhlovu, Zivanai Tsvuura & Karen J Esler

Author contributions: TN conceived study, collected and analysed data and wrote manuscript. ZT supervised TN, and with KJE contributed valuable comments to the manuscript.

Publication: Prepared for publication in the *African Journal of Range and Forage Science*

Vegetation composition change on a small Mediterranean-type South African offshore island following the control of invasive alien European rabbits (*Oryctolagus cuniculus*)

Thabisisani Ndhlovu & Zivanai Tsvuura

Author contributions: TN conceived study, collected and analysed data and wrote manuscript. ZT supervised TN and contributed valuable comments to the manuscript.

Publication: Prepared for publication in the *African Journal of Range and Forage Science*

Change in vegetation species diversity on a small Mediterranean-type South African offshore island following the control of invasive alien European rabbits (Oryctolagus cuniculus)

Thabisisani Ndhlovu & Zivanai Tsvuura

Author contributions: TN conceived study, collected and analysed data and wrote manuscript. ZT supervised TN and contributed valuable comments to the manuscript.

Signed: [redacted]

Thabisisani Ndhlovu

December 2023

ACKNOWLEDGEMENTS

This work was funded and materially supported by the School of Life Sciences (Community of Practice Bursary, 2022) and the College of Agriculture, Engineering and Science (Vice-Chancellor's Bursary, 2023) at the University of KwaZulu-Natal, the Department of Conservation Ecology and Entomology at Stellenbosch University, and Robben Island Management (RIM). I am deeply grateful to my supervisor, Dr. Zivanai Tsvuura from the School of Life Sciences at the University of KwaZulu-Natal, for his unwavering guidance, support, and expertise throughout this research journey. I would like to extend my gratitude to Johannes Philippus Groenewald, Suzaan Kritzinger-Klopper (Centre for Invasion Biology), and Estelle Esterhuysen (RIM) for their invaluable assistance during fieldwork. Special thanks to the late Professor Shaun Jacobs of the Department of Conservation Ecology and Entomology at Stellenbosch University for co-supervising the early phase of this thesis, and to Professor Karen Esler of the same department for her close involvement from the study's inception.

I also acknowledge the support and camaraderie of my colleagues, fellow students, and staff members at both Stellenbosch University and the University of KwaZulu-Natal. The opinions expressed and conclusions drawn in this thesis are my own and do not necessarily reflect the views of the aforementioned funders and contributors.

DEDICATION

This thesis is dedicated
to
my late mother Jennet Faith Ndhlovu (1948-2018)
and
niece Thando Faith Ndhlovu (2022-2023).

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Introduction

I. Background to the study

A significant proportion of the Earth's natural ecosystems have been degraded due to human activities. Approximately 75% of the world's land surface has been affected (Xie, et al. 2020), with over two-thirds of natural grasslands and savannas, and a third of tropical rainforest and natural woodland, having been degraded (Sage 2020). This degradation poses a threat to human well-being since natural ecosystems provide essential services to human societies and economies (Millennium Ecosystem Assessment 2005, Riggio, et al. 2020). These services include air and water purification, crop pollination, nutrient cycling, waste decomposition, soil protection, climate stabilisation, and natural products such as wild fruit and nuts, forage, timber, game, natural fibres, and medicines (Newcome, et al. 2005, Riggio, et al. 2020). The Organisation for Economic Co-operation and Development (OECD) estimates that ecosystem services contribute US$125-140 trillion per year to the global economy, more than one and a half times the size of global GDP (OECD 2023). To mitigate the effects of human-induced ecosystem degradation and safeguard the provision of ecosystem services to human societies and economies, conservation efforts have prioritised the protection and conservation of relict natural ecosystems as reserves (Riggio, et al. 2020, Plumptre, et al. 2021). However, in many areas, the intensity and widespread nature of ecosystem degradation has made conserving relict natural ecosystems insufficient to protect representative biodiversity and ensure ecological integrity and function. In such cases, ecosystem conservation has frequently been supplemented with ecological restoration, which is the process of actively assisting the recovery of degraded, damaged, or destroyed ecosystems (SER 2004).

II. Problem statement

This thesis assessed the outcome of an attempt to ecologically restore degraded vegetation on Robben Island, South Africa, through the control of invasive alien European rabbits (*Oryctolagus cuniculus*). Robben Island is the largest and most environmentally degraded of South Africa's 24 offshore islands (Brooke, et al. 1986, Smith 1997, Crawford, et al. 2000, Williams, et al. 2000). The island has a long history of rabbit occupation dating back to 1654 when Dutch colonial governor Jan van Riebeeck brought them to the island as a source of meat for passing ships and his garrison at the Cape of Good Hope (Skead 1980, Cooper, et al. 1982, Measey, et al. 2020). Long term rabbit herbivory is considered to have eliminated almost all naturally occurring plant species from the island, leaving behind a few native species and weedy aliens that were either unpalatable or could escape or withstand heavy rabbit herbivory (Adamson 1934, Nankivell 1934). Adamson (1934) considered long-term rabbit herbivory on Robben Island to have degraded the island's vegetation beyond a critical threshold, such that the vegetation now existed as an alternative stable degraded state. While several studies have examined the impact of rabbit herbivory on vegetation on Robben Island and other South African offshore islands (Adamson 1934, Nankivell 1934, Gillham 1963), the response of vegetation to rabbit control remains largely unknown. Given that European rabbits are classified as a Category 1b invasive species that must be controlled under South Africa's National Environment Management: Biodiversity Act 10 of 2004, it is crucial to understand how vegetation on South African offshore islands may respond to rabbit control, particularly in the context of the islands' long-standing rabbit occupation and highly degraded ecosystems.

III. Research aim, objectives, and questions

Overall, the thesis aimed to enhance understanding of the impact of European rabbit control on the vegetation of South African offshore islands, using Robben Island as a case study. The objectives were twofold: 1) to empirically observe the pattern of vegetation change following rabbit control on Robben Island, and 2) to develop a general theoretical model and hypotheses on how vegetation may respond to rabbit removal on similar islands. This was facilitated by an attempt to eradicate European rabbits from South Africa's Robben Island between 2008 and 2009, which allowed for the monitoring of vegetation response to the control of alien rabbit herbivory over four years (2010-2013). The period immediately before the study saw Robben Island's rabbit population peak at ~24,100 in 2008, attributed to the removal of top-down control following a series of cat removal exercises that began in 1998 (see Annex III). However, by 2009, the population had drastically reduced to ~1,200, due to food shortages and the culling of 4,786 rabbits (Annex III). This number further plummeted to just three observed rabbits by March 2010, due to continued control measures (Annex III). From November 2010 onwards, no rabbits were observed during the duration of the study, confirming a rabbit-free environment to assess ecological responses (Annex III). This dramatic decrease provided a unique opportunity for research, enabling the observation of the vegetation's response to the eradication of alien rabbit herbivory from 2010 to 2013 on this representative South African offshore island. The study addressed the following questions to achieve its aims and objectives:

1. How did vegetation composition, diversity, and grazing capacity change following rabbit control on Robben Island?
2. What ecological and vegetation processes underpinned the observed changes?
3. What insights do the results offer into the potential response of vegetation on other South African offshore islands?

IV. Hypotheses

Species composition

The study hypothesised that following the eradication of invasive European rabbits, the native vegetation on Robben Island would revert to its historical composition, primarily consisting of evergreen sclerophyllous shrubs along with drought-deciduous shrubs and succulents, known as Cape Flats Dune Strandveld. It was projected that ecological succession would favour late-successional species, such as palatable perennial grasses and shrubs, leading to a decline in early-successional, unpalatable annuals previously thriving under rabbit grazing pressure. However, the extensive and prolonged herbivory by the rabbits has likely pushed the ecosystem beyond critical ecological thresholds (Adamson 1934), making full recovery without human intervention unlikely. Furthermore, the island’s geographic isolation—~7 km from the nearest mainland (Brooke, et al. 1986)—is thought to limit seed dispersal from the mainland, thereby complicating natural recovery. Consequently, the null hypothesis posited that rabbit eradication alone was insufficient for substantial vegetation recovery to the pre-invasion state. This highlighted the potential need for active restoration measures to reintroduce native flora and re-establish ecological balance.

Species diversity

The thesis hypothesised that controlling European rabbits on Robben Island would increase vegetation species diversity. This expectation was based on the premise that reducing intense herbivory would alleviate the suppression of palatable plant species, which had previously led to a simplified ecosystem characterised by early successional stages. It was anticipated that removing this pressure would allow these species to recover, thereby enhancing diversity. However, the prolonged presence of rabbits, coupled with the island's isolation, might have impeded the full restoration of a diverse plant community. Such impediments could have stemmed from the complete loss of palatable species from both the existing plant communities and the seed banks, as well as from the obstruction of plant dispersal from external sources. Given over 350 years of continuous rabbit herbivory, the ecosystem might have undergone irreversible changes (Adamson 1934), potentially preventing a return to its pre-invasion ecological state without significant human intervention. Consequently, the null hypothesis posited that there would have been no significant increase in species diversity, reflecting the severe and potentially irreversible ecological impacts of prolonged herbivory and geographic isolation.

Grazing capacity

The study hypothesised that controlling European rabbits on Robben Island would have increased grazing capacity by allowing the recovery of palatable forage species previously suppressed by rabbit herbivory. It was anticipated that this reduction in herbivory would have enabled native plant species within the seed bank to recover, thereby enhancing forage availability. However, prolonged and intensive herbivory by the rabbits could have critically depleted palatable plant species and degraded the seed bank (Adamson 1934), which might have prevented significant vegetation recovery. Additionally, the island's isolation could have impeded seed dispersal from external sources, further obstructing ecological restoration. Consequently, the null hypothesis posited that grazing capacity on Robben Island might not have improved in response to rabbit control due to the potential complete loss of palatable species in both the vegetation and the seed banks.

Vegetation response on other invaded offshore islands

The thesis hypothesised that the control of European rabbits on Robben Island might have modelled potential vegetation responses on other South African offshore islands, given their classification as a discrete biogeographical unit due to similar climatic conditions and ecological characteristics (Williams et al., 2000). Insights from Robben Island were expected to serve as a benchmark for managing rabbit populations and their ecological effects on comparable islands. The null hypothesis was that differences in specific ecological conditions or climatic features among the islands might have prevented Robben Island's data from providing actionable insights.

V. Justification

The control and management of invasive alien species, such as the European rabbit, are crucial for the restoration and conservation of biodiverse ecosystems globally. In particular, the European rabbit has profoundly impacted vegetation and biodiversity on South African offshore islands, including Robben Island. These rabbits have disrupted ecological balances and damaged vegetation through selective herbivory (Gillham 1963, Brooke and Prins 1986, Cooper and Brooke 1986). Despite widespread recognition of these impacts, there is a notable scarcity of comprehensive studies on vegetation response following the eradication of rabbits, especially in the unique context of South African offshore islands. This research addresses a significant gap in the ecological literature by exploring the dynamics of vegetation recovery after rabbit control, thereby offering insights critical for the development of effective conservation strategies.

The urgency of this study is underscored by the need to understand the ecological aftermath of invasive species eradication—a key yet underexplored aspect of environmental management. Given the ecological significance of South African offshore islands, this timely research is essential for guiding future restoration efforts. The findings will enhance our understanding of island ecosystem recovery processes, providing a valuable framework for enhancing vegetation responses to invasive species control globally. Additionally, this study on Robben Island serves as a pivotal case study for examining ecosystem recovery in environments long subjected to invasive species pressure. By focusing specifically on the European rabbit and its effects on vegetation dynamics, the research contributes significantly to the literature that supports informed, evidence-based conservation practices. The insights gained will be instrumental in shaping policy decisions under the National Environment Management: Biodiversity Act (Act No. 10 of 2004), particularly concerning Category 1b invasive species in South Africa, thereby directly influencing regional and broader conservation policy and practice.

VI. Some notes on the data collection and timeline of the thesis

The data collection for this thesis was conducted between 2010 and 2013, during the author's tenure as a Teaching Assistant and Field Demonstrator in the Department of Conservation Ecology and Entomology at Stellenbosch University. In this role, the author was responsible for demonstrating vegetation sampling techniques to students on the annual 4th-year ecology field trips to Robben Island from 2010 to 2014. After leaving this position, the author pursued a career as an Ecological and Climate Change Adaptation Consultant from 2014 to 2020. It was in this period of professional development and applied ecological practice that the author recognised the unique value and untapped potential of the dataset they had compiled. Inspired by this insight, the author began their PhD in 2021, committing to a detailed analysis of the data and the development of this thesis. This path, though untraditional, has endowed the author with a distinctive combination of practical experience and academic understanding, enhancing the relevance and applicability of the research findings to real-world conservation issues.

VII. Structure of the thesis

The thesis comprises an introduction (Chapter 1), a literature review (Chapter 2), three distinct research papers (Chapters 3, 4, and 5), and a synthesis (Chapter 6). Given that Chapters 3, 4, and 5 were developed as separate research papers, they share some content, notably within the Materials and Methods sections. Despite being primarily the author's work, with the supervisor offering comments and suggestions, Chapters 3, 4, and 5 have been written in a manner that reflects the contributions of multiple authors, as they are intended for submission as co-authored research papers.

Chapter 1 *– Introduction*

In this introductory chapter, the groundwork for the study is laid, first by situating it within the wider context of global ecosystem conservation and restoration challenges. The aims, objectives, and research questions that guide the thesis are then articulated. Finally, a concise outline of the thesis is provided, offering a succinct overview of the research aims and objectives pursued in each chapter.

Chapter 2 *- Impact of invasive alien European rabbits (Oryctolagus cuniculus) on the vegetation of South African offshore islands. A literature review.*

In this chapter, the largely inaccessible or out-of-print literature on European rabbits in Southern African offshore islands is reviewed. Recognising the scarcity and unavailability of relevant resources, a non-systematic approach to literature identification is adopted. Nonetheless, comprehensive and rigorous efforts are undertaken to locate both published and unpublished sources, including the scanning of offline materials into PDF documents and the conducting of extensive online searches. The online search employs the general keywords 'European rabbit' AND 'South Africa' on Google and Google Scholar, yielding online materials that, alongside the scanned offline sources, are managed and analysed using Qiqqa Research and Reference Management Software.

Chapter 3 *- Vegetation composition change on a small Mediterranean-type South African offshore island following the control of invasive alien European rabbits (Oryctolagus cuniculus)*

In this chapter, the impact of rabbit control on Robben Island's vegetation species composition is investigated, and the underlying vegetation dynamics that drive the observed changes are identified. Vegetation species composition refers to the variety and relative abundance of plant species within a particular area. To assess the significance of inter-annual shifts in species composition over the four years following rabbit control, one-way Analysis of Similarities (ANOSIM) is employed. Utilising Similarity of Percentage (SIMPER), the species cover changes that contribute most significantly to compositional change are further identified and ranked. Additionally, multiple regressions are leveraged to evaluate and account for the influence of interannual rainfall variation on compositional change. Finally, multivariate multiple regressions are employed to assess the impact of inter-annual rainfall variation on changes in the mean individual species contributions to the overall compositional shift.

Chapter 4 *- Change in vegetation species diversity on a small Mediterranean-type South African offshore island following the control of invasive alien European rabbits (Oryctolagus cuniculus)*

In this chapter, the impact of rabbit control on vegetation species diversity on Robben Island is assessed, and the underlying vegetation dynamics driving the observed changes are identified. Species diversity quantifies the number and relative abundance of plant species in an area, distinct from species composition, the focus of Chapter 2, which identifies the types and proportions of plants present. The Shannon-Wiener entropy index (H) is employed to quantify species diversity. Species richness (S) is calculated from the number of species encountered along transects at the study sites, and species evenness is measured using Buzas and Gibson's evenness index (E_{BG}). To assess the statistical significance of changes in mean species diversity, richness, and evenness over the four years following rabbit control, the Friedman or Wilcoxon two-sample paired tests are employed. Constrained seriation is then used to optimally arrange presence-absence matrices for analysis, enabling the detection of species presence and cover changes driving the diversity change. Finally, multiple linear regressions are utilised to evaluate and account for the influence of interannual rainfall variation on changes in species diversity, richness, and evenness following rabbit control.

Chapter 5 *- Grazing capacity change on a small Mediterranean-type South African offshore island following the control of invasive alien European rabbits (Oryctolagus cuniculus)*

In this chapter, the impact of rabbit control on Robben Island's grazing capacity and the underlying vegetation dynamics that drove this change are investigated. Grazing capacity, a critical indicator of an ecosystem's productivity and its ability to provide services such as food production, is measured as the maximum number of animals that a given land area can sustainably support without harming the vegetation or soil. Repeated-measures ANOVA tests are employed to assess the statistical significance of the changes in grazing capacity over the four years following rabbit control. Inter-annual differences in the mean contributions of individual species to actual forage production (AFP) are utilised to identify and rank the plant species cover changes that most influenced this shift. Individual species' AFP values are calculated using the Bayer method. To evaluate and account for the influence of inter-annual rainfall variations on the change in grazing capacity after rabbit control, multiple linear regressions are employed. Finally, multivariate multiple regressions are used to assess the influence of inter-annual rainfall variations on the changes in mean individual species contributions to AFP.

Chapter 6 *- Vegetation response to control of invasive alien European rabbits (Oryctolagus cuniculus) on South African offshore islands. A general theoretic model and island-specific hypotheses*

In this chapter, the empirical findings from Chapters 3 to 5 are built upon, synthesising them into a cohesive conceptual model and overarching theoretical framework. This framework acts as a lens, expanding the understanding of vegetation response to rabbit control beyond Robben Island and extracting transferable insights for other invaded South African offshore islands. To achieve this, key observations and results from the empirical chapters are consolidated, establishing a comprehensive understanding of vegetation dynamics on Robben Island following rabbit control. This consolidated knowledge then informs the construction of a coherent conceptual model, depicting the interplay between rabbit control and vegetation response on the island. Drawing upon both the consolidated findings and the conceptual model, a general theoretical framework applicable to other invaded islands is developed. Leveraging this framework, specific hypotheses about vegetation response on other invaded islands (Dassen, Jutten, Schaapen, Seal, and Vondeling) following rabbit control or removal are then formulated.

VIII. References

Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

Brooke RK, Prins AJ. 1986. Review of alien species on South African offshore islands. *South African Journal of Antarctic Research* 16: 102-109.

Cooper J, Brooke RK. 1982. Past and present distribution of the feral European rabbit *Oryctolagus cuniculus* on southern African offshore islands. *South African Journal of Wildlife Research* 12: 5-71.

Cooper J, Brooke RK. 1986. Alien plants and animals on South African continental and oceanic islands: species richness, ecological impacts and management. In: Macdonald IAW, Kruger FJ, Ferrar AA editors. *The ecology and management of biological invasions in southern Africa*. Cape Town: Oxford University Press. p. 133-142.

Crawford R, Dyer B. 2000. Wildlife of Robben Island. In: Underhill L editor. *Bright Continent Guide*. Cape Town: Avian Demography Unit.

Gillham ME. 1963. Some interactions of plants, rabbits and sea-birds on South African islands. *Journal of Ecology* 51: 275-294.

Measey J, Hui C, Somers MJ. 2020. Terrestrial vertebrate invasions in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology* No. 14. Cham, Swtzerland: Springer Open. p. 115-151.

Millennium Ecosystem Assessment. 2005. *Ecosystem and human well-being: Synthesis*. Washington DC: Island Press.

Nankivell JW. 1934. Robben Island. *The South African Geographical Journal* 17: 29-34.

Newcome J, Provins A, Johns H, Ozdemiroglu E, Ghazoul J, Burgess D, Turner K. 2005. *The economic, social and ecological value of ecosystem services: a literature review*. London: Economics for the Environment Consultancy (eftec).

OECD (ed). 2023. *Biodiversity: Finance and the Economic and Business Case for Action* Paris: OECD Publishing.

Plumptre AJ, Baisero D, Belote RT, Vázquez-Domínguez E, Faurby S, Jędrzejewski W, Kiara H, Kühl H, Benítez-López A, Luna-Aranguré C. 2021. Where might we find ecologically intact communities? *Frontiers in Forests and Global Change*: 26.

Riggio J, Baillie JE, Brumby S, Ellis E, Kennedy CM, Oakleaf JR, Tait A, Tepe T, Theobald DM, Venter O. 2020. Global human influence maps reveal clear opportunities in conserving Earth's remaining intact terrestrial ecosystems. *Global Change Biology* 26: 4344-4356.

Sage RF. 2020. Global change biology: A primer. *Global Change Biology* 26: 3-30.

SER. 2004. *The SER international primer on ecological restoration*. Tucson: Society for Ecological Restoration Science and Policy Working Group.

Skead CJ. 1980. *Historical mammal incidence in the Cape Province Vol. 1. The Western and Northern Cape*. Cape Town: Department of Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope.

Smith C. 1997. *Robben Island*. South Africa: Struik Publishers.

Williams AJ, Klages NTW, Crawford RJM. 2000. Functional ecosystems: Coastal islands. In: Durham BD, Pauw JC editors. *Summary Marine Biodiversity Status Report for South Africa*. Pretoria: National Research Foundation.

Xie H, Zhang Y, Wu Z, Lv T. 2020. A bibliometric analysis on land degradation: Current status, development, and future directions. *Land* 9: 28.

CHAPTER 2

Impact of invasive alien European rabbits (*Oryctolagus cuniculus*) on the vegetation of South African offshore islands. A scoping review

Overview

European rabbits have been introduced to five continents and over 800 islands worldwide, where they pose a significant threat to both biodiversity and human livelihoods. While the impact of these invasive rabbits on global environments is well-documented, the region encompassing the 33-plus offshore islands along the southern African coast has received less attention, despite a history of rabbit invasion dating back to the 17th century. This review consolidates scattered literature on European rabbits in this region, offering new insights into their population dynamics and effects on island vegetation. The review includes a brief introduction to South African offshore islands and their general ecology. It also provides a detailed report on the occurrence and impact of invasive alien rabbits on offshore island ecosystems, with a particular focus on Robben Island. Additionally, the review presents information on Robben Island's location, physiography, climate, hydrology, flora, and fauna. It also provides a timeline of significant historical events for ecological and historical context. Lastly, the review contextualises the studies on vegetation response to rabbit control in the current thesis within the broader literature on the impact of European rabbits on South African offshore islands.

Keywords: European rabbits; offshore islands, alien invasive species; vegetation condition; Robben Island; South Africa

I. Introduction

The European rabbit (*Oryctolagus cuniculus*) provides one of the best examples of the disastrous consequences that can result from the introduction of an invasive alien species to new environments

(Flux, et al. 1992, Thompson, et al. 1994, Courchamp, et al. 2003, Long 2003, Schweizer, et al. 2016, Fontanesi, et al. 2021). A small mammal native to the Iberian Peninsula, *O. cuniculus* was released on uninhabited islands as a food source for sailing ship crews during early world explorations (Nowak 1999, Long 2003). This process led to the establishment of rabbits on more than 800 islands and island groups worldwide (Flux, et al. 1983, Nowak 1999, Long 2003, Fontanesi, et al. 2021), where they are commonly regarded as significant threats to biodiversity and human livelihoods (Thompson and King 1994, Williams, et al. 1995, Courchamp, et al. 2003, Schweizer, et al. 2016, Cubas, et al. 2019, Bello-Rodríguez, et al. 2021). This includes the string of over 33 offshore islands that occur along the southern African coast (i.e. along the Namibian, South African and Mozambican coastlines) (de Vos, et al. 1956, Cooper, et al. 1982, Lever 1985, Long 2003, Skead 2011, Davies, et al. 2020, Measey, et al. 2020). The adverse effects of rabbit introductions on island ecosystems have prompted global efforts to remove them where feasible (Schweizer, et al. 2016). There have been at least 90 successful rabbit eradications since the 1800s (Schweizer, et al. 2016). Efficacy and methodology have steadily improved over the years, leading to an almost continuous increase in rabbit eradications (Myers, et al. 2000, Schweizer, et al. 2016).

Ecologists have extensively studied the effects of invasive European rabbits on introduced environments across the globe, resulting in a voluminous literature (see references in, e.g., Flux and Fullagar 1992, Thompson and King 1994, Williams, et al. 1995, Long 2003, Scott, et al. 2013, Fontanesi, et al. 2021). However, the literature on European rabbits on southern African offshore islands is scanty compared to other regions worldwide. Furthermore, much of the literature is scattered in journals and official reports that are difficult to access or out of print. This review chapter identifies, analyses, and synthesises the available scientific literature on European rabbits' impact on South African offshore islands. In addition to providing an overview of the literature, the study presents new insights into European rabbit population dynamics and the ecological processes underlying their impact on island vegetation. The chapter includes a brief introduction to South African offshore islands and their general ecology and a detailed discussion of the occurrence and impact of invasive alien rabbits on offshore island ecosystems, with a particular focus on Robben Island. The chapter also presents information on Robben Island's location, physiography, climate, hydrology, flora, and fauna and a timeline of significant historical events (Annex I) for ecological and historical context. Robben Island, the study site of this thesis, is the largest and most studied of the South African offshore islands (Robben Island Museum 2006, 2013). There are differences in geology, size, distance offshore, and climatic conditions among the South African offshore islands (Williams, et al. 2000). Despite this, I believe that an understanding of vegetation dynamics on Robben Island following rabbit control could provide valuable insight into how vegetation on other South African offshore islands might respond.

A non-systematic approach was used to identify the literature for this review due to its scantiness and inaccessibility, which prevented the use of standardised methods of article selection and data extraction used in systematic reviews. However, rigorous and comprehensive efforts were made to locate relevant published and unpublished literature, with online material identified using the general keywords "European rabbit" AND "South Africa" on Google and Google Scholar search engines. A purposive analysis was then conducted on all publications identified in this manner using the Qiqqa Research and Reference Management Software (Graham 2013).

II. South African Offshore Islands

Of the over 33 offshore islands that occur along the southern African coast, 24 are within South African territory (Cooper, et al. 1986). Offshore islands (also called continental islands) arise from unsubmerged parts of the continental shelf that are surrounded by the ocean. South African offshore islands were part of the mainland during the last Pleistocene glaciation (ca.17 000 YA). They arose from high points on the former coastal plain after the sea level rose following the end of the glacial period, ca. 12000 YA (Tankard 1976, Brooke, et al. 1982, Brooke, et al. 1986). Many of the islands (except for Schaapen, Meeuw, Jutten, Dassen and Seal Islands, which were high enough to remain above sea level) were inundated entirely during the Holocene Climate Optimum (HCO) ca. 6000-2000 YA (Brooke and Crowe 1982). The HCO - a warm period when the mean sea level was at least 3 m higher than the present - ended ca. 2000 YA, and the sea level has since remained constant (Brooke and Crowe 1982).

South African offshore islands are relatively small, low-lying and occur near the mainland (Cooper and Brooke 1986). The largest and furthest offshore, Robben Island, is only 507 ha in size and is located a mere 7 km from the coast (Cooper and Brooke 1986). The islands vary in geology, size, distance offshore and climatic conditions (Williams, et al. 2000). The more northern South African offshore islands are underlain by granite and the southern islands Cape sandstone, but this seems to have little effect on either the plant cover or the vertebrate animals which occur on them (Gillham 1963). Cooper and Brooke (1986) have subdivided South African offshore islands into three groups based on rainfall pattern: islands on which virtually no rain falls though heavy fogs are of regular occurrence (Hollamsbird to Sinclair islands off Namibia); islands on which rainfall is confined to the winter months (Bird to Seal islands off the western coast of the Western Cape Province); islands on which rain may fall at any time of the year (Dyer to Stag islands off the southern and eastern coasts of the Western and Eastern Cape Provinces). A detailed map of the Namibian and South African coastline showing the location of the offshore islands is provided by Brooke and Prins (1986).

Most South African offshore islands are not well-vegetated, especially the smaller ones (Cooper and Brooke 1986). Only four islands, Schaapen and Meeuw in Saldanha, Dassen and Robben just north of Cape Town, were historically vegetated, while the rest were covered with guano (Brooke and Prins 1986). Removal of guano by European sailors and settlers from 1845 onwards allowed crude soils to develop on some islands (Brooke and Prins 1986). The rudimentary soils have enabled plants and animals that could reach the islands either by their own dispersal mechanisms or by an accidental or deliberate human introduction to become established (Brooke and Prins 1986).

Although the actual historical ecology is unknown, it is assumed the islands initially possessed subsets of mainland fauna and flora appropriate to their habitats when the sea rose and cut them off from the mainland (Brooke and Crowe 1982). The fauna and flora would have been altered subsequently by biotic and abiotic factors such as the colonisation of islands by seabirds and seals and salt accumulation from breaking waves and other stochastic events (Brooke and Crowe 1982, Brooke and Prins 1986). Sea-birds deposit droppings with high ammonia content that accumulate to form guano deposits several metres deep (Brooke and Crowe 1982). Guano is inimical to most life forms (Brooke and Crowe 1982). Cape fur seals (*Arctocephalus pusillus*) that move on land by dragging their bodies over the ground severely restrict plants and smaller animals' opportunities to establish themselves (Brooke and Crowe 1982). The complete inundation of many of the islands during the HCO would also have severely affected and altered island fauna and flora.

The seas around South African offshore islands are more dynamic and more difficult to swim or sail across than those of the tropics (Williams, et al. 2000). As a result, South African offshore islands have traditionally been free of the diverse terrestrial mammalian predators found on the mainland (Williams, et al. 2000). The lack of mammalian predators other than introduced feral cats (*Felis catus*) (Gillham 1963, Cooper and Brooke 1986, Skead 2011) has permitted the establishment of populations of Indian peafowl (*Pavo cristatu*), chukar partridges (*Alectoris chukar* Gray, 1830; Cooper and Brooke

1986) and European rabbits (Cooper and Brooke 1982) on the islands. None of these species has become established on the South African mainland with its broad suite of predators and pathogens (Gillham 1963, Cooper and Brooke 1986). The safety from terrestrial predators has also made the islands favourable for breeding colonies of the Cape Fur-seal and seabird species (Gillham 1963). Six of the seabird species are effectively endemic to the islands and are thought to have evolved on them (Williams, et al. 2000).

Many South African offshore islands are of high conservation value as breeding habitats for threatened and endangered seabird species and colonies of Cape fur seals (Cooper and Brooke 1986, Williams, et al. 2000). As a result, many of the islands have been designated as conservation areas and placed under the management of national or provincial conservation agencies. The islands, however, have had a long history of human exploitation, such that much of their terrestrial ecosystems have been severely degraded (Brooke and Prins 1986, Cooper and Brooke 1986). Since the arrival of European sailors in the 17th century, the islands have been used for, among other things, human settlement, farming, ranching and gardening (Cooper, et al. 1983, Brooke and Prins 1986, Cooper and Brooke 1986, Robben Island Museum 2006). Some of the islands have been used for guano, stone and lime quarrying (Brooke and Prins 1986, Robben Island Museum 2006). Alien trees, plants and herbivorous mammals have been intentionally introduced to many islands (Brooke and Prins 1986, Cooper and Brooke 1986). At least 88 terrestrial alien taxa have become established on South African offshore islands (Cooper and Brooke 1986). The most notable impact of human use and settlement on the islands has been the degradation of vegetation by introduced alien mammalian herbivores (Gillham 1963, Brooke and Prins 1986, Cooper and Brooke 1986). Most notorious among the introduced mammalian herbivores has been the European rabbit (Gillham 1963, Brooke and Prins 1986, Cooper and Brooke 1986).

III. European Rabbits on South African Offshore islands

European rabbits were historically introduced to 13 South African offshore islands, but have since become naturally extinct from at least seven islands (de Vos, et al. 1956, Cooper and Brooke 1982, Lever 1985, Long 2003, Skead 2011). Feral populations are currently present on six offshore islands ranging from Possession Island, off Namibia, to Bird Island, Eastern Cape, South Africa (Table 2.1).

Table 2-1 Current status of European rabbit populations on South African offshore islands. Lists compiled from Cooper and Brooke (1982), Skead (2011), Davies, et al. (2020) and Measey, et al. (2020).

Present	Extinct
Schaapen Island	Malgas Island
Jutten Island	Marcus Island
Vondeling Island	Meeuw Island
Dassen Island	St Croix Island[†]
Robben Island	Island on Keurbooms River estuary
Seal Island	Dyer Island
	Possession Island

[†] May be a mistaken reference to Bird Island (see Cooper and Brooke (1982)).

The size and persistence of European rabbit populations on South African offshore islands appear to be controlled by the availability of reliable summer forage. Gillham (1963), in her 1960 survey of South African offshore islands, noted that European rabbits appeared to have been most abundant on Jutten Island, where the drought-tolerant, highly palatable succulent-leaved bulb *Albuca canadensis* (L.) F.M.Leight. supplemented the dominant highly palatable succulent shrub *Prenia pallens* NE. Br. as the main summer forage species (Gillham 1963). *Albuca canadensis* also appeared to be closely associated with well-vegetated offshore islands Robben, Meeuw and Schaapen (Gillham 1963). On Robben Island, where *A. canadensis* was somewhat localised; the drought-tolerant, highly palatable woody shrub *Tetragonia fruticosa* Linn. provided much of the summer feed (Gillham 1963). Rabbit populations were least established on shrub-less guano islands, where succulent halophytes (Chenopodiaceae and Aizoaceae) were almost the only food available during summer (Gillham 1963). Summer is the driest period on winter-rainfall Mediterranean-type southern African offshore islands and the most critical for vegetation cover and rabbit carrying capacity (Cooper and Brooke 1986). European rabbits have not persisted on islands of less than 20 ha, which lack the more complex forage-provisioning vegetation of larger islands (Cooper and Brooke 1982, Skead 2011).

IV. Effects of European Rabbits on South African offshore Island Vegetation

Seminal work on vegetation dynamics on rabbit-invaded South African offshore islands by Adamson (1934), Nankivell (1934) and Gillham (1963) has demonstrated that European rabbits have markedly altered and degraded vegetation on the islands through long-term selective grazing and browsing. These studies compared vegetation on islands under active rabbit herbivory with that on islands and adjacent mainland areas free from or subjected to less prolonged herbivory. The studies concluded that vegetation on the affected islands had either been degraded beyond critical thresholds, existing as alternative stable degraded early developmental states (Adamson 1934) or remained as unstable plagio-seres trapped in early phases of secondary successional development by rabbit herbivory (Gillham 1963). These plagio-seres would undergo secondary succession towards their original species composition once rabbit herbivory had been eliminated (Gillham 1963).

Adamson (1934) compared vegetation on the offshore island, Robben Island, with that on similar soils on the adjacent mainland. He found the flora on rabbit-infested Robben Island to have fewer species than its rabbit-free mainland analogue (Adamson 1934). The vegetation on the island also had a higher percentage of low-growing herbaceous plants and annuals. It also lacked many bushy, woody and succulent plants that occurred in the denser and relatively higher (0.3-1.0 m high) communities on the mainland. Gillham (1963) contrasted vegetation on Schaapen Island, where European rabbits were long-established (introduced in the early 1700s; Cooper and Brooke 1982), and Meeuw Island, where they had only been recently introduced (ca. 1953; Gillham 1963). By 1960 when Gillham (1963) conducted her ecological surveys, both Schaapen and Meeuw Islands had come to carry large populations of European rabbits, their floras representing the late and early stages of rabbit occupation. Gillham (1963) found that the succulent shrub *Roepera morgsana* (L.) Beier & Thulin, that rabbits much favoured as forage, dominated vegetation on Meeuw I., where rabbits had been recently introduced, but was rare on Schaapen Island, where European rabbits had long been established. Like Adamson (1934) and Nankivell (1934) with regards to Robben Island, Gillham (1963) also considered rabbit activity to have been overwhelmingly responsible for vegetation degradation on Schaapen and Meeuw Islands, with shrub nesting cormorants (*Phalacrocorax* spp.) and other sea birds driving the degradation further.

V. Eradication of European Rabbit Populations from South African Offshore Islands

Despite the long-standing realisation that European rabbits negatively affect vegetation on South African offshore islands, there have been no sustained historical attempts to eradicate rabbits from the islands. Given the past use of many of the islands, ecological restoration was not a priority for much of their history. As a result, there would have been no incentive to eradicate rabbits from the islands. The lack of action against rabbits, however, extended into the mid-1980s and '90s when many of the islands had become conservation areas and were under the control of provincial and national conservation agencies (e.g., South African National Parks - Jutten, Malgas, Marcus and Schaapen; Cape Nature Conservation – Bird, Dassen and Vondeling). The reason for the lack of action against rabbits may have lain with their sparse numbers on many of the islands. Hunting (e.g., by human inhabitants on Robben Island), predation (e.g., by feral cats on Robben and Dassen Islands) and seasonal population crashes (e.g. annual dry season die-offs on Dassen Island) most likely kept rabbit populations on many of the islands low for the significant part of their histories, except for episodic irruptions when islands became uninhabited, or predation became somehow curtailed. As a result, rabbit numbers on many islands may have been so low that the animals were seen as not posing any ecological threat. Indeed, numerous evaluations of rabbit impact on island ecosystems published in the 1980s and 90s considered rabbits to be ecologically benign (e.g. Cooper and Brooke 1982, Brooke and Prins 1986, Crawford, et al. 1998, Crawford, et al. 2000).

The notion that rabbit removal was not an urgent ecological priority could have also been bolstered by the commonly held view, expressed by Cooper and Brooke (1982) and Brooke and Prins (1986), that South African offshore islands had already been degraded to such an extent that no conceivable management program could restore them to their pristine condition. Eliminating rabbits after they had existed on some islands for hundreds of years and already caused irreversible vegetation changes would have been considered unnecessary and undesirable. For example, Cooper and Brooke (1982) believed the feral rabbit population on Robben Island, which had "... existed for over 300 years ..." to be "... worthy of study and perhaps also of conservation in its own right." Cooper and Brooke (1982) and Brooke and Prins (1986) even cautioned against rabbit removal, pointing out that such action could potentially cause unforeseen and undesirable ecological effects as rabbits had been part of island ecosystems for long periods and had possibly assumed keystone ecological roles. Instead, Cooper and Brooke (1982) and Brooke and Prins (1986) considered the principal and urgent management problem on South African offshore islands to have been presented by feral cats and their effects on threatened, endangered and endemic seabird species. Unlike the case of European rabbits, the ecological necessity for eliminating feral cats from South African offshore islands was realised and unambiguously prescribed (Brooke 1983, Brooke and Prins 1986, Cooper and Brooke 1986, Crawford, et al. 1998, Crawford and Dyer 2000).

Feral cats have been eradicated from Dassen (Skead 2011) and were for some time thought to have been eradicated from Robben Island in 2008 (Sherley 2016), but have been subsequently observed on the island (Wilke 2022). It had long been realised that eradicating cats from the islands would increase the populations of prey animals such as the European rabbit, black rat (*Rattus rattus*) and chukar partridge. Crawford et al. (1998) recommended that monitoring potential environmentally problematic prey species be instituted as an integral part of cat eradication programmes. Although such surveillance was not rigorously conducted on Robben Island, there is evidence that the eradication of cats from the Island led to a rabbit population explosion in 2008 (de Villiers, et al. 2010, Sherley 2016). The explosion in rabbit numbers caused an environmental crisis on the island (Sherley 2016) that generated considerable bad publicity for the island's Management (see, e.g. Anon 2008a, b, Vosloo 2008, Yeld 2008). The negative publicity from the ecological crisis finally led to a sustained effort to eradicate rabbits from the island between 2009–2019, resulting in the cumulative removal of an estimated 13 600 animals (Anon. 2008a, b, de Villiers, et al. 2010, Sherley 2016, Davies, et al. 2020, Measey, et al. 2020). European rabbits have not been seen (Davies, et al. 2020, Measey, et al. 2020) on the island since 2019.

VI. Robben Island

A. Location and Physiography

Robben Island (33°48’S, 18°22’E; Figure 2.1) lies in Table Bay, approximately 11 km north of Cape Town and 7 km from the nearest mainland at Bloubergstrand (de Villiers 1971, Brooke and Prins 1986, Crawford and Dyer 2000). The island was part of the mainland during the last Pleistocene glaciation (c. 17 000 YA) (Tankard 1976, Brooke and Crowe 1982) when the sea level was ~130 m lower than the present and the coastline tens of kilometres offshore (Miller 1991). The island was then a low hill connected to the Blaauwberg mountain near Bloubergstrand by a ridge now ~15 m below sea level (Miller 1991). When the sea level rose at the end of the glacial period (c. 12 000 YA), Robben Island was cut off from the mainland by roughly 10 km of the South Atlantic Ocean (Dingle, et al. 1972, Tankard 1976). Robben Island is believed to have been periodically inundated (at high tide or spring highs) during the Holocene Climate Optimum (HCO – a warm period beginning ca. 6 000 YA when the mean global sea level was at least 3 m higher than present) (Brooke and Crowe 1982). Since the end of the HCO (c. 2 000 YA), the sea level has remained constant at its current levels (Brooke and Crowe 1982).

Figure 2-1 Map showing the location of Robben Island and satellite image of the island. Satellite image obtained from Google Earth (Version 5.1.3533.1731). Mountain View, CA: Google Inc. (2017).

The island is low-lying and gently undulating to flat (Figure 2.1). It is roughly oval with a north-south axis of ~3.4 km and a width of just over 2 km (Adamson 1934, Miller 1991). The highest point (~30 m above sea level) on the island is a hill (Signal/Light House/Minto Hill) near the southern coast (Adamson 1934, Nankivell 1934, de Villiers 1971). From the hill, the land falls evenly to the south and east and more gradually to the north, where it is punctuated by a series of N.N.E-S.S.E trending dune ridges and troughs (Adamson 1934). The dunes and troughs eventually transition to flat lowlands in the northern part of the island (Nankivell 1934). The coastline (~12 km) is primarily rocky, apart from a small sandy beach on the eastern shore, and devoid of distinctive features (Adamson 1934, Nankivell 1934, Miller 1991).

B. Climate

Robben Island experiences a temperate Mediterranean-type climate (hot, dry summers and cool, wet winters; Figure 2.2) similar to the adjacent mainland (Adamson 1934, Crawford and Dyer 2000, Robben Island Museum 2006). However, the island's climatic conditions are more extreme, with stronger winds and a colder and considerably drier winter (Robben Island Museum 2006). Rainfall is driven by cold fronts from the South Atlantic Ocean and occurs mainly from April to September (Adamson 1934, Robben Island Museum 2006). The mean annual rainfall is ~414 mm (1900–2013, South African Weather Service – unpublished data). The rainfall pattern is strongly seasonal (Adamson 1934). On average, ~80% of the total annual rainfall (~331 mm on average) falls during the six months of April to September (autumn, winter and spring), and only ~20% (~83 mm on average) in the remaining six months (October – March, summer; Figure 2.2). Mean monthly rainfall normally troughs in February (9 mm) and peaks in June (77 mm), while the mean monthly temperature is highest between January and February (25 ^{o}C) and lowest between June and August (17 ^{o}C; Figure 2.2). High winds – NW in winter, S and SE in summer – are common. (Adamson 1934, Nankivell 1934) Equinoctial fogs are usual (Nankivell 1934).

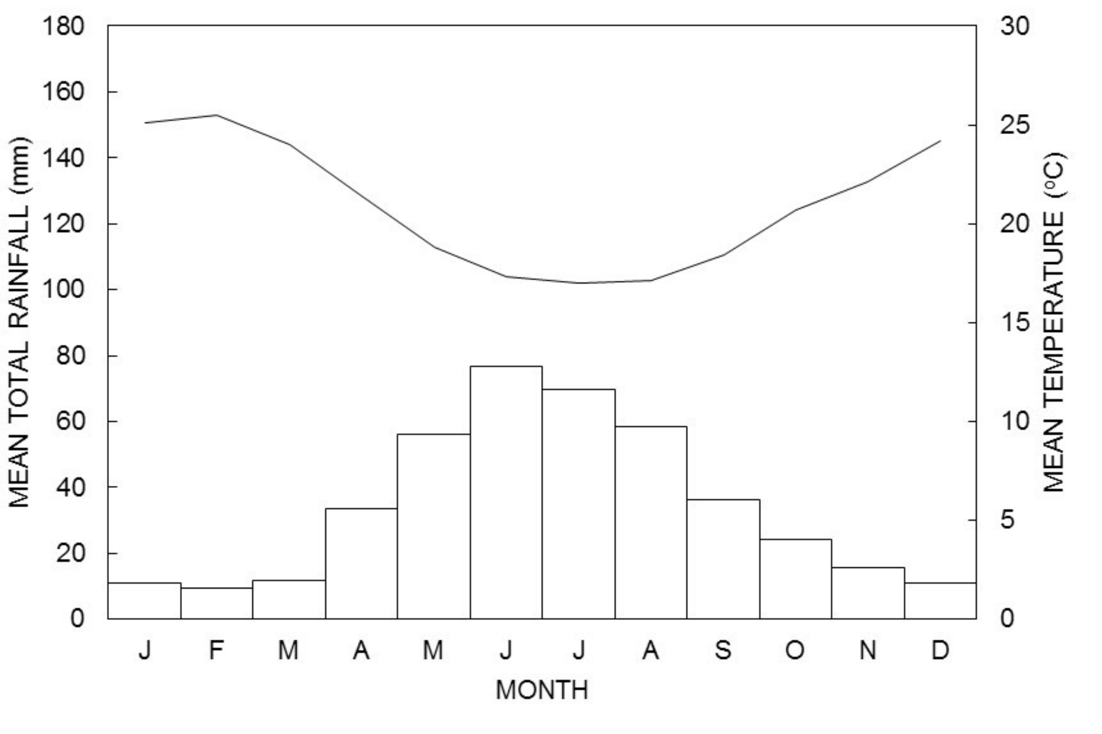


Figure 2-2 Climate of Robben Island, South Africa (unpublished data – South-African Weather Service). Missing monthly rainfall values were substituted by averages of available data.

C. Geology and Soils

Robben Island consists of a bedrock of ancient Late Precambrian shale (Tygerberg Formation) that is unconformably overlain by thick Pleistocene calcareous sandstone and limestone deposits (Langebaan Formation), that are in turn covered by the recent windblown unconsolidated Quaternary beach and dune sands and shell fragments (Miller 1991, Robben Island Museum 2006, Rowe, et al. 2010). The Quaternary sand deposits are shallow, attaining a maximum thickness of about 10 m (Parsons & Associates 1998). The shale bedrock consists of three general lithological groups (tan to grey sandstones, inter-bedded greywacke and siltstone, and fine dark grey slates) that outcrop mainly along the rocky coastline (Rowe, et al. 2010). The sandstone outcrop on the south-eastern and west–north-western coast and the slates on the southern tip and northwest of the island (Rowe, et al. 2010). The bedrock outcrops rarely in the island’s interior (Rowe, et al. 2010). A dolerite dyke cuts across the shale in the island’s southwest corner (Rowe, et al. 2010). Bands of old beach deposits consisting of rounded cobbles, gravel and shell deposits occur in the island’s south, west and north-western parts (Miller 1991). The rock formations on Robben Island are similar to those of the mainland, except that the stratification on the island is virtually horizontal or gently undulating. (Robben Island Museum 2006) Miller (1991) and Rowe et al. (2010) provide geological maps of the island.

The soils over the whole island are sandy or have an admixture of sand (Adamson 1934). Exceptions occur on rock outcrops and locally on the beach, where small stones, gravel, or shells are heaped up (Adamson 1934). Adamson (1934) recognised four soil types – coastal-blown sand (Witzand Formation (Miller 1991)), sand over limestone, sand over shale, and sand within rubble banks. The light-coloured, calcareous, unconsolidated coastal dune sands that constitute coastal-blown sand occur mainly on the island's eastern side (Adamson 1934, Miller 1991). Sand over limestone covers most of the island (Adamson 1934, Miller 1991) and is 0–70 cm thick, pale (lacking humus), without stones or gravel and has no definite stratification (Adamson 1934). The lack of stratification and occurrence of limestone on the surface has been attributed by Adamson (1934) to wind erosion. Sand over slate is similar to sand over limestone, but is shallow (3–5 cm), and has no lime (Nankivell 1934). Sand within rubble banks is dark and occurs between the stones (Adamson 1934). A comparatively recent soil survey of Robben Island was conducted by de Corte et al. (1986). Although references to the study occur in the literature, the report is inaccessible. As a result, we could not include information from the soil survey in this review.

D. Hydrology

Robben Island has no natural surface water except for rain pools in rocks or quarries. Inhabitants of the island have historically relied on rainwater, springs and boreholes for water supply (Adamson 1934, Nankivell 1934, Deacon 1996). Runoff is limited on Robben Island because of its flat terrain (maximum slope ~3%) and sandy soils (Parsons & Associates 1998). Significant runoff occurs only during extremely high-intensity rainfall events (e.g. above 150 mm/hr) or wet antecedent conditions (Parsons & Associates 1998). As a result, a high proportion of rainfall on Robben Island enters the subsurface (Parsons & Associates 1998). Groundwater was the island's primary source of water supply until 2006 when a desalinisation plant was constructed.

The overlying unconsolidated deposits on the island act as a primary aquifer (Vandoolaeghe, et al. 1990). However, the historical abstraction of groundwater resulted in a lowering of groundwater levels to such an extent that groundwater was no longer encountered in the upper part of the geo-hydrological system (Parsons & Associates 1998). Groundwater levels are expected to have risen as the volume of groundwater abstraction has been reduced following the construction of the desalinisation plant (Parsons & Associates 1998). Direct rainfall is the only groundwater recharge source on islands such as Robben Island (Parsons & Associates 1998). The extensive occurrence of sandy material on the island promotes a high proportion of rainfall infiltrating the subsurface and reaching the underlying aquifer system (Parsons & Associates 1998). The underlying fractured hard rocks of the Malmesbury Group act as a secondary aquifer on the island through which groundwater is transmitted through secondary openings derived from weathering, folding and fracturing. (Parsons & Associates 1998) No water-bearing fractures are encountered at depths greater than 40 m below the surface (Vandoolaeghe and Meyer 1990).

E. Flora

Robben Island has undergone considerable change since it was first occupied by humans in the seventeenth century (see Annex I). The island's proximity to Cape Town (~11 km) has resulted in it being altered to a considerably greater extent than any other South African offshore island (Brooke and Prins 1986, Smith 1997, Crawford and Dyer 2000). The island has experienced prolonged and heavy exploitation by humans and alien invasive organisms. Much of the flora now prevalent on the island consists mainly of elements introduced over four hundred years of human habitation (Nankivell 1934, Robben Island Museum 2006). Direct anthropogenic disturbance included human settlement, ranching, gardening and stone- and lime quarrying dating back to the late seventeenth century (Robben Island Museum 2006). Substantial construction began in the mid-seventeenth century, culminating in c. 700 buildings and other human-made sites on the island, covering more than 66 ha (Chapman, et al. 2000). During the early seventeenth century, various alien mammals were introduced, with overgrazing reported in 1659 (Thomb 1954). In addition to alien mammals, portions of the island were afforested with Australian *Eucalyptus* trees to provide shade and wood for residents and hide anti-aircraft guns during World War II (Brooke and Prins 1986, Smith 1997). More than 50 ha of the island is now covered by these alien tree plantations (Chapman, et al. 2000). As a result of its highly degraded nature, vegetation on Robben Island is considered to be of poor conservation value (Smith 1997, Fredericks 1998, Chapman, et al. 2000).

Although it is now impossible to determine the original nature of vegetation on Robben Island, the close similarities in climate and soil between the island and adjacent parts of the mainland have led researchers to believe the vegetation was historically the same (Adamson 1934, Nankivell 1934, Mucina, et al. 2006, Robben Island Museum 2006). The current view is that pre-human settlement vegetation on the island resembled present-day Cape Flats Dune Strandveld (CFDS) (Crawford and Dyer 2000, Mucina and Rutherford 2006, Robben Island Museum 2006). Robben Island's most current vegetation map presents it as CFDS and Cape Seashore Vegetation (Mucina and Rutherford 2006). Cape Flats Dune Strandveld is commonly found on the west coast of the Western Cape, from the Cape Point area to the Olifants River several hundred kilometres to the north (Robben Island Museum 2006). Cape Flats Dune Strandveld is classified as 'Endangered' (SANBI 2011) as it is now constricted by habitat transformation to a narrow band along the mainland's southwestern coast (Mucina and Rutherford 2006, Rebelo, et al. 2011). Cape Seashore Vegetation occurs along the south (from Cape Agulhas to East London) and southwest (from Cape Agulhas to the Olifants River mouth) coasts on the mainland (Mucina, et al. 2006). Unlike CFDS, Cape Seashore Vegetation is classified as 'least threatened' as nearly half of its extent is statutorily conserved in protected areas (Mucina, et al. 2006). Mucina and Rutherford's (2006) map presents the potential and not the existing vegetation of the island and is thus of limited value.

The most comprehensive description of extant vegetation and flora on Robben Island was provided by Professor R.S. Adamson (Adamson 1934) (see van Wilgen et al. (2016) for a brief biography). Professor Adamson conducted floral surveys on the island in spring (September 1933), early summer (October 1933) and late summer (March 1934) as part of a more extensive study of the island by the Cape Geographical Society (Adamson 1934, Nankivell 1934). The vegetation and floral description have been the primary reference for many subsequent ecological studies on the Island (Fredericks 1998). However, the description is outdated, having preceded several significant changes to the island's natural environment. The use of the island has, for example, changed from being a deserted colony for people with Hansen's disease (leprosy; 1931–1939) to a military outpost (1939–1959), maximum-security prison (1961–1995) and National Museum and Monument (1995–present) since Professor Adamson's survey (see Annex I). A new harbour, roads, gun emplacements, observation towers and underground magazines were constructed, and a substantial portion of the island (>50 ha) was afforested with Australian *Eucalyptus* trees and alien mammals such as springbok (*Antidorcas marsupials*), eland (*Taurotragus oryx*) and fallow deer (*Dama dama*) introduced during the period (Annex I).

Professor Adamson divided the island into six broad vegetation habitats based on soil characteristics, underlying geology and species composition (Table 2.2). An important feature of the vegetation habitat classification is that it was based on plant species' eco-physiological potential and limitations. However, more recent classifications of vegetation on the island have been based instead on descriptive and transient features such as vegetation physiognomy, land use and vegetation degradation status (e.g., Chapman, et al. 2000, Robben Island Museum 2006, 2013). Although of some service, vegetation classifications based on such descriptive and transitory features have limited ecological utility compared to eco-physiological descriptions such as Professor Adamson's. For example, Professor Adamson's vegetation habitats can provide a more useful, physiologically based template for directing present-day vegetation sampling and phytosociological classification than purely descriptive classifications. In addition, Professor Adamson's habitat-based vegetation classification provides a valuable framework for ecological restoration on the island. The vegetation habitats in the classification scheme can be used as spatially explicit restoration targets as they represent the condition of vegetation on the island before significant disturbances such as the construction of military installations and afforestation of parts of the island with Australian *Eucalyptus* trees during World War II as well as the introduction of alien mammals such as springbok, eland and fallow deer between 1946 and 1985. However, the utility of the vegetation habitats as pre-disturbance restoration targets is limited as vegetation on Robben Island had already been severely degraded by ~280 years of human occupation by the time of Professor Adamson's survey (Adamson 1934, Nankivell 1934, Gillham 1963). Long-term rabbit herbivory had reduced vegetation composition on the island to a few native species and weedy aliens that were either unpalatable or could escape or withstand heavy rabbit herbivory (Adamson 1934, Nankivell 1934, Gillham 1963). Therefore, Professor Adamson's vegetation habitats most likely missed important compositional and environmental features that a survey of the island's original pre-human settlement vegetation would have revealed. As a result, there is a need to develop restoration targets for island restoration based on reference conditions derived from analogous pristine mainland ecosystems (see, e.g., the research proposal 'Whole-island ecological restoration in South Africa: Opportunities, costs and challenges' available at https://www.researchgate.net/publication/278405845_Whole-island_Ecological_Restoration_in_South_Africa_Opportunities_Costs_and_Challenges).

Table 2-2 Vegetation habitats on Robben Island. Data obtained from Adamson (1934), Nankivell (1934), Miller (1991) and Rowe, et al. (2010).

Habitat	Description	Characteristic species
Sand over limestone	Most extensive Covers whole interior of the island Surface sand 0-70 cm thick, neutral or slightly alkaline, pale (lacking	*Crassula thunbergiana* Schult. *Isolepis incomtula* Nees *Albuca fragrans* Jacq.

	humus), without stones or gravel and no definite stratification	*Brunsvigia orientalis* (L.) Aiton ex Eckl. *Ehrharta villosa* Schult.f. *Physalis peruviana* L. *Cynanchum zeyheri* Schltr. *Solanum americanum* Mill. *Polycarena capillaris* (L.f.) Benth. *Romulea rosea* (L.) Eckl. *Haemanthus coccineus* L. *Phalaris minor* Retz. *Dimorphotheca pluvialis* (L.) Moench *Cissampelos capensis* L.f. *Orobanche ramosa* L.
Sand over shale (Flats over shale)	Forms belt ~300 m wide at the north end of the island Confined to patches near the coast on other parts of the island Covering sand similar to sand over limestone but shallow (3-5cm deep) and lacking lime	*Drosanthemum floribundum* (Haw.) Schwantes *Cyanella lutea* L.f. *Crassula vaillantii* (Willd.) Roth *Hordeum murinum* L. *Wahlenbergia androsacea* A.DC. *Arctotis 27frican* (Harv.) Beauverd *Corydalis decumbens* (Thunb.) Pers. *Ehrharta brevifolia* Schrad.
Rubble bank	Occurs just above the high-tide level along the southwest part of the island	*Frankenia pulverulenta* L. *Orbea variegata* (L.) Haw. *Ballota 27fricana* (L.) Benth.

	Extends for a little less than 700 m parallel to the coast Made up of water-worn stones derived from the Malmesbury slates Dark sand occurs between stones	
Inland rocks and quarries	Apart from the coast, outcrops of bedrock are of a limited extent Exposed bedrock at quarries covers a comparatively negligible portion of the island	*Crassula decumbens* Thunb. *Senecio littoreus* Thunb.
Windblown coastal sand dunes	Consist of sand blown up on the east coast of the island Covering sand is light (white) coloured, calcareous and unconsolidated Occurs in variable quantities but nowhere very deep	*Mesembryanthemum crystallinum* L. *Helichrysum crassifolium* D.Don *Elymus distichus* (Thunb.) Melderis *Tetragonia decumbens* Mill. *Capnophyllum africanum* (L.) Gaertn. *Psoralea repens* P.J.Bergius
Coastal rocks	On rocks at or about the high-tide mark sheltered from direct wave action The coastline on Robben Island is mainly rocky, apart from small shelly beaches at the island's north end	*Chenolea diffusa* Thunb. *Senecio maritimus* L.f. *Erepsia dunensis* (Sond.) Klak *Spergula rubra* J. Presl & C. Presl *Spergularia media* (L.) C.Presl *Atriplex* sp.

	Malva arborea (L.) Webb & Berthel. *Cotula filifolia* Thunb.

The vegetation on Robben Island is considered to be of poor conservation value (Robben Island Museum 2006, Roets and Pryke 2012). The extant flora is thought to represent only a fraction of the original natural vegetation that existed on the island before prolonged and heavy exploitation by humans and invasive organisms (Adamson 1934, Nankivell, 1934, Robben Island Museum 2006; Roets and Pryke 2012). However, three Red Data Book species still occur on the island – *Cynanchum zeyheri* Schltr. (classified as Vulnerable), *Dorotheanthus apetalus* (L.f.) N.E.Br. (classified as Insufficiently Known) and *Psoralea repens* P.J.Bergius (classified as Vulnerable) (Fredericks 1998, Bezeng 2012). Bezeng (2012) has compiled a relatively recent and comprehensive list of Robben Island flora based on an array of 2401 inventory plots systematically placed across the island. The plots were inventoried during mid-summer (December 2010) and autumn, winter and spring (April-September 2011) (Bezeng 2012, Bezeng, et al. 2013). Bezeng's (2012) list also included results from a plant inventory conducted by the South African Council for Scientific and Industrial Research on the island in 2010 (Bezeng, et al. 2013). I present in Annex II a consolidated species list that incorporates Bezeng's (2012) list with Adamson's (1934) list and a more recent but less thorough list developed from species I encountered on the island during my four-year study (2009-2013) of vegetation change on the island following control of European rabbits. The consolidated list is a valuable addition to Bezeng (2012)'s list as it shows species that occurred on the island in 1934 and may have subsequently gone extinct and those that may have re-emerged following the control of European rabbits in 2009. I standardised taxonomy between the lists using the online database The Plant List (2013), Version 1.1 (http://www.theplantlist.org).

Management plans for Robben Island advocate for restoring its vegetation to its original state, thereby enhancing its ecological function and conservation value (Fourtuin 2002, Robben Island Museum 2006, 2013). This restoration would significantly bolster the island's conservation worth, as the target vegetation, Cape Flats Dune Strandveld (CFDS), is classified as 'Endangered' (SANBI 2011). The National Environmental Management Biodiversity Act 10 of 2004 further mandates the restoration and conservation of CFDS (SANBI 2011). However, the island's status as a World Heritage Site complicates the restoration process. The UNESCO Convention Concerning the Protection of the World Cultural and Natural Heritage requires World Heritage Sites to maintain their authenticity and integrity by safeguarding culturally and historically significant artefacts (Robben Island Museum 2013). Despite its ecologically degraded state, the island's vegetation, akin to its buildings and other human-made infrastructure, holds cultural and historical value due to its association with significant events or stories linked to the island's heritage (see Annexe I, Fredericks 1998, Yeld 2008). These elements of the vegetation should be identified, rehabilitated, and preserved in the same manner as other cultural and historical artefacts on the island. Addressing the complex management issues surrounding the restoration of Robben Island's vegetation and the challenges posed by its World Heritage status necessitates a multifaceted approach that balances ecological conservation with cultural and historical preservation. An appropriate method would be to conduct a comprehensive site assessment of the island to identify culturally and historically significant elements of its vegetation. This would involve collaborating with cultural experts and historians to ensure a thorough understanding of the island's heritage. Stakeholder engagement, including with ex-detainees, ex-wardens, Island Management, provincial and national conservation agencies, and the wider public, would be undertaken to determine which elements should be preserved. The site assessment should inform a nuanced restoration plan that safeguards these elements. Selective restoration, based on this plan, can then be carried out on the island. This selective restoration would prioritise the restoration of native vegetation while preserving culturally significant plants and landscapes. This would be achieved by segregating restoration areas from culturally significant ones to minimise disruption to the latter. Cultural and educational programmes, alongside interpretive signage, could also be developed to inform visitors about the cultural and historical significance of the island's vegetation and promote awareness of the intertwined nature of ecological and cultural heritage. In conclusion, Robben Island's unique status demands a thoughtful and collaborative management approach that acknowledges the interwoven nature of its ecological and cultural importance. By carefully balancing these aspects, conservationists and land managers can ensure the island's preservation as a World Heritage Site while also enhancing its ecological function and conservation value.

Similar to ecological restoration, the impact of prolonged human disturbance and extensive environmental alteration on Robben Island has complicated efforts to control and eradicate alien invasive species – a crucial conservation and legislative imperative for the island. The Alien and Invasive Species Regulations under both the South African National Environmental Management: Biodiversity Act (10 of 2004) and the Western Cape Invasive Species Regulations (10 of 2004) mandate landowners and managers to identify, control, and eradicate alien and invasive species on their land. Robben Island hosts numerous such species (listed in Annex II), necessitating control and eradication where possible. However, several alien tree species – including the invasive Rooikrans (*Acacia cyclopis* Cunn. Ex Loudon), Manatoka (*Myoporum laetum* G. Forst.), and *Eucalyptus* spp. – which are virtually the only trees on the island, provide crucial shade for successful African penguin (*Spheniscus demersus*) breeding (Crawford, et al. 1998, Sherley, et al. 2012). Removing these trees would detrimentally impact nesting habitat for the endangered penguins and many other colonial breeders (Sherley, et al. 2012). Consequently, despite their detrimental ecological impact, comprehensive attempts to eradicate these invasive alien plants from the island have not been undertaken (Yeld 2008). Management actions have thus far been limited to thinning stands of invasive trees and clearing firebreaks within *Eucalyptus* plantations. Therefore, Robben Island requires a scientifically informed invasive species management plan that carefully considers the ecological consequences of eradication efforts. Where necessary, the plan should prioritise control over complete eradication, particularly in areas vital for endangered species like African penguins. Additionally, a strategic approach focusing on phased removal of invasive species is crucial, allowing time for indigenous vegetation to regenerate naturally. In areas where invasive species provide essential habitat, a careful balance must be struck, potentially through the creation of artificial habitats to compensate for their removal. This could involve creating and providing access to artificial nesting sites like nest boxes dug into the ground (Sherley, et al. 2012). Such replacement habitats could enable the birds to continue breeding successfully on the island even after the removal of alien tree species (Sherley, et al. 2012). Therefore, rigorous scientific research is urgently needed on the island to identify and develop alternative habitats and nesting sites for endangered species like the African penguin. This should be done before comprehensive action is taken to remove or manage invasive alien vegetation.

Lastly, continuous monitoring and adaptive management are crucial to assess the impact of restoration, alien invasive control, and eradication efforts on both the ecological and cultural aspects of the island, enabling timely adjustments to management plans. This includes ongoing monitoring of the impact of restoration and invasive species control efforts on the island's ecosystem. Collaborations with ecologists and conservationists are essential to adapt management strategies as needed, minimising disruption to native flora and fauna. Additionally, fostering collaboration between ecological scientists and historians can lead to innovative ways to reconcile ecological restoration with cultural and historical preservation. Through a harmonious blend of ecological expertise, cultural sensitivity, stakeholder engagement, and adaptive management, Robben Island's restoration challenges can be effectively addressed, ensuring the island’s ecological and cultural legacy for future generations.

F. Fauna

Robben Island has been reported to have a more diverse avifauna and a greater number of mammals and reptiles than any other southern African offshore island (Crawford and Dyer 2000). In addition to numerous bird species (~168 species; Paijmans, et al. 2017), there have been ~17 reptile, two amphibian, and at some stage ~23 mammal species reported on the island (Crawford and Dyer 2000). It is the only offshore island with a freshwater fish, the Mozambique tilapia (*Oreochromis mossambicus*), which has been reported in artificial pools that have formed within disused quarries (Crawford, et al. 1998, Crawford and Dyer 2000). The island harbours numerous indigenous arthropod species (Roets and Pryke 2012). Some of the arthropod species on the island are suspected of having evolved into unique, genetically distinct sub-lineages following separation from the mainland (Roets and Pryke 2012). Historically, the indigenous fauna on the island appears to have been dominated by Cape fur seals (*Arctocephalus pusillus*, African penguins, white pelicans (*Pelecanus onocrotalus*) and mole snakes (*Pseudaspis cana*) (Robben Island Museum 2006). Seals were hunted to extinction on the island before the nineteenth century (Robben Island Museum 2006). African penguins are thought to have stopped breeding on Robben Island in the early 1800s due to excessive exploitation (Crawford, et al. 1995). However, the penguins, an endangered species, resumed breeding on the island in 1983 (Crawford, et al. 1998).

Robben Island has been identified as an Important Bird Area (Barnes 1998), providing a breeding habitat for several threatened species, including the African penguin and the bank cormorant (*Phalacrocorax neglectus*) (Crawford, et al. 1998, Crawford and Dyer 2000, Robben Island Museum 2006). It is the only place in southern Africa where there is a wild population of chukar partridge (*Alectoris chukar*) and the only easily accessible location in the world where several thousand penguins can readily be seen by the public (Crawford, et al. 1998). The island supports two per cent of the global population of the African black oystercatcher (*Haematopus moquini*) (Crawford, et al. 1998). It provides a breeding site for various egrets and herons that are being steadily displaced from the mainland by habitat destruction (Crawford, et al. 1998). Four of the five sea birds that regularly breed on Robben Island (i.e. African penguin, bank cormorant, crowned cormorant (*Microcarbo* *coronatus*) and Hartlaub's gull (*Chroicocephalus hartlaubii*) are endemic to southern Africa (Crawford, et al. 1998).

Many mammals have been introduced to the island by humans during its long period of habitation (Annex III). Examples include the introduction of dassies (*Procavia capensis*) and sheep (*Ovi aries*) in 1601 (Lloyd 1994), cattle (*Bos taurus*) in 1608 (Lloyd 1994), European rabbits (*Oryctolagus cuniculus*) in 1654 (Skead 1980, Cooper and Brooke 1982, Lloyd 1994), pigs (*Sus scrofa domesticus*) before 1655 (Lloyd 1994), steenbok (*Raphicerus campestris*) in 1658 (Lloyd 1994, Crawford, et al. 1998), cats (*Felis catus* Linnaeus, 1758) in 1881 (Crawford and Dyer 2000), springbok, eland (Cooper and Brooke 1986), Blue wildebeest (*Connochaetes taurinus*) (Crawford and Dyer 2000), fallow deer after World War II (Smithers 1983), ostrich (*Struthio camelus*) in 1967 (Cooper and Brooke 1986) and bontebok (*Damaliscus pygargus pygargus*) in 1985 (Smithers 1986, Crawford, et al. 1998). Annex III presents the population dynamics of several introduced mammals whose details are available in the literature. Many of the introduced animals have since died out or been removed from the island. Only springbok, fallow deer, eland, steenbok and European rabbits were still present on the island in 2010 (Skead 2011, Philander 2017).

Introduced mammals have had a tremendous effect on the Island's other biota, particularly on the avifauna and vegetation (Lloyd 1994). In particular, feral cats and European rabbits have had an especially severe deleterious effect on the Island's birds (Brooke 1983, Brooke and Prins 1986, Cooper and Brooke 1986, Crawford, et al. 1998, Crawford and Dyer 2000) and vegetation (Adamson 1934, Nankivell 1934, Robben Island Museum 2006, Sherley 2016). Feral cats have drastically reduced the breeding success of small ground-nesting sea birds such as swift terns (*Thalasseus bergii*) and Hartlaub's gulls (*Chroicocephalus hartlaubii*) by predating on eggs, chicks and breeding adults (Crawford, et al. 1998). The vegetation and environment on Robben Island have been subjected to various disturbances besides rabbit herbivory since the arrival of the first European sailors in the 16th century (Robben Island Museum 2006). The disturbances also included hunting, human settlement, burning and woodcutting, gardening, ranching, afforestation with Australian Eucalyptus trees and military fortification (see Annex I). However, the effects of these disturbances, which are still evident across the island, are thought to have been of far less consequence than the alterations brought to the island's vegetation and environment by prolonged rabbit herbivory (Adamson 1934, Nankivell 1934, Robben Island Museum 2006). Recommendations for the control of European rabbits on the island have been made since 1889 (Chapman, et al. 2000), and there have been documented attempts at eradication in the early 1930s (Nankivell 1934) and more recently between 2009–2019 (de Villiers, et al. 2010, Sherley 2016, Davies, et al. 2020, Measey, et al. 2020). The recent eradication efforts have resulted in the cumulative removal of an estimated 13600 animals (Davies, et al. 2020, Measey, et al. 2020). European rabbits had reportedly not been seen (Davies, et al. 2020, Measey, et al. 2020) on the island since 2019.

VII. European Rabbits on Robben Island

European rabbits were introduced to Robben Island by the Dutch colonial governor Jan van Riebeeck in 1654 as a meat source for his Cape of Good Hope garrison and passing ships (Skead 1980, Cooper and Brooke 1982). The rabbits, however, only became successfully established in 1661 after numerous supplementations (Skead 1980, Cooper and Brooke 1982, Smithers 1983, Lloyd 1994). European rabbits have since been continuously present on the island. Although the historical record is patchy, rabbit numbers appear to have been low over much of their existence on the island. The island's various human inhabitants and feral cat populations have historically kept rabbit numbers low through trapping, hunting and predation (Apps 1984, Crawford and Dyer 2000, Sherley 2016). Rabbit numbers, however, seem to have intermittently exploded when the island became uninhabited by humans and predation by feral cats curtailed (Adamson 1934, Nankivell 1934, de Villiers, et al. 2010, Sherley 2016). For example, Adamson (1934) and Nankivell (1934) reported explosively high rabbit numbers on the island in 1933 following its desertion by humans after the closure of the General Infirmary in 1931 (Smallberg n.d.). Feral cats, which have intermittently gone extinct and been re-introduced to the island (Crawford and Dyer 2000, de Villiers, et al. 2010), were most probably absent or in low numbers as they were not explicitly mentioned by Adamson (1934). The reference to feral cat predation by Nankivell (1934) during this period appears to have been speculative and not based on direct observation. This is because Nankivell (1934) also mentions the predation of European rabbits by mole snakes and hawks in the same statement. It is doubtful that Nankivell (1934) would have directly observed rabbit predation by mole snakes and hawks and instead appears to have made the claim speculatively. Cats are believed to have been extinct as a feral stock on the island during most of the mid-20th century (Crawford and Dyer 2000).

High rabbit numbers occasioned by the island's abandonment by humans following the General Infirmary's closure in 1931 probably only persisted until 1939, when rabbit hunting and trapping would have resumed following the garrisoning of the island by military personnel and their families after its declaration as an army outpost in 1936 (Smallberg n.d.). Rabbit numbers would have returned to long-term low levels and been subsequently kept low by hunting and trapping by the military (1939-1959) and prison (1961-1995) personnel posted to the island. The military handed over Robben Island to the police in 1959, who converted it into a maximum-security prison in 1961 (Smallberg n.d.). The maximum-security prison was closed in 1995 (Smallberg n.d.). The island was subsequently declared a National Monument in 1995 (Parsons & Associates 1998) and a National Museum in 1996 (Robben Island Museum 2006). Robben Island Museum (RIM) officially assumed responsibility for managing the island from the Department of Correctional Services in 1997 (Parsons & Associates 1998). However, there was no mention of rabbit population explosions in the literature until 2008, when humans again abandoned the island and feral cats were eradicated.

The departure of prison staff in 1995 following the closure of the maximum-security prison would have effectively ended hunting and trapping on the island (Sherley 2016). However, rabbit numbers on the island are thought to have continued to be kept in check by a rapidly increasing feral cat population (Crawford, et al. 1998, Crawford and Dyer 2000, de Villiers, et al. 2010). Feral cats – which had gone extinct from Robben Island during the mid-20th century – had returned to the island in the mid-1980s but been kept at low numbers by hunting and trapping by prison staff (Brooke and Prins 1986, Cooper and Brooke 1986, Crawford, et al. 1998). However, feral cats began to increasingly predate endangered sea birds (Brooke and Prins 1986, Cooper and Brooke 1986, Crawford, et al. 1998). They were soon earmarked by RIM for removal from the island (Crawford and Dyer 2000, de Villiers, et al. 2010, Sherley 2016). Several attempts were made to eradicate feral cats from Robben Island between 1998 and 2007. The first attempt to remove feral cats from the island occurred in 1998/1999 when 107 cats were culled (Crawford and Dyer 2000). However, about ten cats survived the eradication attempt (Crawford and Dyer 2000), leading to the feral population's full recovery within a few years (de Villiers, et al. 2010, Sherley 2016). Cat removals were resumed in 2005, and more than 290 cats were culled between 2005 and 2007 (Sherley 2016). As a result of the cat removal programs conducted from 1998 onwards, predation pressure on the rabbit population is thought to have increasingly diminished, leading to a corresponding rise in rabbit numbers (~31 individuals in 1998, 100 in 1999, 2100 in 2003, 2400 in 2004, 3100 in 2005 and 4100 in 2006) that culminated in a population explosion (~24100 individuals) in 2008 (Crawford and Dyer 2000, de Villiers, et al. 2010, Sherley 2016).

In addition to the removal of feral cats, the explosion in rabbit numbers on Robben Island in 2008 seems to have also been synergistically facilitated by a preceding three-year run of summer rainfall above the long-term average (>86 mm per annum; Table 2.3). Feral rabbit populations are regulated by available forage without robust top-down control by hunting, predation, and disease (Myers, et al. 1977, Villafuerte, et al. 1997, Kontsiotis, et al. 2013). Gilliam (1963) suggested that the size of European rabbit populations on Mediterranean-type South African offshore islands appears to be controlled by the availability of reliable summer forage. As a result, recurrent population bottlenecks caused by inadequate summer forage may dampen annual rabbit population fluctuation in Mediterranean-type South African offshore islands when top-down control by human hunters and feral cats is weak or absent.

Table 2-3 Inter-annual rainfall variation on Robben Island in the period following the closure of the prison (1996), eradication of feral cats and explosion in rabbit numbers (2008), and commencement and end of the rabbit control exercise by RIM (2008-2011). Years of consecutive high summer rainfall (i.e., greater than the long-term average of ~86 mm per annum) are shown in bold.

Year	Total rainfall (mm)					Numbers[†]	
	Summer	Autumn	Winter	Spring	Annual	Cats	Rabbits
1996	117.60	30.00	283.30	64.40	495.30		
1997	97.10	30.60	134.73	22.36	284.79		
1998	80.06	19.30	281.60	19.00	399.96	10	31
1999	76.50	49.90	235.60	0.00	362.00		100
2000	50.60	5.40	186.60	49.80	292.40		
2001	30.30	21.60	432.80	46.80	531.50		
2002	**134.80**	40.10	242.50	22.90	440.30		
2003	**106.80**	12.80	163.60	59.20	342.40		2100
2004	61.20	65.70	221.10	22.60	370.60		2400
2005	**107.10**	47.20	239.80	38.25	432.35	61	3100
2006	**123.25**	26.50	215.50	10.60	375.85	12-15	4100
2007	**224.22**	45.73	285.83	37.90	593.68		
2008	57.20	10.00	278.60	125.80	471.60	0	24100
2009	48.80	19.00	260.70	49.20	377.70	0	1200
2010	61.10	12.00	238.30	6.50	317.90	0	0

2011	46.60	13.70	163.90	17.30	241.50	0	0
Long-term average	86.28	33.85	258.57	35.75	414.56		

†Numbers compiled from Crawford, et al. (1998), Crawford and Dyer (2000) and de Villiers, et al. (2010) (see Annex III).

However, the control of forage-induced summer population bottlenecks on rabbit population size may be broken by a run of seasons that ensures continuity of green forage over at least two summer seasons (Foran 1986, Cooke 2017). When summer rainfall is above the long-term average, the plant growing season is prolonged, and rabbit breeding is extended, resulting in more young and older adults' survival (Cooke 2017). Two years of good summer rainfall together produce such an abundance of rabbits that, on return to regular or drier seasons, the vegetation is over-exploited, and rabbit populations crash (Cooke 2017). The rabbit population explosion on Robben Island in 2008 appears to have been accompanied and followed by summer rainfall below the long-term average (Table 2.3), resulting in a significant population crash. Rabbit numbers are thought to have decreased by ~18000 in 2009 due to shortages in summer forage caused by reduced and low summer rainfall (de Villiers, et al. 2010, Sherley 2016). A similar, albeit less marked, increase and crash in the rabbit population would have probably occurred following the two-year run of above-average summer rainfall in 2002 and 2003 (Table 2.3) but was perhaps moderated by top-down control by a resurgent feral cat population. The run of above-average annual summer rainfall between 2002- 2003 and 2005-2006 most likely accounted for the higher rabbit numbers in 2003 and 2006 compared to 1998 and 1999 despite higher predation by a recovering cat population (see discussion on rabbit population dynamics on Robben Island above).

The rabbit population explosion in 2008 caused an environmental crisis on the island (Sherley 2016) that generated negative press coverage (e.g. Anon 2008a, b, Vosloo 2008, Yeld 2008). In response, RIM conducted a massive rabbit removal exercise between November 2008 and May 2009 in which ~4790 rabbits were culled (Anon 2008a, b, de Villiers, et al. 2010, Sherley 2016). The culling exercise probably contributed significantly (in addition to the rabbits that are thought to have died from starvation due to food shortages resulting from the decline in summer rainfall to below the long-term average in 2008) to the decline in rabbit numbers on the island between 2008 and 2009. Rabbit removal exercises continued into 2010, and by November, rabbit sightings on the island had become rare. As noted in the sections above, further control measures were undertaken until 2009, resulting in the cumulative removal of an estimated 13600 rabbits. European rabbits have not been seen on the island since 2019, but it is not yet certain whether they have been completely extirpated.

III. Effects of Rabbit Herbivory on Robben Island Vegetation

Adamson (1934), Nankivell (1934) and Gillham (1963) viewed extant vegetation on Robben Island to be a relic of over 270 years of heavy rabbit herbivory. They considered feral rabbits to have eliminated almost all naturally occurring plant species from the island, leaving behind a few native species and weedy aliens that were either unpalatable or could escape or withstand heavy rabbit herbivory. European rabbits have a hierarchical diet (Thompson and King 1994) that allows them to progressively switch forage species as preferred species become unavailable (Donlan, et al. 2002). However, despite diet switching, continued rabbit herbivory prevents the recruitment of preferred species (Donlan, et al. 2002). Prolonged suppression of preferred species by rabbit herbivory eventually leads to depletion of their seed banks and extinction (Hunt 2001). Adamson (1934) compared vegetation on Robben Island to vegetation on analogous rabbit-free mainland sites to test this hypothesis. As expected, he found vegetation on Robben Island to be relatively depauperate, more open and simpler in structure and with a higher percentage of annual and early successional species (see discussion on effects of rabbits on offshore island vegetation above). Adamson (1934) considered long-term rabbit herbivory on Robben Island to have degraded the island's vegetation beyond a critical threshold, such that the vegetation now existed as an alternative stable degraded early developmental state.

Although feral rabbits appear to have occurred at low density for much of their existence on Robben Island (see discussion on rabbit population dynamics on Robben Island above), their prolonged occurrence on the island would have been enough to lead to the progressive extinction of preferred species as hypothesised by Adamson (1934), Nankivell (1934) and Gillham (1963). Herbivory by even a few rabbits has been shown to have a considerable cumulative effect on vegetation over time (Farrow 1917, Cooke 2017). Adamson (1934), however, appears to have erroneously assumed a historical status quo of uniformly high rabbit numbers for the island. This explains his surprise at finding vegetation on the island showing signs of ongoing degradation in response to rabbit herbivory during his vegetation survey in 1933/1934 – ~280 years after the introduction of rabbits to the island. If rabbit numbers had been consistently high since their introduction, as thought by Adamson (1934), vegetation on Robben Island would have reached a state of equilibrium after almost three centuries of continuous and heavy herbivory. Rabbit herbivory, therefore, would have had no other effect on vegetation on the island by the time of Adamson (1934)'s survey. Foran (1986), for example, found that rabbits no longer degraded vegetation in arid regions of Australia ~127 years after their introduction but only restricted its development in response to improving seasonal conditions. Adamson (1934), however, observed that certain plant species such as the woody shrub *Tetragonia fruticosa* Linn, and herbs *Oxalis pes-caprae* L., *Satyrium odurum* Sond. and *Ferraria crispa* Burm. were in a state of diminution while others such as the woody shrubs *Cissampelos capensis* L.f., *Trachyandra* and *Conicosia* spp. and geophytes *Moraea collina* Mill. and *Ornithoglossum viride* L.f. appeared to be increasing.

Adamson (1934) appears to have not realised that the vegetation dynamics he was observing were not driven by long-standing heavy rabbit herbivory – but by a recent explosion in rabbit numbers following the desertion of the island by humans after the closure of the General Infirmary (Smallberg n.d.). The General Infirmary had operated on the island for 88 years. During this period, ~500 people had lived on the island at any given time and cared for hundreds of persons with Hansen's disease (leprosy) (Nankivell 1934). The island's human population had reached as many as 1500 people at its peak (Adamson 1934). The large human population would have kept rabbit numbers low during this period through trapping and hunting (see discussion on rabbit population dynamics on Robben Island above). The Infirmary's closure and evacuation of humans from the island would have released rabbits from hunting pressure, leading to the population explosion in the early 1930s. Feral cats, which have intermittently gone extinct and been re-introduced to the island (Crawford and Dyer 2000, de Villiers, et al. 2010), were most probably absent or in low numbers as they were not explicitly mentioned by Adamson (1934) (see discussion on rabbit population dynamics on Robben island above).

The vegetation dynamics observed by Adamson (1934) can, instead, be explained in terms of vegetation response to a recent explosion in rabbit numbers. The decline in cover of the palatable woody shrub *T. fruticosa* and herbs *O. pes-caprae*, *S. odurum* and *F. crispa* was clearly in response to increased rabbit herbivory. *Tetragonia fruticosa* provides much of the summer forage on Robben Island (Gillham 1963). Rabbits browse *Tetragonia* plants to the base of their shoots in the dry season (Adamson 1934). The herbs *S. odurum* and *F. crispa* are eaten freely by rabbits and only existed on Robben Island from 1933-1934 under the protection of bushes, especially the spiny *Asparagus* (Adamson 1934). On the other hand, the increase in cover of the woody shrub *C. capensis,* the herbs *M. collina*, *O. viride*, *Trachyandra,* and *Conicosia* species was evidently in response to release from interspecific competition with rabbit-preferred species such as *T. fruticosa*. Rabbits avoid *Trachyandra* and *Conicosia* spp. because of their astringent and often salty succulent tissue (de Villiers, et al. 2001), while the geophytes *M. collina* and *O. viride* are poisonous to rabbits (Adamson 1934).

Although no empirical information is available on vegetation change on Robben Island after the closure of the maximum-security prison in 1995, vegetation dynamics were most likely similar to those observed by Adamson (1934) following the closure of the General Infirmary and the desertion of the island by humans. However, unlike in 1933, when feral cats appeared to have been absent from the island, cats were present in 1995 and are thought to have kept rabbit numbers low until the commencement of cat removal programmes in 1998-1999 and 2005-2008 (see discussion on rabbit population dynamics on Robben Island above). The 1998-1999 cat removal programme was unsuccessful and would have resulted in a transient and moderate increase in rabbit numbers and their effect on island vegetation. Conditions on Robben Island would have become more like those which prevailed in 1933 following the 2005-2008 cat removals that culminated in the supposed eradication of feral cats from the island. Indeed, like in 1933, vegetation cover over much of the island in 2008 was reported to have been eradicated, and a distinct browse-line was evident at the height of at least 1.2 m (Yeld 2008, Sherley 2016). Fallow Deer and rabbits starved to death, and carcasses were observed on the dry range (Vosloo 2008, Yeld 2008). Rabbits – whose population had exploded to ~24100 individuals – were seen feeding off kelp and climbing acacia thorn trees to feed high up among the thorns (Yeld 2008), indicating a severe shortage of both graze and browse. Fallow Deer (*Dama dama*) on the island were observed breaking branches with antlers to access browse that would have otherwise been outside their reach (Sherley 2016). The deer were also observed eating a variety of other materials, including stranded kelp (*Ecklonia maxima* (Osbeck) Papenfuss), newspaper and cardboard littered on the island, garbage rummaged from rubbish bins and even a rabbit carcase (Sherley 2016). This probably indicated a decline in grazing capacity due to rabbits consuming much of the available graze and browse.

Vegetation conditions on the island would have most likely improved following rabbit control by Island management between 2008-2009 (see discussion on rabbit population dynamics on Robben Island above). This is because, according to the classical equilibrium paradigm (exemplified by the 'range model' in rangeland ecology; sensu Dyksterhuis 1949), a reduction in rabbit herbivory pressure would have resulted in the vegetation reverting through secondary succession to its pre-disturbance state. Assuming vegetation change inverse to that observed during 1933/1934, secondary succession following rabbit control would have consisted of an increase in cover of edible species and a decline in cover of less competitive unpalatable ones. Based on the observation by Adamson (1934), this would have entailed an increase in cover of palatable species such as *T. fruticosa*, *O. pes-caprae*, *S. odurum* and *F. crispa* and a decline in unpalatable species such as *C. capensis*, *Trachyandra*, *Conicosia* spp., *M. collina* and *O. viride*. The former would have most likely increased in response to release from herbivore pressure, while the latter would have declined because of the ensuing inter-specific competition. Generally, a strong positive correlation exists between a species' palatability to rabbits and its competitive ability (Crawley 1990, Pacala, et al. 1992, Diaz 2000). This is because characteristics that expose plant species to rabbit herbivory (e.g., tall vertical shoots) confer a competitive advantage. In contrast, those that protect them (e.g., shoots that grow close to the soil surface) reduce competitive ability. However, these hypothesised vegetation responses have not been empirically tested. The purpose of this thesis is to use plant species cover data collected over a period of four years (2010-2013) following rabbit control between 2008 and 2009 to empirically determine how vegetation responded to rabbit control on the island. As noted in the introduction, I believe an understanding of the vegetation response to rabbit control on Robben Island can provide valuable insights into how vegetation on other South African offshore islands will respond to rabbit removal. This would be particularly the case with other Mediterranean-type offshore islands (e.g., Dassen and Seal) on which rainfall, like on Robben Island, is confined to the winter months. Now that biodiversity conservation strategies increasingly require the removal of European rabbits from invaded South African offshore islands (European rabbits have, for example, been identified under South Africa's National Environment Management: Biodiversity Act 10 of 2004 as Category 1b invasive species that should be controlled), there is a need to understand how vegetation on the islands may respond to rabbit removal within their contexts of long-standing rabbit occupation and highly degraded ecosystems.

IX. Conclusion

Although the impact of invasive European rabbits on introduced environments across the globe has been extensively studied, this has not been the case for southern African offshore islands. As a result, literature on European rabbits in this region is scarce compared to other regions worldwide. Furthermore, the existing literature is scattered in journals and official reports that are difficult to access, making it challenging for policymakers, resource managers, and other stakeholders to utilise. The review chapter presents this information, which has until now been scattered in out-of-print or difficult-to-access journals and reports, in one accessible source. In addition to consolidating the literature into one accessible source, the review provides new insights into European rabbit population dynamics and their impact on island vegetation. For example, the review found that rabbit populations on many offshore islands may have historically been low due to hunting by human inhabitants (such as on Robben Island), predation by feral cats (as on Robben and Dassen Islands), and seasonal population crashes (such as annual dry season die-offs on Dassen Island). Rabbit populations may have instead erupted episodically during periods of island uninhabitation or reduced predation. Consequently, long-term rabbit herbivory has not led to the complete loss of palatable plant species, as periods of high rabbit densities allowed palatable species that could withstand heavy rabbit herbivory to recover and persist in the vegetation and seedbanks. Furthermore, the review reveals that in addition to the cessation of hunting and feral cat removal, the 2008 explosion in rabbit numbers on Robben Island was likely facilitated by a preceding three-year run of above-average summer rainfall, which dampened recurrent annual rabbit population bottlenecks caused by inadequate summer forage. Finally, the review found that while previous studies have examined the impact of rabbit herbivory on vegetation on Robben Island and other offshore islands, little research has been conducted on how vegetation on these islands may respond to rabbit control or removal. Understanding how vegetation responds to rabbit removal is crucial, as biodiversity conservation strategies increasingly require the removal of European rabbits from invaded South African offshore islands. For instance, under South Africa's National Environment Management: Biodiversity Act 10 of 2004, European rabbits have been classified as Category 1b invasive species that require control. The goal of this thesis is to experientially determine how vegetation responded to rabbit control on Robben Island using plant species cover data collected over a four-year period (2010-2013) following rabbit control between 2008 and 2009. As previously stated, an understanding of vegetation dynamics on Robben Island after rabbit control could provide valuable insights into how vegetation on other South African offshore islands, particularly those with a Mediterranean climate (such as Dassen, and Seal), might respond to rabbit removal.

X. References

Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

Anon. 2008a. Rabbits a threat to Robben Island. 'Available at' https://www.iol.co.za/news/south-africa/rabbits-a-threat-torobben-island-420389 [accessed 8 February 2017]

Anon. 2008b. Robben Island's rabbits to be culled. 'Available at' https://www.iol.co.za/news/south-africa/robben-islands-rabbits-to-be-culled-420363 [accessed 8 February 2017]

Apps P. 1984. Cats on Dassen Island. *Acta Zoologica Fennica* 172: 115-116.

Barnes KN (ed). 1998. *The important bird areas of southern Africa*. Birdlife South Africa. Johannesburg.

Bello-Rodríguez V, Mateo RG, Pellissier L, Cubas J, Cooke B, González-Mancebo JM. 2021. Forecast increase in invasive rabbit spread into ecosystems of an oceanic island (Tenerife) under climate change. *Ecological Applications* 31: e02206.

Bezeng BS. 2012. Invasion of alien species on Robben Island: causes and impacts on phylogenetic diversity of native plant communities. Magister Scientiae, University of Johannesburg, Johannesburg.

Bezeng BS, Savolainen V, Yessoufou K, Papadopulos AST, Maurin O, Bank M. 2013. A phylogenetic approach towards understanding the drivers of plant invasiveness on Robben Island, South Africa. *Botanical Journal of the Linnaean Society* 172: 142--152.

Brooke RK. 1983. On the 17th century avifauna of Robben Island, South Africa. *Cormorant* 11: 15-20.

Brooke RK, Crowe TM. 1982. Variation in species richness among the offshore islands of the southwestern Cape. *South African Journal of Zoology* 17: 49-58.

Brooke RK, Prins AJ. 1986. Review of alien species on South African offshore islands. *South African Journal of Antarctic Research* 16: 102-109.

Chapman R, Le Maitre DC, Holmes PM (eds). 2000. *Robben Island: a baseline terrestrial ecology study and recommendations for vegetation rehabilitation*. Environmentek CSIR Report No. ENV-Sc 99115. Stellenbosch.

Cooke B. 2017. Effects of pastoralism and rabbits on the economy and culture of the Diyari people of north-eastern South Australia. *Australian Economic History Review* 57: 65-83.

Cooper J, Brooke RK. 1982. Past and present distribution of the feral European rabbit *Oryctolagus cuniculus* on southern African offshore islands. *South African Journal of Wildlife Research* 12: 5-71.

Cooper J, Brooke RK. 1986. Alien plants and animals on South African continental and oceanic islands: species richness, ecological impacts and management. In: Macdonald IAW, Kruger FJ, Ferrar AA editors. *The ecology and management of biological invasions in southern Africa*. Cape Town: Oxford University Press. p. 133-142.

Cooper J, Hockey PAR, Brooke RK. 1983. Introduced mammals on South and South West African islands: history, effects on birds and control. Paper presented at the Birds and Man Symposium, Johannesburg

Courchamp F, Chapouis JL, Pascual M. 2003. Mammal invaders on islands: impacts, control and control impact. *Biological Reviews* 78: 347-383.

Crawford R, Dyer B. 2000. Wildlife of Robben Island. In: Underhill L editor. *Bright Continent Guide*. Cape Town: Avian Demography Unit.

Crawford RJM, David JHM, Dyer BM, Jarvis JUM, Shannon LJ, Spinks A, Upfold L, Crawford DAE, Crawford PJM, Knoll C*, et al.* (eds). 1998. *Terrestrial vertebrates of Robben Island*. Sea Fisheries Research Institute. South Africa.

Crawford RJM, v D Boonstra HG, Dyer BM, Upfold L. 1995. Recolonisation of Robben Island by African penguins, 1983-1992. In: Dann P, Norman I, Reilly PN editors. *The Penguins: Ecology and Management*. N.S.W. Australia: Surrey Beatty and Sons. p. 333-363

Crawley MJ. 1990. Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology* 27: 803-820.

Cubas J, Severin DH, Villafuerte R, Bello-Rodríguez V, Rodríguez-Luengo JL, del Arco M, Martín-Esquivel JL, González-Mancebo JM. 2019. Endemic plant species are more palatable to introduced herbivores than non-endemics. *Proceedings of the Royal Society B: Biological Sciences* 286: 20190136.

Davies S, Jordaan M, Karsten M, Terblanche J, Turner A, van Wilgen N, Veldtman R, Zengeya T, Measey J. 2020. Experience and lessons from alien and invasive animal control projects in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology*. Cham: SpringerOpen. p. 1302-1381.

de Corte WWM, Schloms BHA, Ellis F, Nell JP (eds). 1986. *A detailed soil survey of Robben Island*. Soil and Irrigation Research Institute Report No. GB/A/86/15. Pretoria.

de Villiers AJ, van Rooyen MW, Theron GK. 2001. Seedbank phytosociology of the Strandveld Succulent Karoo, South Africa: a pre-mining benchmark survey for rehabilitation. *Land Degradation and Development* 12: 119-130.

de Villiers MS, Mecenero S, Sherley RB, Heinze E, Kieser J, Leshoro TM, Merbold L, Nordt A, Parsons NJ, Peter HU. 2010. Introduced European rabbits (*Oryctolagus cuniculus*) and domestic cats (*Felis catus*) on Robben Island: Population trends and management recommendations. *South African Journal of Wildlife Research* 40: 139-148.

de Villiers SA. 1971. *Robben Island: Out of reach, out of mind. A history of Robben Island*. Cape Town: Struik.

de Vos A, Manville RH, Van Gelder RG. 1956. Introduced mammals and their influence on native biota. *Zoologica (New York)* 41: 163-194.

Deacon H. 1996. *The Island - a history of Robben Island 1488-1990*. Cape Town: David Phillip Publishers.

Diaz A. 2000. Can plant palatability trials be used to predict the effect of rabbit grazing on the flora of ex-arable land? *Agriculture, Ecosystems & Environment* 78: 249-259.

Dingle RV, Rogers J. 1972. Pleistocene palaeogeography of the Agulhas Bank. *Transactions of the Royal Society of South Africa* 40: 155–165.

Donlan JC, Tershy BR, Croll DA. 2002. Islands and introduced herbivores: conservation action as ecosystem experimentation *Journal of Applied Ecology* 39: 235-246.

Dyksterhuis EJ. 1949. Condition and management of rangeland based on quantitative ecology. *Journal of Range Management* 2: 104-115.

Farrow E. 1917. On the ecology of the vegetation of Breckland. IV. Experiments mainly relating to the available water supply. *Journal of Ecology* 5: 104-113.

Flux J, Fullagar P. 1992. World distribution of the rabbit Oryctolagus cuniculus on islands. *Mammal Review* 22: 151-205.

Flux JT, Fullagar PJ. 1983. World distribution of the rabbit (*Oryctolagus cuniculus*). *Acta Zoologica Fennica* 174: 75–77.

Fontanesi L, Utzeri VJ, Ribani A. 2021. 1 The evolution, domestication and world distribution of the European rabbit (*Oryctolagus cuniculus*). In: Fontanesi L editor. *The Genetics and Genomics of the Rabbit*. Wallingford, Oxfordshire: CAB International.

Foran BD. 1986. The impact of rabbits and cattle on an arid calcareous shrubby grassland in central Australia. *Vegetatio* 66: 49-59.

Fourtuin H (ed). 2002. *Robben Island Environmental Management Plan*. CSIR Environmentek. Pretoria.

Fredericks F (ed). 1998. *Vegetation of Robben Island*. University of the Western Cape.

Gillham ME. 1963. Some interactions of plants, rabbits and sea-birds on South African islands. *Journal of Ecology* 51: 275-294.

Graham K. 2013. TechMatters:"Qiqqa" than you can say Reference Management: A Tool to Organize the Research Process. *LOEX Quarterly* 40: 1-3.

Hunt LP. 2001. Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. *Journal of Applied Ecology* 38: 238–252.

Kontsiotis V, Bakaloudis D, Tsiompanoudis A. 2013. Key factors determining the seasonal population growth rate of European wild rabbits and their implications for management. *European Journal of Wildlife Research* 59: 495-503.

Lever C. 1985. *Naturalised mammals of the world*. London: Longman.

Lloyd PH (ed). 1994. *A review of non-human mammals on Robben Island*. Unpublished report.

Long JL. 2003. *Introduced mammals of the world: their history, distribution and influence*. Collingwood: CSIRO Publishing.

Measey J, Hui C, Somers MJ. 2020. Terrestrial vertebrate invasions in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology* No. 14. Cham, Swtzerland: Springer Open. p. 115-151.

Miller D. 1991. A geological description of Robben Island. *South African Lapidary Magazine* 23: 5-8.

Mucina L, Adams JB, Knevel IC, Rutherford MC, Powrie LW, Bolton JJ, van der Merwe JH, Anderson RJ, Bornman TG, le Roux A, *et al.* 2006. Coastal vegetation of South Africa. In: Mucina L, Rutherford MC editors. *The vegetation of South Africa, Lesotho and Swaziland*. *Strelitzia 19*. Pretoria: South African National Biodiversity Institute.

Mucina L, Rutherford M (eds). 2006. *Vegetation map of South Africa, Lesotho, and Swaziland*. Pretoria: South African National Biodiversity Institute.

Myers JH, Simberloff D, Kuris AM, Carey JR. 2000. Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution* 15: 316-320.

Myers K, Bults HG. 1977. Observations on the changes in the quality of food eaten by the wild rabbit. *Australian Journal of Ecology* 2: 215-229.

Nankivell JW. 1934. Robben Island. *The South African Geographical Journal* 17: 29-34.

Nowak RM. 1999. *Walker's mammals of the world vol. II*. Baltimore: The Johns Hopkins University Press.

Pacala SW, Crawley MJ. 1992. Herbivores and plant diversity. *American Naturalist* 40: 243-260.

Paijmans DM, Bolton D. 2017. First observation of Cape Batis *Batis capensis* on Robben Island. *Biodiversity Observations* 8: 40: 41-43.

Parsons & Associates (ed). 1998. *Assessment of the groundwater resources of Robben Island*. Somerset West, South Africa.

Philander R. 2017. Robben Island to cull deer. 'Available at' https://www.iol.co.za/capeargus/news/robben-island-to-cull-deer-9940208 [accessed 26 October 2017]

Rebelo AG, Holmes PM, Dorse C, Wood J. 2011. Impacts of urbanization in a biodiversity hotspot: conservation challenges in Metropolitan Cape Town *South African Journal of Botany* 77: 20–35.

Robben Island Museum (ed). 2006. *Integrated Conservation Management Plan (ICMP) for the Robben Island World Heritage Site*. Robben Island Museum Cape Town.

Robben Island Museum (ed). 2013. *Robben Island Integrated Conservation Management Plan. Natural Environment Management Plan*. Robben Island Museum. Cape Town.

Roets F, Pryke JS. 2012. The rehabilitation value of a small culturally significant island based on the arthropod natural capital. *Journal of Insect Conservation* 17: 53-65.

Rowe CD, Backeberg NR, van Rensburg T, Maclennan SA, Faber C, Curtis C, Viglietti PA. 2010. Structural geology of Robben Island: implications for the tectonic environment of Saldanian deformation. *South African Journal of Geology* 113: 57-72.

SANBI. 2011. Threatened terrestrial ecosystems for South Africa, Cape Flats Dune Strandveld (FS6). Available at http://bgis.sanbi.org/ecosystems/showecosystem.asp?id=63 [accessed 18 October 2017].

Schweizer D, Jones HP, Holmes ND. 2016. Literature review and meta-analysis of vegetation responses to goat and European rabbit eradications on islands. *Pacific Science* 70: 55-71.

Scott JJ, Kirkpatrick JB. 2013. Changes in cover of plant species associated with climate change and grazing pressure on the Macquarie island coastal slopes, 1980 – 2009. *Polar Biology* 36: 127-136.

Sherley RB. 2016. Unusual foraging behaviour in two introduced mammals following degradation of their island habitat. *Biodiversity Observations* 7: 1-10.

Sherley RB, Barham BJ, Barham PJ, Leshoro TM, Underhill LG. 2012. Artificial nests enhance the breeding productivity of African Penguins (*Spheniscus demersus*) on Robben Island, South Africa. Emu-Austral Ornithology 112: 97-106.

Skead CJ. 1980. *Historical mammal incidence in the Cape Province Vol. 1. The Western and Northern Cape*. Cape Town: Department of Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope.

Skead CJ. 2011. Historical incidence of the larger land mammals in the broader Western and Northern Cape In: Boshoff AF, Kerley GIH, Lloyd PH editors. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.

Smallberg M. n.d. *Robben Island: history summary*. Robben Island Education Department.

Smith C. 1997. *Robben Island*. South Africa: Struik Publishers.

Smithers RHN (ed). 1983. *The mammals of the southern African sub-region*. University of Pretoria. Pretoria.

Smithers RHN (ed). 1986. *South African red data book - terrestrial mammals*. National Scientific Programmes: CSIR Report No. SANSP 125.

Tankard AJ. 1976. Cenozoic sea-level changes: a discussion. *Annals of the South African Museum* 71: 1–17.

Thomb HB. 1954. *The journal of Jan van Riebeeck. Vol. II. 1656-1658*. South Africa: AA Balkema.

Thompson HV, King CM. 1994. *The European rabbit: the history and biology of a successful colonizer*. New York: Oxford University Press.

van Wilgen BW, Carruthers J, Cowling RM, Esler KJ, Forsyth AT, Gaertner M, Hoffman MT, Kruger FJ, Midgley G, Palmer G, *et al.* 2016. Ecological research and conservation management in the Cape Floristic Region between 1945 and 2015: History, current understanding and future challenges. *Transactions of the Royal Society of South Africa* 71: 207-303.

Vandoolaeghe MAC, Meyer PS (eds). 1990. *Robbeneiland en grondwater*. Directorate of Geohydrology Report No. GH 3487. Pretoria: Forestry DoWAa.

Villafuerte R, Lazo A, Moreno S. 1997. Influence of food abundance and quality on rabbit fluctuations: conservation and management implications in Doñana National Park (SW Spain). *Rev Ecol (Terre Vie)* 52: 345-356.

Vosloo E. 2008. Eco-xenophobia' for island's deer 'Available at' https://www.iol.co.za/news/south-africa/eco-xenophobia-for-islands-deer--403624 [accessed 8 February 2017]

Wilke C 2022. A review of more than a decade of problem causing animal control on Robben Island. Unpublished Video Presentation: Wilke's Eco Solutions.

Williams AJ, Klages NTW, Crawford RJM. 2000. Functional ecosystems: Coastal islands. In: Durham BD, Pauw JC editors. *Summary Marine Biodiversity Status Report for South Africa*. Pretoria: National Research Foundation.

Williams K, Parer I, Coman B, Burley J, Braysher M. 1995. *Managing vertebrate pests: rabbits* Canberra: Australian Government Publishing Service

Yeld J. 2008. Robben Island conservation 'in a shambles'. 'Available at' http://www.iol.co.za/news/south-africa/robben-island-conservation-in-a-shambles-1.398514#.Utf_RYWRa1s [accessed 8 February 2017]

CHAPTER 3

Vegetation composition change on a small Mediterranean-type South African offshore island following the control of invasive alien European rabbits (*Oryctolagus cuniculus*)

Thabisisani Ndhlovu[1] and Zivanai Tsvuura[2]

[1]School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa.

[2]Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa.

Formatted for submission to the African Journal of Range and Forage Science.

Abstract

Biological invasions pose a significant threat to global biodiversity and ecosystems. Invasive species such as the European rabbit (*Oryctolagus cuniculus*) not only drive global extinctions and disrupt ecosystem functioning but also adversely affect human livelihoods. Introduced to 13 of South Africa's 24 offshore islands in the 17th century, European rabbits have become extinct on seven but continue to persist on six. This study investigated vegetation changes on Robben Island, the most ecologically impacted of these islands, over four years (2010–2013) following rabbit eradication attempts in 2008–2009. Despite eradication efforts, our findings reveal an increase in early successional species rather than a return to the late-successional vegetation that was originally present, suggesting a significant alteration in seed banks and competitive plant dynamics due to prolonged rabbit herbivory. This alteration likely pushed the ecosystem past a critical ecological threshold, preventing the recovery of late-successional vegetation even after reducing the rabbit population. Furthermore, the vegetation composition at eucalyptus sites remained unchanged post-rabbit control, implying that the inhibitory effects of these alien trees on understory dynamics might be contributing to this lack of change. The results of this study highlight the complex challenges involved in the ecological restoration of islands that have long been affected by invasive species and underscore the need for comprehensive restoration strategies that include both the eradication of invasive species and the reintroduction of native plants. Additionally, these findings may provide valuable insights into how vegetation species composition might respond to rabbit control on other invaded South African offshore islands.

Keywords: European rabbits; invasive alien species; ecological restoration; vegetation composition; Robben Island; South Africa

Introduction

Biological invasions pose a significant threat to global biodiversity and ecosystems (Lurgi, et al. 2018). Throughout the world, invasive alien species (IAS) have negatively impacted native populations, communities, and ecosystems due to competition, predation, hybridisation, disease, and disruption to ecological services (Lurgi, et al. 2018, Thresher 2020). Consequently, IAS are now acknowledged as major drivers of animal and plant extinctions globally, with introduced mammals having the most severe impact (Cubas, et al. 2019, Cleeland, et al. 2020, Thresher 2020). Among invasive mammals, the European rabbit (*Oryctolagus cuniculus*) stands out as particularly problematic. It has been introduced to five continents and over 800 islands worldwide, where it poses a significant threat to both biodiversity and human livelihoods (Flux, et al. 1992, Schweizer, et al. 2016, Cubas, et al. 2019, Bello-Rodríguez, et al. 2021). In areas where they have been introduced, European rabbits have, among other impacts, been observed to modify the composition, diversity, and structure of plant species (Farrow 1917, Gillham 1955, Hobbs, et al. 1981, Lange, et al. 1983, Foran, et al. 1985, Foran 1986, Cubas, et al. 2018). They have also diminished grazing capacity (Farrow 1917, Friedel 1985, Foran 1986, Williams, et al. 1995, Williams 2011, Pennell, et al. 2016) and contributed to the degradation of landscapes (Cooke 1991, Strive, et al. 2019). Although research on the impact of invasive European rabbits on biodiversity and ecosystems has been extensive globally, its distribution has been uneven. Certain regions, such as the string of offshore islands along Africa's southern coast, have been studied less compared to others.

There exist more than 33 offshore islands along the southern African coast, 24 of which fall within South African territory (Cooper, et al. 1986). Offshore islands, also known as continental islands, are formed from unsubmerged portions of the continental shelf that are surrounded by the ocean. Southern African offshore islands were part of the mainland during the last Pleistocene glaciation, which occurred ~17,000 years ago. Subsequently, as sea levels rose following the glacial period's end, around 12,000 years ago, the highest points of the former coastal plain became isolated, forming the extant offshore islands (Tankard 1976, Brooke, et al. 1982, Brooke, et al. 1986). Most of the islands hold significant conservation value as breeding habitats for threatened and endangered seabird species, as well as colonies of Cape fur seals, *Arctocephalus pusillus* (Cooper, et al. 1986, Williams, et al. 2000). European rabbits were introduced to 13 South African islands, but they have since become naturally extinct on seven (de Vos, et al. 1956, Cooper, et al. 1982, Lever 1985, Long 2003, Skead 2011). Currently, feral rabbit populations are present on six South African offshore islands: Jutten, Dassen, Vondeling, Schaapen, Robben, and Seal Islands (Davies, et al. 2020, Measey, et al. 2020). European rabbits have not established on the South African mainland, most likely due to its broader suite of predators and pathogens (Gillham 1963, Cooper and Brooke 1986). The detrimental impact of European rabbits on the vegetation of South African offshore islands has long been known. Studies by Adamson (1934) and Gillham (1963) have demonstrated that European rabbits substantially alter and deplete vegetation communities on islands where they are present through selective grazing and browsing. More recently, an expert opinion evaluation conducted during the process of listing invasive alien species under the South African National Environment Management: Biodiversity Act 10 of 2004 (NEM:BA) (Kumschick, et al. 2020) identified rabbits as having a significant environmental impact on the islands due to their adverse effects on vegetation (Bruton 2021). Consequently, European rabbits were listed under the NEM:BA as Category 1b invasive species that require control. However, while we have some understanding of how long-term rabbit herbivory has impacted vegetation composition on South African offshore islands, our knowledge regarding how the vegetation might respond to rabbit control or removal is limited.

The impact of European rabbit herbivory on vegetation composition can be attributed to its influence on the relative abundance of different plant species and life forms (Farrow 1917, Fenton 1940, Gillham 1955, Ranwell 1960, Thomas 1960, Thomas 1963, Watt 1981, Bishop, et al. 1984, Foran 1986, Crawley 1990, Diaz 2000, Cubas, et al. 2018). European rabbits exhibit high selectivity in their herbivorous behaviour (Bhadresa 1977, Soane 1980, Cubas, et al. 2019), favouring soft, low-fibre, and highly nutritious herbaceous plants such as grasses, herbs, and succulents (Myers, et al. 1977, Friedel 1985, Foran 1986, Duffy, et al. 1996, Mátrai, et al. 1998, Gidenne, et al. 2020). Consequently, they intensively consume these highly nutritious plant forms, leading to the dominance of less palatable or unpalatable high-fibre annual grasses and unpalatable or low-growing herbs in plant communities (Hobbs and Grace 1981, Lange and Graham 1983, Friedel 1985, Foran 1986, Leigh, et al. 1989, Williams, et al. 1995, Diaz 2000, Eldridge, et al. 2002). Moreover, their selective herbivory on shoots or seedlings of trees and shrubs suppresses forest and shrubland regeneration, resulting in vegetation with fewer shrubs and trees (Cubas, et al. 2018, Gidenne, et al. 2020). In extreme cases, intensive and sustained herbivory can induce complete species turnover, leading to vegetation and seedbanks solely composed of unpalatable or toxic plant species (Acocks 1975, Skarpe 1986). Conversely, a reduction in rabbit herbivory often triggers a reversion of vegetation composition, characterised by the resurgence of palatable perennial grasses, herbs, and succulents through secondary succession (Farrow 1917, Ranwell 1960, Watt 1962, Bishop, et al. 1978, Bishop and Davy 1984, Norbury, et al. 1996, Finlayson, et al. 2021). This shift is usually accompanied by an increased recolonisation of tree and shrub species (Foran 1986, Denham, et al. 2004, Mesléard, et al. 2011, Strive and Cox 2019). The resurgence of palatable perennial grasses, herbs, and succulents corresponds with a reduction in the abundance of unpalatable or low-growing annual grasses and herbs (Ranwell 1960). This decline is attributed to the competitive advantage possessed by plant species more susceptible to rabbit herbivory. Generally, the more palatable a plant species is to rabbits, the more ecologically competitive it is. This is because many characteristics that make plants vulnerable to rabbit herbivory, such as tall vertical shoots, also make them competitive, whereas those that protect them, such as shoots close to the soil surface, make them less competitive. Consequently, a strong positive correlation exists between a species' palatability to European rabbits and its competitive ability (Crawley 1990, Pacala, et al. 1992, Diaz 2000). Therefore, as the palatable species rebound in response to reduced herbivory pressure following rabbit control, they outcompete and reduce the abundance of the less ecologically competitive unpalatable species that would have dominated the vegetation during rabbit herbivory.

In our study, we monitored changes in vegetation composition on Robben Island, the largest and most ecologically degraded South African offshore island (Crawford, et al. 2000), over a four-year period (2010–2013) following an attempt to eradicate invasive European rabbits from the island between 2008 and 2009 (Anon 2008a, b, de Villiers, et al. 2010, Sherley 2016). We had two objectives: (1) to determine the effect of rabbit control on the species composition of vegetation on the island and (2) to identify the changes in species cover underlying the observed change. Although South African offshore islands vary in size, distance offshore, and climate, Williams, et al. (2000) considered them similar enough to form a discrete biogeographical unit. Therefore, we believe that the vegetation dynamics on Robben Island offer valuable insights into the potential response of vegetation species composition to rabbit control on other invaded South African offshore islands. At present, Robben Island is the only South African offshore island from which sustained attempts have been made to deliberately eradicate European rabbits.

Following rabbit control, we expected that vegetation on Robben Island would undergo secondary succession towards its original species composition or its projection over time. Given that the original vegetation on the island, Cape Flats Dune Strandveld, is a grassy shrubland primarily dominated by evergreen sclerophyllous shrubs in its southern region and drought-deciduous shrubs and succulents in the north (Liengme 1987, Robben Island Museum 2006), our prediction was that the compositional shift would involve the re-establishment of palatable late-successional perennial grasses, succulents, and herbs, alongside increased recolonization by shrub species (see, e.g., Kämpfer, et al. 2019). This change would coincide with a decrease in the abundance of less ecologically competitive unpalatable or low-growing early successional annual grasses and herbs, which would have proliferated before rabbit control due to decreased competition with rabbit-favoured plants. However, concerns have been raised (see, for e.g., Adamson 1934, Nankivell 1934, Cooper and Brooke 1982, Brooke and Prins 1986) that prolonged rabbit herbivory on South African offshore islands may have pushed their ecosystems beyond critical ecological thresholds, meaning that merely removing rabbits may no longer lead to unaided succession back to the original natural vegetation. In general, the longer the duration of herbivory before rabbit control, the less likely it is that vegetation composition will recover without external intervention (Fenton 1940). This is because vegetation that has been intensively browsed and grazed over a significant period can completely lose species that are sensitive to rabbit herbivory (Watt 1957). In such cases, plant species susceptible to rabbit herbivory would have been entirely removed from both vegetation and seed banks, reducing the possibility of successional changes in species composition when vegetation is protected from herbivory (Leigh, et al. 1989, Norbury and Norbury 1996, Latham, et al. 2020, Finlayson, et al. 2021). Rabbit herbivory had been ongoing on Robben Island for over 350 years before rabbit control began in 2008. The island is also separated from the mainland by ~7 km of the South Atlantic Ocean (Crawford and Dyer 2000), which restricts plant dispersal. Therefore, it was possible that vegetation composition on the island would not have changed after rabbit control, since herbivory-sensitive palatable species would have been absent from the vegetation and seed banks, and unavailable to respond positively to reduced herbivory pressure.

Materials and Methods

Study site

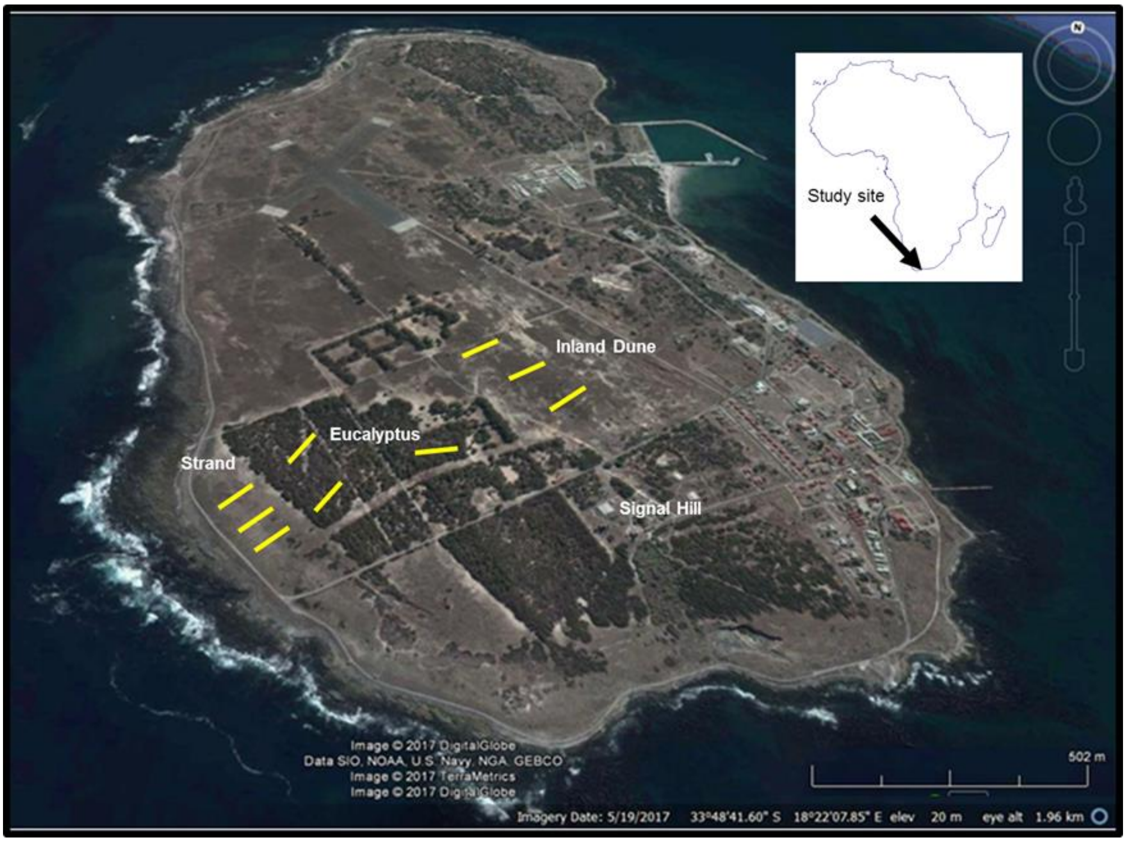


Figure 3-1 Map showing the location of the study site and placement of fixed transects. Satellite image obtained from Google Earth (Version 5.1.3533.1731). Mountain View, CA: Google Inc. (2009).

Robben Island (33°48'S, 18°22'E; Figure 3.1) is the largest (~507 ha) of the chain of offshore islands that occur along South Africa's coast. It lies in Table Bay, about 11 kilometres north of Cape Town and ~7 kilometres from the nearest mainland (de Villiers 1971, Brooke and Prins 1986, Crawford and Dyer 2000). The island experiences a temperate Mediterranean climate with hot, dry summers and cool, wet winters, much like the adjacent mainland (Adamson 1934, Crawford and Dyer 2000, Robben Island Museum 2006). Robben Island's environment has changed considerably since humans settled there in the 17th century (Robben Island Museum 2006). However, geographical, and climatic similarities between the island and adjacent parts of the mainland have led researchers to believe that their vegetation was historically contiguous (Adamson 1934, Nankivell 1934, Mucina, et al. 2006, Robben Island Museum 2006). It is, therefore, currently believed that pre-human settlement vegetation on the island resembled present-day mainland Cape Flats Dune Strandveld (CFDS) and Cape Seashore Vegetation (CSV; Crawford and Dyer

2000, Mucina and Rutherford 2006, Robben Island Museum 2006). The present vegetation on Robben Island is considered to be only a fraction of what it was in terms of species richness before heavy exploitation and disturbance by humans and invasive alien species (Adamson 1934, Nankivell 1934, Robben Island Museum 2006, Roets, et al. 2012). While vegetation on Robben Island has been affected by various elements, including several other introduced large herbivores, since the 17th century, the alterations resulting from extended rabbit herbivory are thought to have had the greatest impact on the island's environment (Adamson 1934, Nankivell 1934, Robben Island Museum 2006).

European rabbits were introduced to Robben Island in 1654 by the Dutch colonial governor, Jan van Riebeek (Measey, et al. 2020). Historically, rabbit numbers on the island remained low due to trapping, hunting, and predation by humans and feral cats (Apps 1984, Crawford and Dyer 2000, Sherley 2016). However, periodic surges in rabbit numbers occurred when the island was uninhabited, and predation by feral cats was minimal or absent (Adamson 1934, Nankivell 1934, de Villiers, et al. 2010, Sherley 2016). One such surge happened in 2008 following the desertion of the island in 1998 due to the closure of the island prison and the culmination of a series of cat removal exercises that began in 1998. This population explosion triggered an environmental crisis on the island, resulting in negative press coverage (Anon 2008a, b, Yeld 2008). In response to the crisis in 2008, when rabbit numbers had surged to ~24100, Robben Island Management conducted a massive rabbit removal exercise between November 2008 and May 2009. During this period, ~4790 rabbits were culled (de Villiers, et al. 2010, Sherley 2016), and around 18000 rabbits are thought to have died from starvation due to food shortages, which were most likely a consequence of the decline in summer rainfall to significantly below the long-term average (see Chapter 2). Rabbit removal exercises on the ~1,200 remaining rabbits continued into 2010 (Sherley 2016), and by November, rabbit sightings on the island had become extremely rare, with only three rabbits observed during field exercises in March and none by November. No rabbits were observed during field sampling from November 2010 until 2013, when the study ended. Subsequent efforts to eradicate rabbits from the island have resulted in the removal of ~13600 animals by 2019 (Davies, et al. 2020, Measey, et al. 2020). Since 2019, European rabbits have not been sighted on the island (Measey, et al. 2020), and the prevailing belief is that they have been successfully eradicated.

Field sampling and data analysis

Plant species cover change was monitored at nine sites (strand (n=3), eucalyptus (n=3), and inland dune (n=3)) on the south-eastern portion of Robben Island over four years (2010-2013), following an attempt to eradicate invasive alien European rabbits from Robben Island between 2008 and 2009 (see Figure 3.1 for location of sites). The sites were positioned along a deliberately selected transect that extended across major ecological land units on the island, utilising the gradsect method (Gillison and Brewer 1985) to capture ecological variability across the study site along a gradient. Species cover at each site was determined annually in early summer (November) using line point intercepts (see Herrick, et al. 2005) along three 100-metre transects, each separated by 50 metres. This 50-metre spacing was a methodological choice designed to improve data quality and representativeness by ensuring the independence of data points and capturing ecological variability across sites. The point intercept method was implemented by placing points at 1-metre intervals along each transect, resulting in 100 points per transect and a total of 300 recordings per site. Plant species cover referred to the cover of the upper layer of each plant species, regardless of the overhanging cover of other species (Herrick, et al. 2005, Fehmi 2010). Plant nomenclature followed The Plant List (2013), Version 1.1 (http://www.theplantlist.org).

Inter-annual rainfall variation

Variations in inter-annual rainfall play a significant role in the vegetation dynamics of Mediterranean ecosystems (Mucina and Rutherford 2006, Esler, et al. 2018). Therefore, analyses and interpretations of vegetation dynamics in Mediterranean-type ecosystems must always take into account inter-annual rainfall variation (Austin, et al. 1981, Foran 1986). Total annual, summer, winter, autumn, and spring rainfall for Robben Island were computed using unpublished data sourced from the South African Weather Service. Yearly rainfall totals were determined by adding up the monthly rainfall data from the preceding 12 months before the vegetation monitoring period. Similarly, total summer (TSUR), winter (TWR), autumn (TAUR), and spring (TSR) rainfall were calculated by summing the rainfall recorded during the respective months preceding the monitoring period. Summer occurred from October to March, followed by autumn in April, winter between May and August, and spring in September. In cases were rainfall data was missing, the means of available non-missing data were used as substitutes. Long-term rainfall averages were computed over a period of 113 years (1900 - 2013).

Statistical analyses

The change in vegetation composition was determined from differences in mean species cover between the four years that proceeded rabbit control. Inter-annual species compositional change was assessed within the strand, eucalyptus and inland dune sites using one-way Analysis of Similarities (ANOSIM, 999 permutations, Bray-Curtis distances; (Clarke 1993)). Species cover changes that drove compositional change were identified and ranked using Similarity of Percentage (SIMPER; Clarke 1993). The non-parametric ANOSIM was used instead of repeated-measures one-way Multivariate Analysis of Variance

(MANOVA) because data remained multivariate non-normal even after transformation. Data were transformed using Box-Cox power transformation (Box, et al. 1964, Sakia 1992) and tested for multivariate normality using the Doornik and Hansen omnibus test (Doornik, et al. 1994). To focus the analysis on the most important composition changes, only plant species that accounted for the top 95% of inter-annual compositional Bray Curtis dissimilarities were considered. Significant differences in individual plant species' contributions to composition change (i.e., mean annual species cover) were determined using repeated-measures ANOVA tests. The Exact Wilcoxon two-sample paired test was used for species with only two years of mean cover values above zero. The magnitude of overall species compositional differences between years was assessed based on mean annual non-metric multidimensional scaling axis one scores (NMDS, two dimensions, Bray-Curtis distances; (Kruskal 1964)), with an addition of 1.50 to NMDS axis scores to prevent negative values. Significant differences in mean annual NMDS axis scores were determined using repeated-measures ANOVA tests after testing for normality using the Shapiro-Wilk test. The NMDS axis scores were log transformed before analysis. Principal Components Analysis (PCA) biplots were used to graphically portray the contributions of individual plant species to inter-annual vegetation compositional differences following rabbit control.

The role of interannual rainfall variation in influencing changes in species composition in the years following rabbit control was evaluated using multiple regressions. Multivariate multiple regressions were used to assess the influence of inter-annual rainfall variation on changes in mean individual species contributions to compositional change. Total summer rainfall, TAUR and TWR were used as independent variables in all regressions. Total annual rainfall and TSR, which Redundancy Analysis (RDA; McCune, et al. 2002) identified as collinear and, therefore, potentially redundant, were excluded from regressions. Rao's F statistic was used to test for overall multivariate significance, while t-tests were used to determine the significance of separate combinations of independent and dependent variables. To achieve distributional normality and homoscedasticity, interannual rainfall and species cover data utilised in the regressions were subjected to Box-Cox power transformations. Tests for multivariate normality and homoscedasticity were conducted using the Doornik and Hansen omnibus test (Doornik and Hansen 1994). Regression residuals were tested for serial correlation using Durbin-Watson tests (Durbin, et al. 1951). Redundancy Analysis (RDA) tri-plots (ter Braak, et al. 1994) were used to graphically represent species cover-rainfall relationships.

Significance, normality, regression and serial correlation tests were carried out using the Paleontological Statistics Software Package for Education and Data Analysis (PAST; Hammer, et al. 2001). False discovery rate-based adjustments for multiple comparisons were made using the spreadsheet provided by Pike (2011). Principal Components Analysis and RDA were conducted using vegan (Oksanen, et al. 2015) in R

(R Core Team 2020). We used PCA and RDA because Detrended Correspondence Analysis confirmed species cover data underlying species composition change conformed to the linear model (see Annex VIII Figure S1). Analyses were conducted separately for strand, eucalyptus and inland dune sites to evaluate the effects of landscape variation on vegetation composition dynamics across the island.

Multiple comparison and serial correlation

In this study, the effects of multiple comparisons and serial correlation were not considered in the interpretation of statistical results. This was because, as the study was exploratory in nature, there was greater concern about making Type II errors (false negatives) than Type I errors (false positives; see Nakagawa 2004). Type I errors occur when a genuine effect is non-existent, yet the analysis implies its presence. Conversely, Type II errors arise when a true effect exists but goes unnoticed by the analysis. Multiple comparisons inflate Type I errors. However, while adjustments for multiple comparisons, such as the Bonferroni correction, limit Type I errors, they also increase Type II errors. Similarly, serial correlation may result in over-optimistically low *P*-values (Type I error; Weissgerber, et al. 2016, Forstmeier, et al. 2017). However, adjusting for serial correlation — like adjusting for multiple comparisons — leads to inflated Type II error rates. Multiple comparison-adjusted *P* values (Annex IV Table S2) and evaluations of serial correlation (Annex IV Table S1 and S4) are provided for reference.

Modelled before-after, control-impact (BACI) design and correlative statistical control

The study was opportunistically based on the attempt to remove invasive alien European rabbits from Robben Island, which led to several methodological challenges. Firstly, owing to its unplanned nature, the study commenced a full year after the rabbit removals had started. Consequently, the well-established before-after, control-impact (BACI) design (Stewart-Oaten, et al. 1986, Stewart-Oaten, et al. 2001, Smith 2002), commonly used in longitudinal observational studies, could not be employed (Johnson 2002). Secondly, the opportunistic nature of the study precluded the use of planned treatments and randomisation to eliminate confounding variables. Particularly, there were constraints in evaluating and cancelling out the confounding effects of rainfall variation on vegetation response. To address the first methodological challenge, island vegetation was modelled as a longitudinal time series, utilising data from a previous vegetation survey conducted by Adamson (1934) in 1933-1934, a period when the island was overrun by rabbits. Assuming that the conditions during 1933-1934 resembled those prior to rabbit control in 2009 and 2010, the survey results were used as a BACI-like control (see Annex V). However, this assumption is precarious, as the Adamson (1934) survey was conducted 77 years prior to the present study's sampling, and the island has undergone significant environmental changes since then. Moreover, the island was uninhabited during the 1933-1934 survey (Nankivell 1934), resulting in the complete absence of rainfall records for that period, which limits the comparability between these periods. Nevertheless, the Adamson (1934) survey remains the only detailed vegetation study on the island that provides a viable baseline. Addressing the second challenge involved using correlative statistical control, providing plausible mechanisms, and citing independent evidence from published literature to support interpretations of correlative rainfall-vegetation interactions (Annex V).

Results

Inter-annual rainfall variation

Inter-annual rainfall varied considerably during the four years following rabbit control (Table 3.1). Total summer rainfall was significantly below the long-term average in the first- and second years following rabbit control (Table 3.1). It then increased to moderately above or equal to the average in the third and fourth years, respectively (Table 3.1). Total autumn rainfall followed the same pattern as total summer rainfall. Total winter rainfall was slightly to moderately below the long-term average in the first- and second years following rabbit control and substantially increased to above average in the third and fourth years (Table 3.1).

Table 3-1 Inter-annual rainfall following the control of invasive alien European rabbits on Robben Island. Long-term (1900– 2013) rainfall averages are provided for comparative purposes.

Rainfall (mm)	Year				Long term average
	2010	2011	2012	2013	
Total summer rainfall	22	10	61	51	50
Total autumn rainfall	12	14	42	31	34
Total winter rainfall	238	164	270	354	258

Vegetation composition change following rabbit control

Strand sites

Vegetation species composition changed significantly (R = 0.51, *P* = 0.001) following rabbit control. Mean annual NMDS axis one scores changed moderately across the sites between the first- and second years following rabbit control (change by 0.15 NMDS axis scores), slightly more markedly between the second- and third (change by 0.16 NMDS axis scores) and slightly between the third- and fourth (change by 0.04 NMDS axis scores; Table 3.2). The increase in cover of the woody shrub *Tetragonia fruticosa* Linn. between the first- and second years and emergence of the annual grass *Ehrharta longiflora* Sm between the second-and third and subsequent increase in cover mainly drove vegetation composition change following rabbit control (Figure 3.2; Annex IV Table S2). Emergence of the perennial grass *Ehrharta villosa* Schult.f. between the first- and second years, increase in cover of the annual herb *Oncosiphon suffruticosum* (L.) Kallersjo between the second, third and fourth, and decline in cover of the perennial herb *Conicosia pugioniformis* (L.) N. E. Br. between the first- and second were of intermediate (but considerably lesser) importance (Figure 3.2; Annex IV Table S2). Temporary disappearances of the perennial grass *Cynodon dactylon* (L.) Pers., herb *Zantedeschia aethiopica* (L.) Spreng. and emergence of the alien annual grass *Bromus diandrus* Roth and annual alien herb *Silene cretica* L. between the first- and second years were of minor importance (Figure 3.2; Annex IV Table S2).

Inter-annual rainfall variation accounted for ~83% of vegetation composition change, with TSUR accounting for ~42%, TAUR ~67% and TWR ~29% (Table 3.3). At the species level, inter-annual rainfall variation accounted for ~98%, ~33% and ~32% of the change in cover of *E. longiflora*, *C. pugioniformis* and *S. cretica,* respectively, following rabbit control (Annex IV Table S3). An increase in TAUR and TWR accounted for ~90% and ~67% of the increase in cover of *E. longiflora* between the second-and third years following rabbit control (Figure 3.3; Annex IV Table S3). In contrast, increase in TAUR suppressed (i.e., was negatively correlated with) the increase in cover of *C. pugioniformis* by ~13% during the same period (Figure 3.3; Annex IV Table S3). An increase in TSUR suppressed (i.e., was negatively correlated with) the increase in the cover of *E. longiflora* by ~80%, while the overall increase in rainfall accounted for the increase in cover of *S. cretica* between the second- and third-years following rabbit control (Figure 3.3; Annex IV Table S3). Inter-annual rainfall variation had no significant influence on the change in cover of *B. diandrus*, *O. suffruticosum*, *Z. aethiopica*, *E. villosa*, *C. dactylon* and *T. fruticosa* (Annex IV Table S3).

A decline in cover of *C. pugioniformis* was correlated with an increase in cover of *T. fruticosa* (strongly), *E.* longiflora an*d B. diandrus* (moderately), *E. villosa* and *O. suffruticosum* (weakly; Figure 3.2). Increase in cover of *O. suffruticosum* was weakly correlated with a decline in cover of *T. fruticosa* (Figure 3.2).

Eucalyptus sites

Vegetation composition did not change significantly (R = 0.15, *P* = 0.104) following rabbit control. However, mean annual NMDS axis one scores changed moderately across the sites between the first- and second years following rabbit control (change by 0.13 NMDS axis scores), more markedly between the second- and third (change by -0.36 NMDS axis scores) and slightly between the third and fourth (change by 0.01 NMDS axis scores; Table 3.2). The increase in cover of the perennial herb *P. canaliculatus* and emergence and subsequent increase in cover of the woody shrub *T. fruticosa* between the second-and third years mainly drove vegetation composition change following rabbit control (Figure 3.2; Annex IV Table S2). The temporary disappearance of the perennial herb *O. pes-caprae* during the second year was of intermediate importance (Figure 3.2; Annex IV Table S2). Emergence of the annual herbs *O. suffruticosum, Euphorbia peplus* L. (alien) and *Chenopodium murale* L. (alien) between the second- and third years and in the fourth were of minor importance (Figure 3.2; Annex IV Table S2).

Inter-annual rainfall variation accounted for ~58% of vegetation composition change, with no significant effects at the seasonal level (Table 3.3). At species level, inter-annual rainfall variation accounted for ~52%, ~43% and ~42% of the change in cover of *T. fruticosa*, *P. canaliculatus* and *O. pes-caprae* respectively, following rabbit control (Annex IV Table S3). A decrease in TWR accounted for ~31% of the decline in cover of *O. pes-caprae* during the second year following rabbit control (Annex IV Table S3). Although inter-annual rainfall variation accounted for ~52% and ~43% of the emergence and increase in cover of *T. fruticosa* and *P. canaliculatus* between the second-and third years following rabbit control, there was no significant statistical relationship at the seasonal level (Annex IV Table S3). Inter-annual rainfall variation had no significant influence on the change in cover of *O. suffruticosum*, *E. peplus* and *C. murale* (Annex IV Table S3).

Inland dune sites

Vegetation species composition changed significantly (R = 0.21, *P* = 0.012) following rabbit control. Mean annual NMDS axis one scores changed moderately across the sites between the first- and second years following rabbit control (change by 0.17 NMDS axis scores) and the changes were progressively lesser between the second -, third- and fourth years (changed by 0.06 and 0.01 NMDS axis scores, respectively; Table 3.2). The increase in cover of the woody shrub *T. fruticosa* between the first-, second and third years and perennial grass *E. villosa* across the years mainly drove vegetation composition change following rabbit control (Figure 3.2; Annex IV Table S2). Emergence of the alien annual grass *B. diandrus* between the second-and third years and decline in cover of the perennial herb *C. pugioniformis* between the first- and second were of intermediate (but considerably lesser) importance (Figure 3.2; Annex IV Table S2). The temporary disappearance of the annual grass *E. longiflora* between the first- and second years was of minor importance (Figure 3.2; Annex IV Table S2).

Inter-annual rainfall variation accounted for ~37% of vegetation composition change, with TAUR accounting for ~25% (Table 3.3). At the species level, inter-annual rainfall variation accounted for ~39%, ~31%, ~54%, ~45% and ~31% of the change in cover of *T. fruticosa*, *E. villosa*, *B. diandrus*, *C. pugioniformis* and *E. longiflora* respectively, following rabbit control (Annex IV Table S3). An increase in TAUR accounted for ~23% and ~21% of the increase in cover of *T. fruticosa* and *E. villosa* respectively, between the second- and third years following rabbit control (Figure 3.3; Annex IV Table S3). In contrast, the increase in TAUR suppressed (i.e., was negatively correlated with) increase in cover of *C. pugioniformis* by ~18% during the same period (Figure 3.3; Annex IV Table S3). An increase in TWR accounted for ~24% of the increase in cover of *E. longiflora* between the second- and third years following rabbit control (Figure 3.3; Annex IV Table S3). Although inter-annual rainfall variation accounted for ~45% of the emergence and subsequent increase in cover of *B. diandrus* between the second- and third years following rabbit control, there was no significant statistical relationship at the seasonal level (Annex IV Table S3).

A decline in cover of *C. pugioniformis* was correlated with increase in cover of *T. fruticosa* (strongly) and *E. villosa* and *B. diandrus* (weakly; Figure 3.2). The increase in cover of *E. longiflora* was weakly correlated with a decline in the cover of *T. fruticosa* (Figure 3.2).

Table 3-2 Change in plant species composition (mean NMDS axis one score (+1.50) ± SE) following the control of invasive alien European rabbits on Robben Island. Significant differences ($P \leq 0.05$) between years determined using repeated-measures ANOVA.

Site	Year				*F*	*P*
	2010	2011	2012	2013		
Strand	1.30 ± 0.03	1.45 ± 0.03	1.61 ± 0.02	1.65 ± 0.02	48.67	<0.001
Eucalyptus	1.58 ± 0.09	1.71 ± 0.07	1.35 ± 0.01	1.36 ± 0.01	11.04	<0.001
Inland dune	1.34 ± 0.07	1.51 ± 0.07	1.57 ± 0.05	1.58 ± 0.03	10.31	<0.001

Table 3-3 Relationship between inter-annual rainfall variation and plant species composition change (mean NMDS axis one score) following the control of invasive alien European rabbits on Robben Island. Significant differences ($P \leq 0.05$) were determined using Rao's *F* statistic and *t* tests.

Sites	Multiple Regressions														
	Overall Rainfall			TSUR				TAUR				TWR			
	Adj. R^2	*F*	*P*	R^2	*Coeff*	*T*	*P*	R^2	*Coeff*	*t*	*P*	R^2	*Coeff*	*t*	*P*
Strand	0.83	33.18	< 0.001	0.42	-0.257	-4.40	< 0.001	0.67	0.358	6.99	< 0.001	0.29	0.262	3.76	0.001
Eucalyptus	0.58	9.36	< 0.001	0.58	-0.059	-0.60	0.556	0.48	-0.045	-0.53	0.600	0.48	-0.075	-0.56	0.584
Inland dune	0.37	3.95	0.023	0.10	-0.221	-1.84	0.080	0.25	0.298	2.83	0.010	0.05	0.172	1.20	0.243

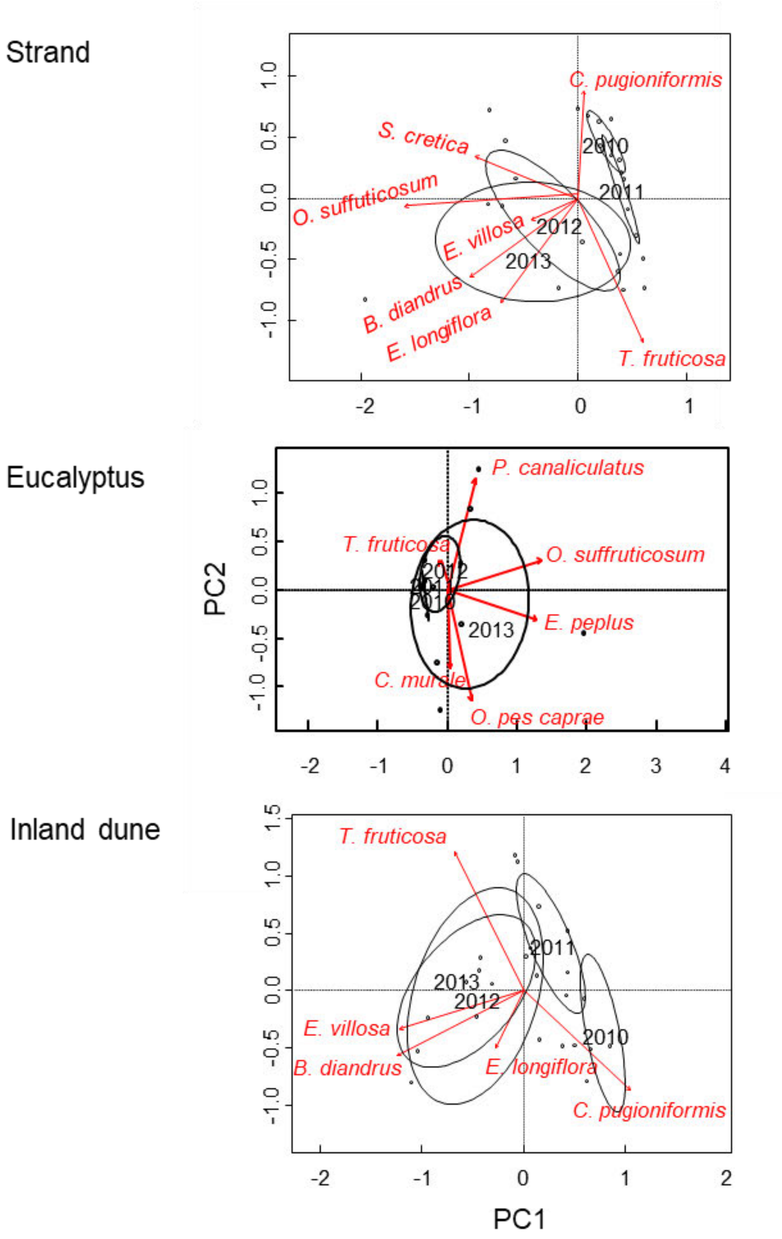


Figure 3-2 Principal Components Analysis plots showing species cover changes that underlay vegetation compositional change following the control of European rabbits on Robben Island. Arrows point towards directions of maximum species cover change, the length of arrows indicates rates of change and angles between arrows represent correlations between cover changes (< 90^0 = positively correlated, 90^0 = uncorrelated, > 90^0 = negatively correlated). Only species accounting for the top 95% of compositional change are shown. Also shown are 95% confidence ellipses for annual vegetation composition. PCA axes 1 ($T = 0.43$, $p < 0.001$) and 2 ($T = 0.51$, $p < 0.001$) with eigenvalues of 2.118 and 1.524 represented 35% and 18% of the total variance, respectively, at strand sites, while the axes (PCA 1: $T = 0.55$, $p < 0.001$ and PCA2: $T = 0.56$, $p <= 0.001$) had eigenvalues of 1.798 and 1.595 and represented 30% and 27% of the total variance at eucalyptus sites. At inland dune sites, eigenvalues for

PCA axes 1 ($T = 0.43$, $p < 0.001$) and 2 ($T = 0.57$, $p < 0.001$) were 2.170 and 1.922, and represented 31% and 27% of the total variance, respectively. The significance of PCA axes was tested using a simple parametric bootstrap method (999 bootstraps, unscaled variables, Hellinger transformed data) (see Forkman, et al. 2019).

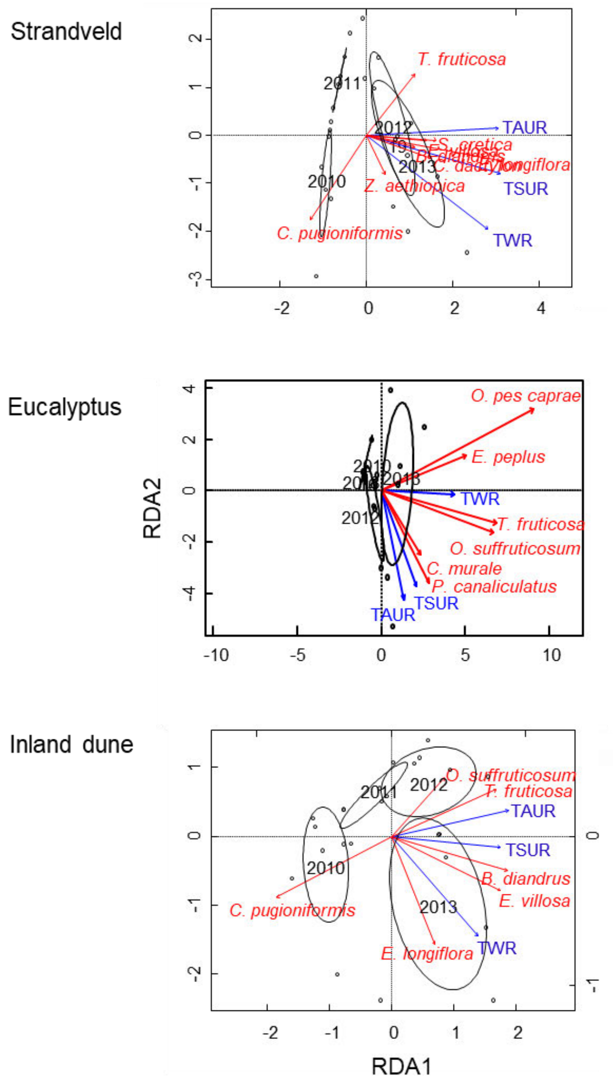


Figure 3-3 Redundancy Analysis plots showing relationships between inter-annual rainfall dynamics and plant species cover changes that underlay vegetation compositional change following the control of European rabbits on Robben Island. Arrows point towards directions of maximum change, the length of arrows indicates rates of change and angles between arrows represent correlations (<90 = +vely correlated, 90 = uncorrelated, > 90 = -vely correlated). Only species accounting for the top 95% of compositional change are shown. Also shown are 95% confidence ellipses for annual vegetation composition. The Monte Carlo permutation test showed evidence of non-randomness of the ordination for the strand ($F = 2.22$, $p = 0.007$) and inland dune sites ($F = 2.90$, $p = 0.001$) but not the Eucalyptus

sites (*F* = 0.80, *p* = 0.596), based on 999 permutations. RDA axes 1 and 2 with eigenvalues of 1.925 and 0.517 represented 19% and 5% of the total variance, respectively, at strand sites, while eigenvalues of 0.853 and 0.143 represented 14% and 2% of the total variance, respectively, at eucalyptus sites. At inland dune sites, eigenvalues for RDA axes 1 and 2 were 1.300 and 0.505, which represented 19% and 7% of the total variance, respectively. Values for species–rainfall correlations are shown in Annex IV Table S3.

Effects of inter-annual rainfall variation on vegetation composition response

Inter-annual rainfall variation significantly complicated vegetation dynamics across our study sites following rabbit control (Annex V). The complicating effects of this variation included the suppression and delay of species responses (*T. fruticosa*, *E. longiflora*, *C. pugioniformis*, *B. diandrus*, *S. cretica* and *E. villosa*), the facilitation of unusual emergences (*O. suffruticosum*, *C. murale* and *E. peplus*), and the occurrence of transient disappearances (*C. dactylon*, *Z. aethiopica*, *O. pes-caprae* and *E. longiflora*), as well as unusual increases in *P. canaliculatus* and *B. diandrus* in response to drought conditions during the first two years and above-average winter, autumn, and summer rainfall events during the third and fourth years following rabbit control (Annex V).

We determined that vegetation composition would have changed moderately across strand sites following rabbit control, given constant and average inter-annual rainfall (Annex V). The increase in *T. fruticosa* and *E. longiflora* cover would have been of major importance in driving the change in vegetation composition (Annex V). The emergence of *E. villosa* would have been of intermediate importance, while the emergence of *C. dactylon* and the decline in *O. suffruticosum* and *C. pugioniformis* cover would have been of minor importance (Annex V). Specifically, the cover of *T. fruticosa* and *E. longiflora* would have increased moderately and markedly between the first and second years, while the cover of *E. villosa* and *C. dactylon* would have slightly increased from zero (Annex V). In contrast, the cover of *O. suffruticosum* and *C. pugioniformis* would have sharply decreased between the first- and second years following rabbit control. The cover of all six species would have remained constant thereafter (Annex V).

Additionally, we surmised that the vegetation composition would have moderately changed across inland dune sites in response to rabbit control, given constant and average inter-annual rainfall (Annex V). The increase in the cover of *T. fruticosa* and *E. villosa* would have been of major importance, the decline of *B. diandrus* and *C. pugioniformis* of intermediate importance, and the emergence of *E. longiflora* of minor importance in driving the change in vegetation composition (Annex V). Specifically, the cover of *T. fruticosa* would have increased markedly between the first and second years and remained constant thereafter, whereas the cover of *E. villosa* would have increased moderately across the years following rabbit control (Annex V). In contrast, the cover of *B. diandrus* and *C. pugioniformis* would have decreased moderately and sharply between the first- and second years following rabbit control and remained at reduced and low cover thereafter (Annex V). The cover of *E. longiflora* would have slightly increased from zero between the first- and second years following rabbit control and would have remained constant in subsequent years (Annex V).

Lastly, we deduced that vegetation composition would not have changed at eucalyptus sites following rabbit control in the absence of inter-annual rainfall variation (Annex V). The lack of change in composition was due to subdued responses of *P. canaliculatus*, *O. pes-caprae* and *T. fruticosa* to rabbit control (Annex V).

Discussion

Impact of rabbit control on vegetation composition

We had anticipated that vegetation on Robben Island would undergo secondary succession towards its original or projected undisturbed composition in response to rabbit control. Specifically, our hypothesis was that this succession would involve the re-establishment of late-successional perennial grasses, succulents, and herbs, as well as the recolonisation or increase in cover of woody shrubs. However, contrary to our expectations, changes in plant species composition across our study sites in response to rabbit control were primarily driven by increases in the abundance of early successional species i.e., the woody shrub *T. fruticosa* and grasses *E. longiflora*, *C. dactylon*, and *E. villosa*), rather than the hypothesised late-successional ones. This outcome confirmed suspicions previously raised by researchers such as Adamson (1934), Nankivell (1934), and Cooper and Brooke (1982, 1986) that prolonged rabbit herbivory on South African offshore islands had pushed island ecosystems beyond critical ecological thresholds, so that the removal of rabbits from the islands would no longer result in a return to the original natural vegetation. In the case of Robben Island, long-term rabbit herbivory appears to have driven the island's vegetation beyond such a threshold by cumulatively eliminating ecologically competitive late successional species from the island's vegetation and seed banks, making these species unavailable to drive successional change after rabbit control. Therefore, the observed changes in vegetation composition in response to rabbit control across our study sites were not indicative of successional processes but rather reflected responses to reduced rabbit herbivory within an alternative stable degraded state. Indeed, the absence of late successional species from all our study sites underscored this observation, as all the plant species we encountered across the sites during our study were early successional species adapted to disturbed or naturally open habitats, including the woody shrub species. Our findings, therefore, supported Adamson (1934)'s deduction that prolonged rabbit herbivory had depleted vegetation on Robben Island by almost eliminating all native plant species, leaving only a few native species and weedy aliens that were either unpalatable or could escape or withstand heavy rabbit grazing (see below). Furthermore, Adamson (1934) noted, through comparison of the vegetation of Robben Island with that of analogous rabbit-free mainland sites, that the degradation of the vegetation had resulted in increased openness, a simpler structure, and a higher proportion of annual and early successional species.

Prolonged rabbit herbivory can result in the complete loss of herbivory-sensitive species from both vegetation and seed banks, leading to degraded alternative stable vegetation states solely composed of unpalatable relic plant species. However, this was not the case at our study sites on Robben Island. Despite over 270 years of rabbit herbivory, a few palatable species (e.g., *T. fruticosa* (van Breda, et al. 1990, Germishuizen, et al. 2003), *E. longiflora* (Germishuizen, et al. 2003, van Oudtshoorn 2012), *C. dactylon* (van Breda, et al. 1990, Simmonds, et al. 2000, Germishuizen, et al. 2003) and *E. villosa* (Louw, et al. 1988 Germishuizen, et al. 2003) seemed to have survived and persisted in the island's vegetation and seed banks. The occurrence and persistence of these palatable plant species across our study sites can be attributed to the intermittent, rather than persistent, occurrence of heavy rabbit herbivory on the island. Historical records suggest that rabbit populations on the island remained consistently low due to human hunting and trapping, as well as predation by feral cat populations (Apps 1984, Crawford and Dyer 2000, Sherley 2016). However, occasional, intermittent increases in the rabbit population occurred during periods when human presence was reduced, and cat predation on the island was limited (Adamson 1934, Nankivell 1934, de Villiers, et al. 2010, Sherley 2016).

The intermittent nature of historical episodes of high rabbit populations on Robben Island evidently facilitated the survival and persistence of the palatable species found across our sites. For example, European rabbits can browse *T. fruticosa* shrubs to the shoot base but cannot consume the entire plant (Adamson 1934). Consequently, under intense rabbit herbivory, *T. fruticosa* can persist as heavily browsed ground-level shoot bases, from which it later recovers once herbivory pressure subsides (Adamson 1934). Additionally, *T. fruticosa* produces seeds with durable seed coats, resulting in delayed germination due to slow soil moisture penetration (van Breda, et al. 1991). Therefore, *T. fruticosa* can endure short periods of intense herbivory as long-lived soil seed banks. The annual grass *E. longiflora* produces abundant, persistent soil-stored seeds, facilitating the species' re-establishment after intense rabbit herbivory through mass germination of its seeds (Moore, et al. 2007a, Fisher, et al. 2009). *Erhrarta longiflora*'s brief annual growth period exposes it to rabbit grazing for a much shorter duration than most other plants.

Consequently, a significant proportion of adult *E. longiflora* plants survive intense rabbit herbivory, allowing them to flower and produce fresh seeds (Halvorson, et al. 2003a, Fisher, et al. 2009, Winston, et al. 2014). These seeds germinate freely without the need for disturbance or fire cues (Fisher, et al. 2009). On the other hand, the ability of *C. dactylon* and *E. villosa* to regenerate from underground rhizomes and stolons (Hodder 1997, Brown, et al. 2002, Halvorson, et al. 2003b) likely underpinned their capacity to withstand intense periods of rabbit herbivory. This is because their underground rhizomes could regenerate even after complete removal of above-ground biomass during episodes of intense rabbit herbivory (see, e.g., Belsky 1986, Hodder 1997, Zwerts, et al. 2015). Furthermore, both grasses exhibit limited palatability to herbivores due to their tough, fibrous leaves and stems, which possess a high silica content (Ellis 1987, Babu, et al. 2018). Moreover, grazing, and rabbit herbivory specifically, have minimal effect on the growth of rhizomatous and stoloniferous plants with a prostrate growth form, such as the two perennial grasses (Farrow 1917, White 1973). Therefore, because of their capacity to escape and withstand occasional intense rabbit herbivory, the palatable woody shrub *T. fruticosa* and annual and perennial grasses *E. longiflora*, *C. dactylon* and *E. villosa* would have managed to persist within the island vegetation and seed banks throughout the prolonged period of rabbit herbivory, alongside unpalatable species such as *O. suffruticosum*, *C. pugioniformis*, *B. diandrus, P. canaliculatus* and *O. pes-caprae*.

Although the changes in vegetation composition across our study sites in response to rabbit control were not successional, they partly aligned with our hypothesised responses for the island's plant species. We hypothesised that controlling rabbit herbivory would lead to the re-establishment of late successional palatable perennial grasses, succulents, and herbs that were previously suppressed by herbivory. Additionally, we expected this change to coincide with a decrease in the abundance of less ecologically competitive, unpalatable, or low-growing annual grasses and herbs, which would have proliferated before rabbit control due to reduced competition with suppressed rabbit-favoured plants. While the changes in vegetation composition across our sites were limited to early successional species and did not encompass the late-successional species as hypothesised, they involved the re-establishment and increased cover of the palatable woody shrub *T. fruticosa* and perennial grasses *E. longiflora*, *C. dactylon*, and *E. villosa*. These changes were accompanied by reductions in the abundance of the unpalatable annual grass *B. diandrus* and perennial herbs *O. suffruticosum* and C. *pugioniformis*.

Tetragonia fruticosa is highly palatable to European rabbits, which browse it down to its shoot base (Adamson 1934). Moreover, it produces relatively few large seeds that render it susceptible to the adverse effects of intense summer grazing, leading to reduced recruitment as it is unable to set seed (Todd 2000). The plant demonstrates substantial interspecific competitiveness, aided by its extensive root systems that penetrate deep into the soil (van Breda and Barnard 1991).

Cynodon dactylon exhibits limited palatability to herbivores, including rabbits, due to the tough, fibrous texture and high fibre content of its leaves (van Breda, et al. 1990, Simmonds, et al. 2000, Germishuizen and Meyer 2003). However, while *C. dactylon* is resilient to grazing, excessive grazing negatively impacts its growth and survival (Melak, et al. 2019). *Cynodon dactylon* demonstrates strong interspecific competitive ability, effectively competing for resources such as water, nutrients, space, and soil oxygen due to its expansive rhizomes and stolons (Kumar, et al. 1982).

Ehrharta longiflora is palatable to herbivores and was the preferred rabbit feed on Robben Island (Adamson 1934). The annual grass struggles to persist under grazing due to its easily uprooted creeping branched roots and rhizomes (Gillham 1963, Moore and Moore 2007a, van Oudtshoorn 2012). *Ehrharta longiflora* is a poor interspecific competitor, requiring open ground for germination and disturbed sites for successful establishment (Winston, et al. 2014). Nevertheless, as a rapidly growing annual grass, it can swiftly colonise open areas and dominate when grazing pressure is removed (California Invasive Plant Council 2023). It is typically one of the first annual grasses to flower, enabling it to effectively compete with other plant species for open space (California Invasive Plant Council 2023).

Ehrharta villosa, like *C. dactylon*, is not highly palatable to herbivores but is similarly negatively affected by intense grazing and tends to thrive under lenient grazing conditions (Louw and Beukes 1988, Tainton, et al. 1990). A coastal dune specialist, *E. villosa* displays strong interspecific competitive ability (Verboom, et al. 2003). Its positive response to sand burial and deep rhizome system, accessing water from deep below the soil surface, contribute to its competitiveness (Hertling 1997, Harrington, et al. 1998). Additionally, *E. villosa*'s lengthy stems, often exceeding a height of 2 m, allow it to overshadow surrounding vegetation, augmenting its competitive ability (Harrington, et al. 1998).

Bromus diandrus is generally unpalatable to most herbivores due to its high fibre content, although rabbits consume its seeds (Myers, et al. 1963, van Breda, et al. 1990, Martin, et al. 2007, Muhl 2008). The alien annual grass is tall and has deep roots, enabling it to shade out and outcompete other species for limited soil resources (Menke 1992, Jackson, et al. 2006). Furthermore, it outcompetes native species for soil moisture through early germination and sheer volume (Menke 1992, Jackson, et al. 2006). *Bromus diandrus* exhibits high seed production, with a single plant capable of producing up to a thousand seeds (Jackson, et al. 2006). Consequently, in contrast to other less ecologically competitive unpalatable species, *B. diandrus*, which dominated vegetation before rabbit control, most likely declined moderately in response to the resurgence of more competitive palatable species following rabbit control.

Oncosiphon suffruticosum is unpalatable to herbivores, including livestock and rabbits (Le Roux 2005, Anon 2014, Western Australian Herbarium 2022); thus, it would have tolerated rabbit herbivory without significant impacts on growth and reproduction. The plant is a weak competitor, typically found in disturbed, open localities where grasses or perennial vegetation have been reduced, especially due to heavy grazing (Moore, et al. 2007b, Anon 2014).

Lastly, *Conicosia pugioniformis* exhibits extremely limited palatability to livestock and European rabbits due to the astringent and salty quality of its succulent tissue (Louw and Beukes 1988, de Villiers, et al. 2001). The species possesses relatively poor competitive ability and is typically found in disturbed open localities where grasses or perennial vegetation have been reduced, particularly by heavy grazing (Schmalzer, et al. 1987).

In summary, although the changes in vegetation composition across our study sites in response to rabbit control were not indicative of succession, they did reflect responses to diminished herbivory pressure by relic species within the alternative stable degraded vegetation state. This was demonstrated by the responses of the early successional palatable woody herb *T. fruticosa* and perennial grasses *E. longiflora*, *C. dactylon*, and *E. villosa*, as well as the unpalatable annual grass *B. diandrus* and perennial herbs *O. suffruticosum* and C. *pugioniformis*. These species increased and decreased in abundance in response to rabbit control in partial alignment with our hypothesis.

Effect of landscape variation on vegetation composition dynamics

As expected, the dynamics of plant species underlying changes in vegetation composition in response to rabbit control varied across the landscape. For example, the cover of the annual grass *E. longiflora* increased significantly at strand sites, while it remained low at inland dune sites. In contrast, the annual grass *E. villosa* emerged with low cover at strand sites, while it increased moderately at inland dune sites. The perennial grass *B. diandrus* maintained low cover at strand sites but decreased moderately from high cover at inland dune sites. This variation in species dynamics can be largely attributed to differences in soil depth between these two sites. Strand sites had shallow soils ranging from 3 to 5 cm deep, whereas inland dune sites had comparably deeper soils ranging from 0 cm (at dune troughs) to 70 cm (at dune crests) (Adamson 1934).

Ehrharta villosa possesses a robust rhizomatous root system characterised by thick and fleshy rhizomes that can extend several meters horizontally and reach depths of up to 50 cm (Harrington, et al. 1998). These rhizomes create a dense network of roots, providing the plant access to water and nutrients across the soil profile (Harrington, et al. 1998). Due to its deep roots, the less palatable *E. villosa* was most likely unable to fully respond to reduced herbivory pressure at strand sites after rabbit control, owing to the limited availability of habitats with soils deep enough to support its roots. However, the tall-stemmed perennial grass, which shades and outcompetes other species for soil moisture and nutrients (Hertling 1997, Harrington, et al. 1998, Coetzee 2008), could have fully responded to rabbit control at inland dune sites due to the greater availability of deep-soil habitats.

The root system of *E. longiflora* is shallow (Moore and Moore 2007a) and is located in the top 10 cm of the soil. Although *E. longiflora* is a strong competitor for light and space due to its sprawling rhizomes and rapidly sprouting long shoots (Fisher, et al. 2009, DiTomaso, et al. 2013), it requires disturbed open sites for successful germination (Winston, et al. 2014). Therefore, due to the scarcity of suitable open habitats at inland dune sites caused by higher vegetation density, *E. longiflora*, which is palatable to European rabbits, most likely could not fully respond to reduced herbivory pressure following rabbit control, beyond re-establishing at low cover in the few available open sites. However, the shallow-rooted *E. longiflora* was most likely able to fully respond to rabbit control at strand sites due to the greater availability of open habitats and the absence of more competitive deeper-rooted species.

Bromus diandrus possesses an extensive fibrous root system that penetrates deep into the soil (Menke 1992, Jackson, et al. 2006). Like *E. villosa*, the deep-rooted *B. diandrus* most likely exhibited varying responses to rabbit control at strand and inland dune sites due to differences in the availability of deep-soil habitats. Before rabbit control, *B. diandrus* occurred with high cover and maintained medium cover after rabbit control at inland dune sites, where deep-soil habitats were abundant. However, at strand sites where suitable deep-soil habitats were limited, *B. diandrus* occurred with low cover both before and after rabbit control. Since *B. diandrus* is unpalatable to herbivores, it was most likely able to increase to high cover during rabbit herbivory at inland dune sites, while remaining constrained to low cover at strand sites due to the unavailability of suitable deep-soil habitats. *Bromus diandrus* most likely maintained medium cover at inland dune sites because of its strong interspecific competitive ability for space, light, and soil moisture (Menke 1992, Jackson, et al. 2006), unlike other unpalatable species that declined to low cover or were displaced by recovering and more competitive palatable species.

There were exceptions to the above-mentioned pattern of shallow- and deep-rooted plants occurring exclusively or responding differently to rabbit herbivory and control on strand and inland dune sites. For instance, the deep-rooted perennial grass *C. dactylon* (Corr 1993) persisted or emerged exclusively at shallow-soiled strand sites following rabbit control. The seemingly anomalous distribution of *C. dactylon* can be attributed to its relatively weak ability to compete for sunlight. Adult *C. dactylon* plants are highly sensitive to shading (Burton, et al. 1988) and their low stature limits their ability to compete with taller plants (Guglielmini, et al. 2002). Consequently, this low-growing, shade-intolerant perennial grass would have been unable to establish itself in inland dune sites due to the denser and taller vegetation cover. However, the root systems of *C. dactylon* plants are more efficient and versatile than those of the other deep-rooted species, being more fibrous and having masses of dense, slender rootlets that are evenly distributed throughout the soil (Kamchoom, et al. 2022). Because of their more adaptable roots, *C. dactylon* would have been able to establish and outcompete shallow-rooted plant species on marginal habitats at strand sites where the soil was deep enough to support them rather than their deep-rooted, superior competitors.

Overall, our findings demonstrated that changes in vegetation composition in response to rabbit control on Robben Island were most likely strongly influenced by differences in soil depth across the landscape. The results highlight the importance of considering soil depth as a key factor influencing plant community dynamics in Mediterranean-type South African offshore islands and the need for landscape-scale management strategies that take these spatial heterogeneities into account.

Vegetation composition response under *Eucalyptus* plantations

Unlike the differences in species dynamics between strand and inland dune sites, which were primarily attributed to variations in soil depth, the absence of change in vegetation composition at eucalyptus sites can be attributed to the inhibitory effects of alien *Eucalyptus* trees on understory vegetation dynamics. *Eucalyptus* plantations inhibit understory vegetation through shading (Loumeto, et al. 1997), allelopathy (Sasikumar, et al. 2001, Khan, et al. 2008 , Zhang, et al. 2010), and alteration of nutrient cycling regimes (Bernhard-Reversat 1996, Guo, et al. 2001, Marchante, et al. 2008), resulting in lower soil nutrient content, pH, and base saturation (Alexander 1989, Guo and Sims 2001, Marchante, et al. 2008 , Zhang, et al. 2010). Furthermore, *Eucalyptus* trees rapidly deplete soil moisture following rainfall events (Le Maitre, et al. 2002, Dye, et al. 2004, Dye, et al. 2007) due to their high water consumption rates and extensive root systems (del Moral, et al. 1969).

At our study sites, *Eucalyptus* trees appear to have suppressed the response of the four species that occurred there: the early successional woody shrub *T. fruticosa* and the annual and perennial low-growing herbs *C. natans*, *O. pes-caprae*, and *P. canaliculatus* to the effects of rabbit control. These species maintained low cover both before and after rabbit control. This suppression was likely due to the *Eucalyptus* trees creating drier-than-usual soil conditions and shading the understory vegetation. The ephemeral herb *C. natans* and woody shrub *T. fruticosa* require high soil moisture conditions to germinate (Toelken 1981, van Breda and Barnard 1991), while the perennial herbs *O. pes-caprae* and *P. canaliculatus* perform poorly under shade (Verdaguer, et al. 2010, UWC Cape Flats Indigenous Nursery 2021). *Crassula natans*, *T. fruticosa*, *O. pes-caprae* and *P. canaliculatus* may have established at the eucalyptus sites due to unique adaptations to the environmental conditions, such as the ability to tolerate low light levels, dry soil conditions, acidic soils, and the presence of terpenes in the soil. *Crassula natans* is a succulent plant that can store water in its leaves, allowing it to tolerate dry soil conditions (Gardenia.net. 2023). It also has the ability to photosynthesise in low light levels (Gardenia.net. 2023). *Tetragonia fruticosa* is a drought-tolerant plant that can also tolerate acidic soils (South African National Biodiversity Institute 2023b). It has deep roots that allow it to tap into groundwater, helping it survive during periods of drought (South African National Biodiversity Institute 2023a). *Oxalis pes-caprae* is a highly adaptable plant that can tolerate a wide range of environmental conditions, including low light levels, dry soil conditions, and acidic soils (Verdaguer, et al. 2010, Vahamidis, et al. 2024). Similarly, *P. canaliculatus*, a native South African coastal dune specialist (Fernkloof Nature Reserve 2024), demonstrates significant resilience in dry environments. This species possesses tuberous roots (Fernkloof Nature Reserve 2024) which store water and nutrients essential for surviving prolonged dry periods. Additionally, its leaves are equipped with pronounced bladder cells (Fernkloof Nature Reserve 2024), presumed to play a critical role in water conservation. These adaptations greatly enhance the plant's ability to cope with the limited moisture availability in its native coastal dune habitats.

In addition to the aforementioned adaptations, these plants might have established themselves at the *Eucalyptus* sites because of their root systems' ability to access the scarce resources present in the top layer of soil beneath *Eucalyptus* plantations. *Eucalyptus* trees have a very aggressive root system that can quickly deplete the soil of moisture and nutrients, making it difficult for other plants to survive (del Moral, et al. 1969). Shallow-rooted plants can avoid this competition by rooting in the top few centimetres of soil, where the *Eucalyptus* roots are less abundant. *Crassula natans*, *O. pes-caprae* and *P. canaliculatus*, for instance, have shallow root systems. These shallow roots would have allowed them to access the limited water and nutrients available in the top layer of soil and avoid more intense competition with *Eucalyptus* roots in the soil below. *Tetragonia fruticosa*, on the other hand, has a well-developed and versatile root system that would have allowed it to establish under *Eucalyptus* trees. In sandy soil, it typically has shallow, long-spreading roots (van Breda and Barnard 1991). However, in harder soil conditions, it develops a deeper root system, including a taproot that penetrates the soil to a considerable depth (van Breda and Barnard 1991). However, the shallow root systems that may have enabled the annual and perennial herbs *C. natans* and *O. pes-caprae* to persist under the *Eucalyptus* plantation likely resulted in their exclusion from the more diverse plant communities found at strand

and inland dune sites. These plant communities featured a wider array of plant species with varying root depths, leading to intensified competition for soil resources among the different species.

Further research needs

Our findings indicate that prolonged rabbit herbivory has driven Robben Island's vegetation beyond a critical ecological threshold. This threshold represents a point at which the loss of late-successional native plant species is so severe that the ecosystem's ability to self-regenerate is compromised. Consequently, the vegetation has shifted to an alternative stable state dominated by early successional species more resistant to rabbit grazing. Therefore, merely removing the rabbits will not suffice to facilitate natural succession back to the original vegetation; this is because the new stable state does not support the natural processes necessary for the re-establishment of the island's original, diverse plant community. The rabbits appear to have induced this ecological transition by gradually eliminating ecologically competitive, late-successional, and palatable species from both the island's vegetation and seed banks during their 270-year presence on the island. This interpretation of our results is supported by the observation that late-successional species were absent from all our study sites, and the vegetation response to rabbit control was limited to changes in early successional species cover. However, the validity of this interpretation of the study's results is uncertain due to the relatively short period between the implementation of rabbit control on the island and our evaluation of vegetation response (see Schweizer, et al. 2016). Given the degraded state of vegetation on Robben Island, the four-year monitoring period for vegetation composition response following rabbit control might have been insufficient for previously eradicated late successional and palatable species to re-establish at our sites from refugia on the island or the mainland. Therefore, it is reasonable to assume that our results might have differed if vegetation composition response had been evaluated after a longer interval following rabbit control.

However, it is crucial to note that the possibility of relic palatable and late-successional plant species being present in refugia on the island is highly unlikely. This is because, while species that spread vegetatively would have taken a considerable amount of time to reach affected areas, many other relic palatable species that spread through seed and wind dispersal would have recolonised the sites during the four years that followed rabbit control given the island's small size (~507 ha). The fact that such species did not recolonise our study sites within the four years is strong evidence that late successional and palatable species had indeed been eliminated from the island. Likewise, the possibility of late-successional and palatable species dispersing from refugia on the mainland to the island is equally improbable. This is because Robben Island is separated from the mainland by ~7 km of the South Atlantic Ocean, a situation that severely restricts the possibilities for palatable species to disperse from the mainland to the island.

Consequently, our interpretation that the island's vegetation has been pushed into a stable early-successional alternative degraded state by long-term rabbit herbivory is more plausible than the possibility that the results are merely an artefact of the short time interval between rabbit control and the assessment of vegetation response. Nevertheless, there is a need for further monitoring of vegetation composition on the island to assess the long-term robustness of our findings. Such long-term monitoring would clarify management issues such as whether the removal of European rabbits alone is enough to restore vegetation composition on the island or if additional measures, such as replanting or reseeding missing native late-successional and palatable species, are necessary.

Conclusion

Contrary to expectations, rabbit control on Robben Island did not lead to the re-establishment of the original late-successional vegetation but rather resulted in an increase in early successional species. The changes in vegetation composition across strand and inland dune sites involved the re-establishment and increase in cover of the early-successional palatable woody shrub *T. fruticosa* and perennial grasses *E. longiflora*, *C. dactylon*, and *E. villosa*. These changes were accompanied by reductions in the abundance of the early-successional unpalatable annual grass *B. diandrus* and perennial herbs *O. suffruticosum* and *C. pugioniformis*. The vegetation composition at eucalyptus sites remained unchanged. The four species present at the eucalyptus sites – the early-successional woody shrub *T. fruticosa*, and the annual and perennial low-growing herbs *C. natans*, *O. pes-caprae*, and *P. canaliculatus* – appeared to be suppressed by the *Eucalyptus* trees, maintaining low cover both before and after rabbit control. *Eucalyptus* plantations suppress understory vegetation through shading, allelopathy, and alteration of nutrient cycling regimes, resulting in lower soil nutrient content, pH, and base saturation. Additionally, *Eucalyptus* trees rapidly deplete soil moisture following rainfall events due to their high water consumption rates and extensive roots. The unexpected outcome across strand and inland dune sites indicates that prolonged rabbit herbivory may have pushed the island's ecosystem beyond a critical ecological threshold, making a natural return to the original vegetation impossible. This observation was further bolstered by the absence of late-successional species from all study sites, signifying that the island's vegetation is presently solely comprised of early-successional species, which were either unpalatable or capable of evading or enduring intense rabbit grazing. Therefore, the observed changes in vegetation composition in response to rabbit control across our study sites were most likely not indicative of successional processes but rather reflected responses to reduced rabbit herbivory pressure within an alternative degraded early successional state. Our study results underscore the need for a holistic restoration approach on Robben Island. This approach should not only focus on the elimination of invasive alien herbivores like European rabbits but also actively promote the reintroduction of extirpated native late-successional and palatable plant species. Reintroducing these species from off-island sources is crucial in this restoration process. Additionally, our findings highlight the importance of thoroughly evaluating the potential long-term ecological consequences of introducing or managing alien herbivores in island ecosystems, given their unique ecological characteristics and limited species diversity.

Despite their diverse sizes, distances from the mainland, and climates, we hypothesise that vegetation responses to rabbit control on invaded South African offshore islands will broadly resemble those observed on Robben Island. On these diverse islands, comparable durations and intensities of rabbit herbivory suggest a common initial surge in early successional, herbivory-resistant species, particularly those with persistent seed banks. However, island-specific factors like size and distance from the mainland may influence and modify the establishment patterns of late successional species. For example, islands closer to the mainland, such as Jutten, Schaapen, and Vondeling, are likely to have greater potential for re-establishment by late successional and palatable species from the mainland source compared to Robben Island. On many invaded islands, like on Robben Island, less ecologically competitive species will likely decline due to competition from recovering palatable species, though the specific plant species involved, and their roles will differ due to each island's unique composition (see for e.g., Gillham 1963). Similarly, within these invaded islands, species responses to rabbit control will also vary spatially on the presence of sufficient habitat heterogeneity influenced by environmental factors, such as soil depth and vegetation structure.

References

Acocks JPH. 1975. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* 40: 1-128.

Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

Alexander JM. 1989. The long-term effect of *Eucalyptus* plantations on tin-mine spoil and its implication for reclamation. *Landscape and Urban Planning* 17: 413–433.

Anon. 2008a. Rabbits a threat to Robben Island. 'Available at' https://www.iol.co.za/news/south-africa/rabbits-a-threat-torobben-island-420389 [accessed 8 February 2017]

Anon. 2008b. Robben Island's rabbits to be culled. 'Available at' https://www.iol.co.za/news/south-africa/robben-islands-rabbits-to-be-culled-420363 [accessed 8 February 2017]

Anon 2014. Declared Plant Policy under the Natural Resources Management Act 2004. Calomba daisy (*Oncosiphon suffruticosum*). Government of South Australia.

Apps P. 1984. Cats on Dassen Island. *Acta Zoologica Fennica* 172: 115-116.

Austin MP, Williams OB, Belbin L. 1981. Grassland dynamics under sheep grazing in an Australian Mediterranean type climate. *Vegetatio* 47: 201-211.

Babu RH, Yugandhar P, Savithramma N. 2018. Synthesis, characterization and antimicrobial studies of bio silica nanoparticles prepared from *Cynodon dactylon* L.: a green approach. *Bulletin of Materials Science* 41: 65.

Bello-Rodríguez V, Mateo RG, Pellissier L, Cubas J, Cooke B, González-Mancebo JM. 2021. Forecast increase in invasive rabbit spread into ecosystems of an oceanic island (Tenerife) under climate change. *Ecological Applications* 31: e02206.

Belsky AJ. 1986. Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania: I. Colonization of grazed and ungrazed Plots. *Journal of Ecology* 74: 419-437.

Bernhard-Reversat F. 1996. Nitrogen cycling in tree plantations grown on a poor sandy savanna soil in Congo. *Applied Soil Ecology* 4: 161–172.

Bhadresa R. 1977. Food preferences of rabbits *Oryctolagus cuniculus* L. at Holkham sand dunes, Norfolk. *Journal of Applied Ecology* 14: 287-293.

Bishop G, Davy A, Jefferies R. 1978. Demography of *Hieracium pilosella* in a Breck grassland. *Journal of Ecology* 66: 615-629.

Bishop GF, Davy AJ. 1984. Significance of rabbits for the population regulation of *Hieracium pilosella* in Breckland. *Journal of Ecology* 72: 273-284.

Box G, Cox D. 1964. An analysis of transformations. *Journal of the Royal Statistical Society* 26: 211-234.

Brooke RK, Crowe TM. 1982. Variation in species richness among the offshore islands of the southwestern Cape. *South African Journal of Zoology* 17: 49-58.

Brooke RK, Prins AJ. 1986. Review of alien species on South African offshore islands. *South African Journal of Antarctic Research* 16: 102-109.

Brown K, Brooks K. 2002. *Bushland weeds. A practical guide to their management. With case studies from the Swan Coastal Plain and beyond*. Perth: Environmental Weeds Action Network (Inc).

Bruton M. 2021. Biological invasions in South Africa. *Transactions of the Royal Society of South Africa* 76: 301-305.

Burton GW, Hook JE, Butler JL, Hellwig R. 1988. Effect of temperature, daylength and solar radiation on production of coastal bermuda grass. *Agronomy Journal* 80: 557–560.

California Invasive Plant Council. 2023. *Ehrharta longiflora*. Available at https://www.cal-ipc.org/plants/profile/ehrharta-longiflora-profile/ [accessed 17 October 2023]

Clarke KR. 1993. Non-parametric multivariate analysis of changes in community structure. *Journal of Ecology* 18: 117-143.

Cleeland JB, Pardo D, Raymond B, Terauds A, Alderman R, McMahon CR, Phillips RA, Lea M-A, Hindell MA. 2020. Introduced species and extreme weather as key drivers of reproductive output in three sympatric albatrosses. *Scientific Reports* 10: 8199.

Coetzee K. 2008. Blaauwberg Conservation Area: management guidelines for larger wildlife and their habitats. *Report prepared for the Biodiversity Management Branch, City of Cape Town*.

Cooke BD. 1991. Rabbits: indefensible on any grounds. *Search* 22: 193–194.

Cooper J, Brooke RK. 1982. Past and present distribution of the feral European rabbit *Oryctolagus cuniculus* on southern African offshore islands. *South African Journal of Wildlife Research* 12: 5-71.

Cooper J, Brooke RK. 1986. Alien plants and animals on South African continental and oceanic islands: species richness, ecological impacts and management. In: Macdonald IAW, Kruger FJ, Ferrar AA editors. *The ecology and management of biological invasions in southern Africa*. Cape Town: Oxford University Press. p. 133-142.

Corr BE. 1993. *Zantedeschia* research in the United States: past, present and future. *Acta Horticulturae* 337: 177-188.

Crawford R, Dyer B. 2000. Wildlife of Robben Island. In: Underhill L editor. *Bright Continent Guide*. Cape Town: Avian Demography Unit.

Crawley MJ. 1990. Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology* 27: 803-820.

Cubas J, Martín-Esquivel JL, Nogales M, Irl SDH, Hernández-Hernández R, López-Darias M, Marrero-Gómez M, del Arco MJ, González-Mancebo JM. 2018. Contrasting effects of invasive rabbits on endemic plants driving vegetation change in a subtropical alpine insular environment. *Biological Invasions* 20: 793-807.

Cubas J, Severin DH, Villafuerte R, Bello-Rodríguez V, Rodríguez-Luengo JL, del Arco M, Martín-Esquivel JL, González-Mancebo JM. 2019. Endemic plant species are more palatable to introduced herbivores than non-endemics. *Proceedings of the Royal Society B: Biological Sciences* 286: 20190136.

Davies S, Jordaan M, Karsten M, Terblanche J, Turner A, van Wilgen N, Veldtman R, Zengeya T, Measey J. 2020. Experience and lessons from alien and invasive animal control projects in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa. Invading Nature - Springer Series in Invasion Ecology*. Cham: SpringerOpen. p. 1302-1381.

de Villiers AJ, van Rooyen MW, Theron GK. 2001. Seedbank phytosociology of the Strandveld Succulent Karoo, South Africa: a pre-mining benchmark survey for rehabilitation. *Land Degradation and Development* 12: 119-130.

de Villiers MS, Mecenero S, Sherley RB, Heinze E, Kieser J, Leshoro TM, Merbold L, Nordt A, Parsons NJ, Peter HU. 2010. Introduced European rabbits (*Oryctolagus cuniculus*) and domestic cats (*Felis catus*) on Robben Island: Population trends and management recommendations. *South African Journal of Wildlife Research* 40: 139-148.

de Villiers SA. 1971. *Robben Island: Out of reach, out of mind. A history of Robben Island*. Cape Town: Struik.

de Vos A, Manville RH, Van Gelder RG. 1956. Introduced mammals and their influence on native biota. *Zoologica (New York)* 41: 163-194.

del Moral R, Muller CH. 1969. The allelopathic effect of *Eucalyptus camaldulensis*. *American Midland Naturalist* 83: 254–282.

Denham AJ, Auld TD. 2004. Survival and recruitment of seedlings and suckers of trees and shrubs of the Australian arid zone following habitat management and the outbreak of rabbit calicivirus disease (RCD). *Austral Ecology* 29: 585-599.

Diaz A. 2000. Can plant palatability trials be used to predict the effect of rabbit grazing on the flora of ex-arable land? *Agriculture, Ecosystems & Environment* 78: 249-259.

DiTomaso JM, Kyser GB, Oneto SR, Wilson RG, Orloff SB, Anderson LW, Wright SD, Roncoroni JA, Miller TL, Prather TS (eds). 2013. *Weed control in natural areas in the Western United States*. Weed Research and Information Center, University of California. Davis.

Doornik JA, Hansen H. 1994. An omnibus test for univariate and multivariate normality. *W4&91 in Nuffield Economics Working Papers*.

Duffy S, Fairley J, O'Donnell G. 1996. Food of rabbits *Oryctolagus cuniculus* on upland grasslands in Connemara. *Biology and Environment: Proceedings of the Royal Irish Academy* 96B: 69-75.

Durbin J, Watson GS. 1951. Testing for serial correlation in least squares regression. *Biometrika* 37: 409-428.

Dye P, Jacobs S, Drew D. 2004. Verification of 3-PG growth and water-use predictions in twelve *Eucalyptus* plantation stands in Zululand, South Africa. *Forest Ecology and Management* 193: 197-218.

Dye P, Versfeld D. 2007. Managing the hydrological impacts of South African plantation forests: An overview. *Forest Ecology and Management* 251: 121-128.

Eldridge DJ, Simpson R. 2002. Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands. *Basic and Applied Ecology* 3: 19-29.

Ellis R. 1987. Leaf anatomy of the genus *Ehrharta* (Poaceae) in southern Africa: the Villosa group. *Bothalia* 17. 195-204.

Esler KJ, Jacobsen AL, Pratt RB. 2018. *The biology of Mediterranean-type ecosystems*. Oxford University Press.

Farrow EP. 1917. On the ecology of the vegetation of Breckland. III. General effects of rabbits on the vegetation. *Journal of Ecology* 5: 1-18.

Fehmi JS. 2010. Confusion among three common plant cover definitions may result in data unsuited for comparison. *Journal of Vegetation Science* 21: 273-279.

Fenton EW. 1940. The influence of rabbits on the vegetation of certain hill-grazing districts of Scotland. *Journal of Ecology* 28: 438-449.

Fernkloof Nature Reserve. 2024. *Mesembryanthemum canaliculatum*. 'Available at' https://www.fernkloof.org.za/index.php/all-plants/plant-families/item/phyllobolus-canaliculatus [accessed 3 May 2024]

Finlayson G, Taggart P, Cooke B. 2021. Recovering Australia's arid-zone ecosystems: learning from continental-scale rabbit control experiments. *Restoration Ecology* 30: e13552.

Fisher JL, Loneragan WA, Dixon K, Veneklaas EJ. 2009. Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. *Biological Conservation* 142: 256-269.

Flux J, Fullagar P. 1992. World distribution of the rabbit *Oryctolagus cuniculus* on islands. *Mammal Review* 22: 151-205.

Foran BD. 1986. The impact of rabbits and cattle on an arid calcareous shrubby grassland in central Australia. *Vegetatio* 66: 49-59.

Foran BD, Low WA, Strong BW. 1985. The response of rabbit populations and vegetation to rabbit control on a calcareous shrubby grassland in central Australia. *Wildlife Research* 12: 237-247.

Forkman J, Josse J, Piepho H. 2019. Hypothesis tests for Principal Component Analysis when variables are standardized. *Journal of Agricultural, Biological, and Environmental Statistics* 24: 289-308.

Forstmeier W, Wagenmakers E-J, Parker TH. 2017. Detecting and avoiding likely false-positive findings - a practical guide. *Biological Reviews* 92: 1941-1968.

Friedel MH. 1985. The population structure and density of central Australian trees and shrubs, and relationships to range condition, rabbit abundance and soil. *Australian Journal of Wildlife Research* 7: 130-139.

Gardenia.net. 2023. *Crassula*: The delightful succulent perfect for any setting. Available at https://www.gardenia.net/plants/genera/crassula [accessed 4 December 2023]

Germishuizen G, Meyer NL. 2003. *Plants of southern Africa: an annotated checklist*. Pretoria: National Botanical Institute.

Gidenne T, Lebas F, Fortun-Lamothe L. 2020. Feeding behaviour of rabbits. In: De Blas JC, Wiseman J editors. *Nutrition of the rabbit* No. 3: CAB International. p. 978-0851992792.

Gillham EM. 1955. Ecology of the Pembrokeshire Islands. III. The effect of grazing on the vegetation. *Journal of Ecology* 43: 172-207.

Gillham ME. 1963. Some interactions of plants, rabbits and sea-birds on South African islands. *Journal of Ecology* 51: 275-294.

Gillison AN, Brewer KR. 1985. The use of gradient directed transects or gradsects in natural resource surveys. *Journal of Environmental Management* 20: 103-127.

Guglielmini AC, Satorree H. 2002. Shading effects on spatial growth and biomass partitioning of *Cynodon dactylon*. *Weed Research* 42: 123-134.

Guo LB, Sims REH. 2001. Effects of light, temperature, water and meat works effluent irrigation on eucalypt leaf litter decomposition under controlled environmental conditions. *Applied Soil Ecology* 17: 229–237.

Halvorson WL, Guertin P. 2003a. Factsheet for: *Avena fatua* L. . *USGS Weeds in the West project: status of introduced plants in Southern Arizona parks*. Tucson: U.S. Geological Survey / Southwest Biological Center.

Halvorson WL, Guertin P (eds). 2003b. *Factsheet for: Cynodon dactylon (L.) Pers.* U.S. Geological Survey / Southwest Biological Center. Tucson.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Palaeontological Statistics Software Package for Education and Data Analysis. *Available at http://palaeo-electronica.org/2001/past/issue101.htm [Accessed 24 August 2010]*.

Harrington KC, Hodder LM, Outred HA. Biology and control of pypgrass*, 1 August 1998*: New Zealand Plant Protection Society. pp. 259-259.

Herrick JE, van Zee JW, Havstad KM, Burkett LM, Whitford WG. 2005. *Monitoring manual for grassland, shrubland and savanna ecosystems: Volume 1 Quickstart*. Las Cruces: USDA-ARS Jornada Experimental Range.

Hertling UM. 1997. *Ammophila arenaria* (l.) Link (Marram grass) in South Africa and its potential invasiveness. DPhil, Rhodes University, Grahamstown.

Hobbs RJ, Grace J. 1981. A study of pattern and process in coastal vegetation using principle components analysis. *Vegetatio* 44: 137-153.

Hodder LM. 1997. The biology and control of *Ehrharta villosa*, South African pypgrass. MSc, Massey University.

Jackson N, Cudney D, DiTomaso J, C. B, Lee V, Drewitz J, Bossard S, Randall L, Hansen-Winter B, Faber P, *et al.* 2006. *Invasive plants of California's wildland*. California Invasive Plant Council.

Johnson DH. 2002. The importance of replication in wildlife research. *The Journal of Wildlife Management* 66: 919-932.

Kamchoom V, Boldrin D, Leung AK, Sookkrajang C, Likitlersuang S. 2022. Biomechanical properties of the growing and decaying roots of *Cynodon dactylon*. *Plant and Soil*: 1-18.

Kämpfer S, Fartmann T. 2019. Breeding populations of a declining farmland bird are dependent on a burrowing, herbivorous ecosystem engineer. *Ecological Engineering* 140: 105592.

Khan MA, Hussain I, Khan EA. 2008 Allelopathic effects of *Eucalyptus* (*Eucalyptus camaldulensis* L.) on germination and seedling growth of wheat (*Tricum aestivum* L.). *Pakistan Journal of Weed Science Research* 14: 9-18.

Kruskal J. 1964. Nonmetric multidimensional scaling: A numerical method. *Psychometrika* 29: 115-129.

Kumar A, Abrol IP. 1982. Relative tolerance of grasses to sodic soils. *Indian Farming* 32: 41-43.

Kumschick S, Foxcroft LC, Wilson JR. 2020. Analysing the risks posed by biological invasions to South Africa. *Biological Invasions in South Africa*: 573-596.

Lange RT, Graham CR. 1983. Rabbits and the failure of regeneration in Australian arid zone *Acacia*. *Australian Journal of Ecology* 8: 377-381.

Latham ADM, Latham MC, Norbury GL, Forsyth DM, Warburton B. 2020. A review of the damage caused by invasive wild mammalian herbivores to primary production in New Zealand. *New Zealand Journal of Zoology* 47: 20-52.

Le Maitre DC, van Wilgen BW, Gelderblom C, Bailey C, Chapman R, Nel J. 2002. Invasive alien trees and water resources in South Africa: case studies of the costs and benefits of management. *Forest Ecology Management* 160: 143-159.

Le Roux A. 2005. *Namaqualand – South African Wild Flower Guide 1*. Cape Town: Botanical Society of South Africa.

Leigh JH, Wood DH, Holgate MC, Slee A, Stanger MG. 1989. Effects of rabbit and kangaroo grazing on two semi-arid grass- land communities in central-western New South Wales. *Australian Journal of Botany* 37: 375-396.

Lever C. 1985. *Naturalised mammals of the world*. London: Longman.

Liengme CA. 1987. West Coast Strandveld: its utilization and management. MSc. Thesis, University of Cape Town, Cape Town.

Long JL. 2003. *Introduced mammals of the world: their history, distribution and influence*. Collingwood: CSIRO Publishing.

Loumeto JJ, Huttel C. 1997. Understory vegetation in fast-growing tree plantations on savanna soils in Congo. *Forest Ecology and Management* 99: 65–81.

Louw G, Beukes T. 1988. Ken ons veldplante. *Die Noordwester*: 6-12.

Lurgi M, Ritchie EG, Fordham DA. 2018. Eradicating abundant invasive prey could cause unexpected and varied biodiversity outcomes: The importance of multispecies interactions. *Journal of Applied Ecology* 55: 2396-2407.

Marchante E, Kjoller A, Struwe S, Freitas H. 2008 Short- and long- term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. *Applied Soil Ecology* 40: 210–217.

Martin GR, Twigg LE, Lena Z. 2007. Seasonal changes in the diet of the European rabbit (*Oryctolagus cuniculus*) from three different Mediterranean habitats in south-western Australia. *Wildlife Research* 34: 25-42.

Mátrai K, Altbäcker V, Hahn I. 1998. Seasonal diet of rabbits and their browsing effect on juniper in Bugac Juniper Forest (Hungary). *Acta Theriologica* 43: 107-112.

McCune B, Grace JB, Urban DL. 2002. *Analysis of ecological communities* Gleneden Beach: MjM Software Design.

Measey J, Hui C, Somers MJ. 2020. Terrestrial vertebrate invasions in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology* No. 14. Cham, Swtzerland: Springer Open. p. 115-151.

Melak Y, Angassa A, Abebe A. 2019. Effects of grazing intensity to water source on grassland condition, yield and nutritional content of selected grass species in Northwest Ethiopia. *Ecological Processes* 8: 1-13.

Menke JW. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia* 20: 22-25.

Mesléard F, Mauchamp A, Pineau O, Dutoit T. 2011. Rabbits are more effective than cattle for limiting shrub colonization in Mediterranean xero-halophytic meadows. *Ecoscience* 18 37-41.

Moore CB, Moore JH. 2007a. Annual veldgrass: *Ehrarta longiflora* Smith. HerbiGuide - The Pesticide Expert on a Disk Available at http://www.herbiguide.com.au/Descriptions/hg_Annual_Veldtgrass.htm. [accessed 25 September 2017]

Moore CB, Moore JH. 2007b. Colombia Daisy: *Oncosiphon suffruticosum* (L.) Kallersjo. HerbiGuide - The Pesticide Expert on a Disk. Available at http://www.herbiguide.com.au/Descriptions/hg_Colomba_Daisy.htm. [accessed 25 September 2017]

Mucina L, Rutherford M (eds). 2006. *Vegetation map of South Africa, Lesotho, and Swaziland*. Pretoria: South African National Biodiversity Institute.

Muhl SA. 2008. Alien grass invasion of Renosterveld: Influence of soil variable gradients. MSc Thesis, Stellenbosch University, Stellenbosch.

Myers K, Bults HG. 1977. Observations on the changes in the quality of food eaten by the wild rabbit. *Australian Journal of Ecology* 2: 215-229.

Myers K, Poole WE. 1963. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations IV. The effects of rabbit grazing on sown pastures. *Journal of Ecology* 51: 435-451.

Nakagawa S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology* 15: 1044-1045.

Nankivell JW. 1934. Robben Island. *The South African Geographical Journal* 17: 29-34.

Norbury DC, Norbury GL. 1996. Short-term effects of rabbit grazing on a degraded short-tussock grassland in Central Otago. *New Zealand Journal of Ecology* 20: 285-288.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H 2015. vegan: Community Ecology Package. R package version 2.2-1. http://CRAN.R-project.org/package=vegan.

Pacala SW, Crawley MJ. 1992. Herbivores and plant diversity. *American Naturalist* 40: 243-260.

Pennell CGL, Rolston MP, Latham ADM, Mace WJ, Vlaming B, van Koten C, Latham MC, Brown S, Card SD. 2016. Novel grass–endophyte associations reduce the feeding behaviour of invasive European rabbits (*Oryctolagus cuniculus*). *Wildlife Research* 43: 681.

Pike N. 2011. Using false discovery rates for multiple comparisons in ecology and evolution. *Methods in Ecology and Evolution* 2: 278–282.

R Core Team 2020. R: A Language and Environment for Statistical Computing. Vienna http://www.R-project.org/: R Foundation for Statistical Computing

Ranwell DS. 1960. Newborough Warren, Anglesey, Ill. Changes in vegetation on parts of the dune system after the loss of rabbits by myxomatosis. *Journal of Ecology* 48: 385-397.

Robben Island Museum (ed). 2006. *Integrated Conservation Management Plan (ICMP) for the Robben Island World Heritage Site*. Robben Island Museum Cape Town.

Roets F, Pryke JS. 2012. The rehabilitation value of a small culturally significant island based on the arthropod natural capital. *Journal of Insect Conservation* 17: 53-65.

Sakia RM. 1992. The Box-Cox transformation technique: A review. *The Statistician* 41: 169-178.

Sasikumar K, Vijayalakshmi C, Parthiban KT. 2001. Allelopathic effects of *Eucalyptus* on Redgram (*Cajanus cajan* L.). *Journal of Tropical Agriculture* 39: 134-138.

Schmalzer PA, Hinkle CR (eds). 1987. *Species biology and potential for controlling four exotic plants (Ammophila Arenaria, Carpobrotus Edulis, Cortaderia Jubata, And Gasoul Crystallinum) on Vandenberg Air Force Base, California*. National Aeronautics and Space Administration, John F. Kennedy Space Center. Florida.

Schweizer D, Jones HP, Holmes ND. 2016. Literature review and meta-analysis of vegetation responses to goat and European rabbit eradications on islands. *Pacific Science* 70: 55-71.

Sherley RB. 2016. Unusual foraging behaviour in two introduced mammals following degradation of their island habitat. *Biodiversity Observations* 7: 1-10.

Simmonds H, Holst P, Bourke C. 2000. *The palatability, and potential toxicity of Australian weeds to goats*. Kingston: Rural Industries Research and Development Corporation.

Skarpe C. 1986. Plant community structure in relation to grazing and environmental changes along a north-south transect in the western Kalahari. *Vegetatio* 68: 3-18.

Skead CJ. 2011. Historical incidence of the larger land mammals in the broader Western and Northern Cape In: Boshoff AF, Kerley GIH, Lloyd PH editors. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.

Smith EP. 2002. BACI design. In: El-Shaarawi AH, Piegorsch WW editors. *Encyclopedia of environmetrics*. Chichester: Wiley p. 141-148.

Soane GA. 1980. Food selection by the rabbit. Ph.D. thesis, University College of North Wales.

South African National Biodiversity Institute. 2023a. *Tetragonia fruticosa* - PlantZAfrica. Available at http://redlist.sanbi.org/species.php?species=1989-13 [accessed 4 December 2023]

South African National Biodiversity Institute. 2023b. *Tetragonia fruticosa* - Useful and harmful plants of South Africa. . Available at http://redlist.sanbi.org/species.php?species=1989-13 [accessed 4 December 2023]

Stewart-Oaten A, Bence JR. 2001. Temporal and spatial variation in environmental impact assessment. *Ecological Monographs* 71: 305-339.

Stewart-Oaten A, Murdoch WW, Parker KR. 1986. Environmental impact assessment: "pseudoreplication" in time? *Ecology* 67: 929-940.

Strive T, Cox TE. 2019. Lethal biological control of rabbits – the most powerful tools for landscape-scale mitigation of rabbit impacts in Australia. *Australian Zoologist* 40: 118-128.

Tainton NM, Bransby DI, Booysen Pd. 1990. *Common veld and pasture grasses of Natal* (2nd edn). Pietermaritzburg: Shuter and Shooter.

Tankard AJ. 1976. Cenozoic sea-level changes: a discussion. *Annals of the South African Museum* 71: 1–17.

ter Braak CJF, Looman CWN. 1994. Biplots in reduced-rank regression. *Biometrical Journal* 36: 983-1003.

Thomas AS. 1960. Changes in vegetation since the advent of myxomatosis. *Journal of Ecology* 48: 287-307.

Thomas AS. 1963. Further changes in vegetation since the advent of myxomatosis. *Journal of Ecology* 51: 151-186.

Thresher AC. 2020. When extinction is warranted: Invasive Species, Suppression-Drives and the Worst-Case Scenario. *Ethics, Policy & Environment* 25: 1-21.

Todd SW. 2000. Patterns of seed production and shrub association in two palatable Karoo shrub species under contrasting land use intensities. *African Journal of Range and Forage Science* 17: 22-26.

Toelken HR. 1981. The species of *Crassula* L. in Australia. *Journal of the Adelaide Botanic Garden* 3: 57-90.

UWC Cape Flats Indigenous Nursery. 2021. Propagating *Phyllobolus canaliculatus* (Vingerkanna). Available at https://www.pinterest.co.uk/pin/593490057135262691/ [accessed 22 March 2021]

Vahamidis P, Chachalis D, Akrivou A, Karanasios E, Ganopoulou M, Argiri A, Mandoulaki A, Hatzigiannakis E, Arampatzis G, Panagopoulos A, Mantzouni I. 2024. Weed species' diversity and composition as shaped by the interaction of management, site, and soil variables in Olive groves of Southern Greece. *Agronomy* 14: 640

van Breda PAB, Barnard SA. 1991. *100 veld plants of the winter rainfall region: A guide to the use of veld plants for grazing*. Pretoria: Department of Agricultural Development.

van Breda PAB, Nel EJ, Bayer MB (eds). 1990. *Palatability of plant species – winter rainfall region: Little Karoo and Ceres Karoo* Elsenburg Agricultural Development Institute

van Oudtshoorn F. 2012. *Guide to grasses of southern Africa*. Pretoria: Briza Publications.

Verboom GA, Linder HP, Stock WD. 2003. Pylogenetics of the grass genus *Ehrarta*: evidence for radiation in the summer-arid zone of the South African Cape. *Evolution* 57: 1008-1021.

Verdaguer D, Sala A, Vilà M. 2010. Effect of environmental factors and bulb mass on the invasive geophyte *Oxalis pes-caprae* development *Acta Oecologica* 36: 92–99.

Watt AS. 1962. The effect of excluding rabbits from Grassland A (Xerobrometum) in Breckland (1936-60). *Journal of Ecology* 50: 181-198.

Watt AS. 1981. A comparison of grazed and ungrazed Grassland A in East Anglian Breckland. *Journal of Ecology* 69: 499–508.

Weissgerber TL, Garovic VD, Milin-Lazovic JS, Winham SJ, Obradovic Z, Trzeciakowski JP, Milic NM. 2016. Reinventing biostatistics education for basic scientists. *PLoS Biology 14, e1002430*.

Western Australian Herbarium. 2022. *Oncosiphon suffruticosum* (L.) Kallersjo. Available at https://florabase.dpaw.wa.gov.au [accessed 12 January 2022]

White LM 1973. Carbohydrate Reserves of Grasses: A Review. Society for Range Management. p. 13-18.

Williams AJ, Klages NTW, Crawford RJM. 2000. Functional ecosystems: Coastal islands. In: Durham BD, Pauw JC editors. *Summary Marine Biodiversity Status Report for South Africa*. Pretoria: National Research Foundation.

Williams K (ed). 2011. *Managing Rabbits in Canberra Nature Park*. Office of the Commissioner for Sustainability and the Environment. Canberra.

Williams K, Parer I, Coman B, Burley J, Braysher M. 1995. *Managing vertebrate pests: rabbits* Canberra: Australian Government Publishing Service

Winston R, DesCamp W, Andreas J, Randall CB, Milan J, Schwarzländer M. 2014. *New invaders of the Southwest*. Washington, DC: Forest Health Technology Enterprise Team, United States Department of Agriculture.

Yeld J. 2008. Robben Island conservation 'in a shambles'. 'Available at' http://www.iol.co.za/news/south-africa/robben-island-conservation-in-a-shambles-1.398514#.Utf_RYWRa1s [accessed 8 February 2017]

Zhang D, Zhang J, Yang W, Wu F. 2010. Potential allelopathic effect of *Eucalyptus grandis* across a range of plantation ages. *Ecological Research* 25: 13-23.

Zwerts JA, Prins HHT, Bomhoff D, Verhagen I, Swart JM, de Boer WF. 2015. Competition between a lawn-forming *Cynodon dactylon* and a tufted grass species *Hyparrhenia hirta* on a South African dystrophic savanna. *PLOS ONE* 10: e0140789.

CHAPTER 4

Change in vegetation species diversity on a small Mediterranean-type South African offshore island following the control of invasive alien European rabbits (*Oryctolagus cuniculus*)

Thabisisani Ndhlovu[1], Zivanai Tsvuura[2]

[1]School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa.

[2]Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal,
Pietermaritzburg, South Africa.

Formatted for submission to the African Journal of Range and Forage Science.

Abstract

Island ecosystems, which are hotspots of global biodiversity and endemism, are threatened by invasive species such as the European rabbit (*Oryctolagus cuniculus*). Introduced to over 800 islands, this species has become a major disruptor, significantly affecting these habitats. Since the 1800s, at least 90 successful rabbit eradications have been documented, with methods improving over time. However, the impact of these eradications on vegetation species diversity has been less explored, despite biodiversity protection being a primary goal of such efforts. Our study examined changes in vegetation diversity on Robben Island from 2010 to 2013, following an attempted eradication of European rabbits between 2008 and 2009. Robben Island is the most ecologically degraded of South Africa's 24 offshore islands and the only one where sustained eradication efforts have been made. Contrary to our initial hypothesis that rabbit eradication would enhance native vegetation diversity, we observed a decrease in species diversity at strand and inland dune sites, while it remained unchanged at eucalyptus sites. These changes are primarily attributed to the prolonged effects of rabbit herbivory, which appear to have depleted palatable plant species and left a community dominated by ecologically less competitive, marginally palatable, and unpalatable species. Generally, the more palatable a plant species is to European rabbits, the more ecologically competitive it is. The release from herbivory pressure following the control of European rabbits appears to have provided a competitive advantage to the few remaining palatable species that had survived the prolonged rabbit herbivory on the island, enabling them to outcompete the less competitive, less palatable species and leading to a decline in species diversity. Eucalyptus sites showed no change in diversity likely due to the inhibitory effects of the *Eucalyptus* trees on understory vegetation dynamics. These findings from Robben Island offer insights into the potential effects of invasive species control on vegetation diversity across similar ecosystems and highlight the importance of considering unintended consequences of such interventions on heavily impacted ecosystems.

Keywords: European rabbits; invasive alien species; ecological restoration; vegetation species diversity; Robben Island; South Africa

Introduction

Island ecosystems have long been prioritised in global biodiversity conservation (El-Lakany 2002, Kier, et al. 2009). This has been primarily because of their ability to offer high returns for conservation efforts that are disproportionate to their small area (El-Lakany 2002, Kier, et al. 2009, Cubas, et al. 2019). Despite accounting for only 5% of the global terrestrial surface, islands are home to 17% of all plant species (Cubas, et al. 2019), 37% of all critically endangered species (Barbraud, et al. 2021, Travers, et al. 2021), and a disproportionate number of range-restricted endemics (~10 times more than those found on continents; El-Lakany 2002, Kier, et al. 2009). However, this exceptional contribution of islands to global biodiversity is threatened by several environmental factors, such as land-use change, overexploitation, climate change, pollution, and, above all, the impacts of invasive alien species (McGill, et al. 2015, Cubas, et al. 2019, Russell, et al. 2019). One of the most widely introduced invasive alien species that has had devastating effects on island biodiversity is the European rabbit, *Oryctolagus cuniculus* (Schweizer, et al. 2016). European rabbits have been released on over 800 islands and island groups worldwide, where they are widely considered significant pests (Schweizer, et al. 2016, Cubas, et al. 2019, Bello-Rodríguez, et al. 2021).

European rabbits are a keystone species in their native range in southwestern Europe (Delibes, et al. 2007, Carro, et al. 2019, Marín-García, et al. 2021). In addition to being essential drivers of vegetation composition, structure, and function in their native areas (Ruiz-Aizpurua, et al. 2018, Carro, et al. 2019), European rabbits are an important prey species for over 40 carnivores, including rabbit specialists (Prada, et al. 2018, Marín-García and Llobat 2021). European rabbits are also critical 'ecosystem engineers' whose activities significantly impact native ecosystems (Cubas, et al.

2018, Delibes-Mateos, et al. 2018, Cubas, et al. 2019). For example, rabbit burrowing provides refuge for many species, such as the Montpellier snake (*Malpolon monspessulanus*) and common toad (*Bufo bufo*), while their feeding habits facilitate the dispersion of important Mediterranean plants (Marín-García and Llobat 2021). Their faeces also improve soil fertility significantly (Marín-García and Llobat 2021). European rabbits are also a valuable small-game species in their native range in Spain and Portugal, where they are hunted in their millions and generate ~US$1.25 billion in revenue annually (Villafuerte, et al. 2017, Delibes-Mateos, et al. 2018).

In contrast, in areas where they have been introduced, European rabbits have become one of the most severe threats to biodiversity and human livelihoods (Thompson, et al. 1994, Williams, et al. 1995, Courchamp, et al. 2003, Schweizer, et al. 2016, Marín-García and Llobat 2021). European rabbits have, among other impacts, been shown to reduce pastoral productivity (Williams, et al. 1995, Pennell, et al. 2016) and compete with ecologically similar native and domestic mammals (Myers, et al. 1963, Dawson, et al. 1979, Thresher 2020), change plant species composition (Farrow 1917, Fenton 1940, Gillham 1955, Ranwell 1960, Watt 1981, Foran 1986, Crawley 1990, Diaz 2000, Schweizer, et al. 2016), diversity (Farrow 1917, Gillham 1955, Hobbs, et al. 1981, Foran 1986) and structure (Farrow 1917, Tansley, et al. 1925, Fenton 1940, Crawley 1990, Norbury 1996, Diaz 2000, Schweizer, et al. 2016), limit regeneration of trees and shrubs (Lange, et al. 1983, Foran, et al. 1985, Cubas, et al. 2018) and increase landscape degradation (Cooke 1991, Strive, et al. 2019) in their introduced areas. In Australia, annual economic losses caused by rabbits are estimated to be ~US$146 million (Delibes-Mateos, et al. 2018). Financial losses of between US$130–169 million were reported for the United Kingdom in 1986 (Delibes-Mateos, et al. 2018), while annual losses are estimated to have ranged between US$23–49 million in New Zealand during the 1990s (Latham, et al. 2020). The adverse ecological and economic effects of introduced rabbits have spurred concerted efforts to eradicate them from affected areas (Schweizer, et al. 2016). Since the 1800s, there have been at least 90 successful rabbit eradications worldwide (Schweizer, et al. 2016). Eradication methodology and efficacy have steadily improved over the years, resulting in a nearly constant increase in successful rabbit eradication over time (Myers, et al. 2000, Schweizer, et al. 2016). However, few studies have been conducted to evaluate the effects of rabbit eradication on vegetation species diversity, despite biodiversity protection being an intrinsic goal of invasive alien species removals across the globe (Schweizer, et al. 2016).

In this study, we took advantage of an attempt to eradicate invasive European rabbits from Robben Island between 2008 and 2009 to monitor changes in vegetation species diversity over four years (2010-2013) following rabbit control. Robben Island is the largest and most ecologically degraded of the string of 24 South African offshore islands that occur along the southern African coast. Our objectives were to (1) determine the effect of rabbit control on vegetation species diversity on the island and (2) identify the vegetation dynamics that underlay the observed change. Although South African offshore islands vary in geology, size, distance from the coast, and climatic conditions, Williams, et al. (2000) considered them to have enough similarities to constitute a discrete bio-geographical unit. As a result, we believe that vegetation dynamics on Robben Island can provide valuable insights into the potential response of vegetation species diversity on other South African offshore islands to rabbit control. European rabbits were historically introduced to 13 South African offshore islands but are currently present on six (Jutten, Dassen, Vondeling, Schaapen, Robben, and Seal Islands, de Vos, et al. 1956, Cooper, et al. 1982, Lever 1985, Long 2003, Skead 2011, Davies, et al. 2020, Measey, et al. 2020). To date, Robben Island is the only South African offshore island from which there has been a deliberate and sustained attempt to eradicate European rabbits as extinctions from other islands (i.e., Malgas, Marcus, Meeuw, Dyer, Possession, St Croix/Bird, and an unnamed island on the Keurbooms River estuary) have been natural.

Vegetation species diversity has been shown to be highest in areas under moderate herbivory and poorest in those under heavy or light herbivory (Tansley and Adamson 1925, Zeevalking, et al. 1977). These observations are consistent with the intermediate disturbance hypothesis (IDH; Suzuki, et al. 2013). Herbivory is a bidirectional process that reduces diversity by favouring a few herbivory-tolerant species when heavy and facilitating a few competitively dominant species when light or non-existent (Suzuki, et al. 2013). This is because there is a strong positive correlation between the competitive ability of plant species and their palatability to European rabbits (Crawley 1990, Pacala, et al. 1992, Diaz 2000). The IDH proposes that at intermediate herbivory pressure, the bidirectional processes counterbalance each other and enhance plant species diversity by allowing for mixed species compositions with different interspecific competitive abilities (Suzuki, et al. 2013). Thus, depending on the intensity of the initial herbivory, rabbit control can either increase or decrease plant species diversity (Watt 1957, Zeevalking and Fresco 1977). In cases where the initial herbivory pressure is high, rabbit control would increase species diversity by enabling the re-establishment of previously suppressed edible species, resulting in a richer species mix (Tansley and Adamson 1925, Watt 1957, Zeevalking and Fresco 1977, Hobbs and Grace 1981). However, if the initial herbivory pressure is below intermediate level or initially high herbivory pressure is reduced beyond intermediate to low or non-existent levels, rabbit control would result in less restrained or unrestrained re-establishment and growth of previously suppressed edible species, leading to the elimination of less competitive herbivory-tolerant species and less diverse plant communities (Watt 1957, Hobbs and Grace 1981).

In accordance with the findings in the literature mentioned above, we expected vegetation species diversity on Robben Island to increase following rabbit control. This was because there was evidence that herbivore pressure on the island was high before rabbit control. For instance, Yeld (2008) and Sherley (2016) reported that vegetation cover over much of the island had been severely reduced and a distinct browse line evident at the height of at least 1.2 m in 2008. Low vegetation cover is indicative of high herbivore pressure and vegetation at low levels of diversity in areas under rabbit herbivory (Tansley and Adamson 1925, Zeevalking and Fresco 1977, Hobbs and Grace 1981). Under heavy rabbit herbivory, palatable species are selectively consumed and can be completely removed from vegetation, resulting in a loss of species diversity (Tansley and Adamson 1925, Fenton 1940, Friedel 1985, Foran 1986, Williams, et al. 1995, Williams 2011, Cubas, et al. 2019). Under such conditions, controlling rabbit herbivory would have led to increased species diversity by enabling the re-establishment of previously suppressed palatable plant species. Since, in addition to European rabbits, Robben Island hosts a variety of large mammalian herbivores, such as springbok (*Antidorcas marsupials*), fallow deer (*Dama dama*) and steenbok (*Raphicerus campestris*), we postulated that residual herbivory pressure would prevent re-establishing palatable species from completely replacing less competitive unpalatable species from the vegetation. However, even under these circumstances, species diversity may not respond positively to rabbit control in insular areas, such as Robben Island, which have been subjected to long-term intense rabbit herbivory and have limited options for plant dispersal from outside. In such situations, long-term rabbit herbivory may have caused a complete loss of palatable species from plant communities and seedbanks, so that the diversity of species would not change even if the vegetation was protected from rabbit herbivory (Hobbs and Grace 1981, Leigh, et al. 1989, Norbury, et al. 1996, Hunt 2001, Williams 2011, Latham, et al. 2020, Finlayson, et al. 2021). At the inception of rabbit control in 2008, Robben Island had been exposed to more than 350 years of continuous rabbit herbivory. Additionally, the island has been separated from the mainland by ~7 km of the South Atlantic Ocean since the end of the Holocene Climate Optimum (~2000 years ago; Brooke, et al. 1982).

Materials and Methods

Study site

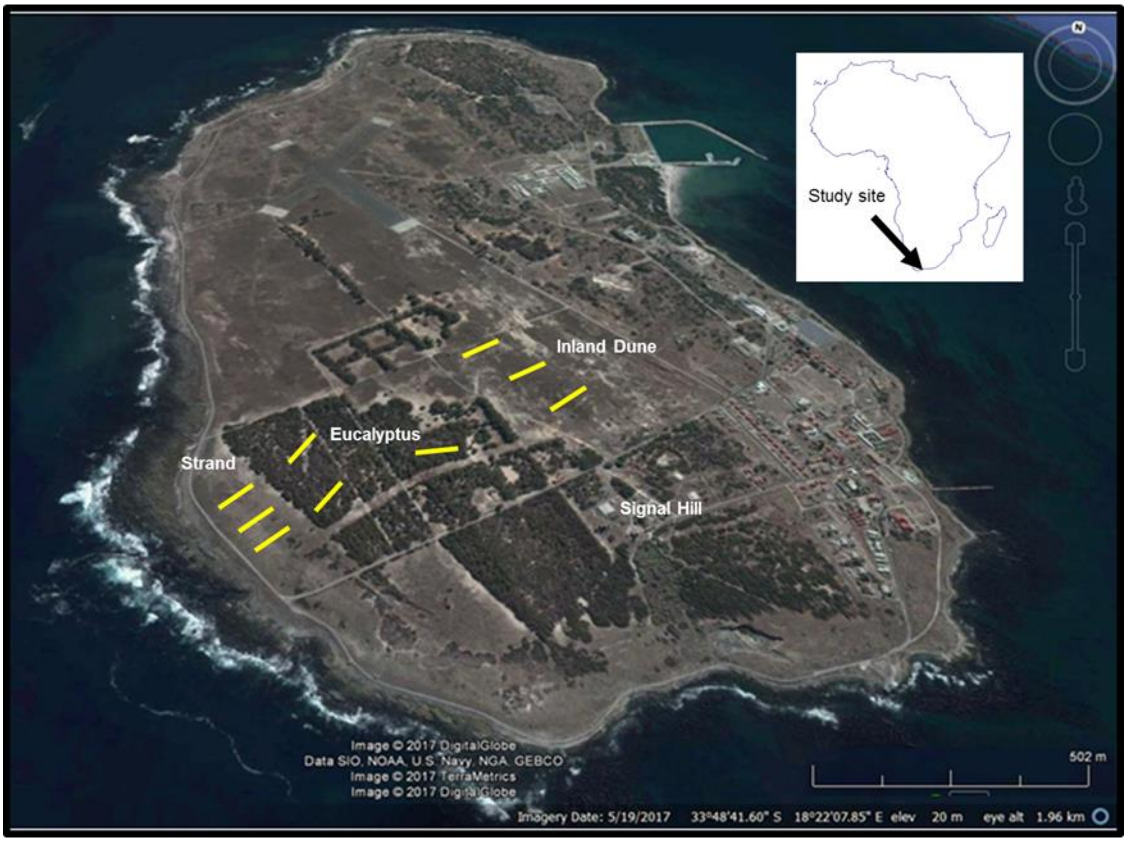


Figure 4-1 Location of the study site and the placement of sampling transects. Satellite image obtained from Google Earth (Version 5.1.3533.1731). Mountain View, CA: Google Inc. (2009).

Robben Island (33° 48′S, 18° 22′E; Figure 4.1) is the largest (507 ha) of the offshore islands that lie off South Africa's southern coast (Crawford, et al. 2000). It is located in Table Bay, ~11 km north of Cape Town and ~7 km from the nearest mainland (de Villiers 1971, Brooke, et al. 1986, Crawford and Dyer 2000). The island, which experiences a temperate Mediterranean climate, is low-lying and gently undulating to flat (Robben Island Museum 2006). The soils on the island are sandy (Adamson 1934). The map by Mucina, et al. (2006) presents the Island's vegetation as Cape Flats Dune Strandveld and Cape Seashore Vegetation. However, the vegetation on Robben Island has undergone considerable changes since the island was first occupied by humans in the 17th century (Robben Island Museum 2006). Much of the flora now prevalent on the island consists mainly of elements introduced over four hundred years of human habitation and is considered to represent only a fraction of the original natural vegetation (Adamson 1934, Nankivell 1934, Robben Island Museum 2006, Roets, et al. 2012).

Cape Flats Dune Strandveld, which has been reduced to a narrow band along South Africa's southwestern coast due to habitat transformation, is classified as 'endangered' (SANBI 2011). Cape Seashore Vegetation is considered 'least threatened' (SANBI 2011) because nearly half of its range is conserved in protected areas (Mucina, et al. 2006, Mucina and Rutherford 2006, Rebelo, et al. 2011). Although the island's vegetation has been influenced by various factors, including several other introduced large herbivores since the 17th century, the changes caused by prolonged rabbit herbivory are thought to have had the most profound impact on the island's environment (Adamson 1934, Nankivell 1934, Robben Island Museum 2006).

European rabbits were introduced to Robben Island by the Dutch colonial governor, Jan van Riebeeck, in 1654 (Measey, et al. 2020). Rabbit numbers appear to have been low for much of their existence on the island due to trapping, hunting, and predation by humans and feral cats (Apps 1984, Crawford and Dyer 2000, Sherley 2016). Numbers exploded intermittently when the island was uninhabited by humans and predation by feral cats was curtailed (Adamson 1934, Nankivell 1934, de Villiers, et al. 2010, Sherley 2016). A recent explosion in rabbit numbers (up to ~24100) occurred on the island in 2008, following the closure of the island prison in 1998 and the culmination of a series of feral cat eradication exercises that began in the same year. This explosion in rabbit numbers caused an environmental crisis on the island (Sherley 2016) that generated negative publicity. The crisis involved the eradication of vegetation cover over a significant portion of the island and substantial die-offs of rabbits and other introduced mammalian herbivores, including fallow deer, bontebok, and springbok, due to the reduced grazing capacity of the vegetation (Vosloo 2008, Yeld 2008, Sherley 2016). In response, Robben Island management (RIM) conducted a massive rabbit control exercise from November 2008 through May 2009, during which ~4790 rabbits were culled (de Villiers, et al. 2010, Sherley 2016). This period also saw around 18000 rabbits die from starvation due to food shortages, which were a consequence of the decline in summer rainfall to significantly below the long-term average (see Chapter 2). The rabbit control efforts on the ~1200 remaining rabbits continued into 2010, culminating in further reductions in the population. By November 2010, rabbit sightings on the island had become extremely rare, with only three rabbits observed during field exercises in March and none by November. No rabbits were observed during field sampling from November 2010 until 2013, when the study ended. Additional culls have been conducted on the island since the initial cull in 2009-2010, resulting in the removal of ~13600 rabbits cumulatively (Davies, et al. 2020, Measey, et al. 2020). European rabbits have not been observed on the island since 2019 (Davies, et al. 2020, Measey, et al. 2020).

Field sampling

Plant species cover change at nine sites (strand (n=3), eucalyptus (n=3), and inland dune (n=3)) on the southeastern portion of Robben Island was monitored over four years (2010-2013) following an attempt to eradicate invasive alien European rabbits from Robben Island between 2008 and 2009 (see Figure 4.1 for the location of sites). The sites were positioned along a deliberately selected transect that extended across the major ecological land units on the island, utilising the gradsect method (Gillison and Brewer 1985), which is designed to capture ecological variability across the entire study site along a gradient. Species cover at each of the sites was assessed annually in early summer (November) using line point intercepts (see Herrick, et al. 2005) along three 100-metre transects, with a 50-metre gap between them. This spacing was methodologically chosen to enhance data quality and representativeness by ensuring the independence of data points and capturing ecological variability across the sites. The point intercept method involved placing points at 1-metre intervals along each transect, resulting in 100 points per transect and a total of 300 recordings per site. Plant species cover in this study referred to the cover of the upper layer of each plant species independent of the overhanging cover of other species (Herrick et al. 2005, Fehmi 2010). Plant nomenclature followed The Plant List (2013), Version 1.1 (http://www.theplantlist.org).

Data analysis

Species diversity, richness, and evenness

Species diversity is one of the most frequently used indicators of ecological conservation value (Mace, et al. 2012). Measures of species diversity typically combine species richness (the total number of species in an area) and evenness (the relative frequency of occurrence of species in an area) (Hayek, et al. 2010, Tuomisto 2012). In general, the greater the number of species and the more evenly distributed their individual abundances are, the higher the value of diversity metrics (Hayek and Buzas 2010, Tuomisto 2012).

Species diversity was quantified using the Shannon-Wiener entropy index (*H*):

$$H = -\sum \frac{n_i}{n} \ln \frac{n_i}{n}$$

where n_i is the number of individuals of taxon i. and n is the total number of individuals across all taxa in the sample. The Shannon-Wiener index (Shannon 1948, Magurran 2004)) is the most commonly used diversity measure and represents the minimum number of yes/no questions required, on average, to determine the identity of a sampled species (Jost 2006). The index ranges from 0 for communities with only a single taxon to high values (often less than 5 in the field, Magurran (2004)) for communities with numerous taxa, each with few individuals. While the Simpson index, which does not assume that all species are represented in the sample (Magurran 2004), was more suitable for the study's small sample size, preference was given to the Shannon-Wiener index due to its prevalent use in the literature and extensive application in ecological studies to evaluate species diversity. Furthermore, the Shannon-Wiener index provides a simpler and more intuitive measure of diversity that considers both species richness and evenness, offering a comprehensive assessment of community diversity (Magurran 2004). The preference for the Shannon-Wiener index was also driven by its flexibility in using species cover as a measure of species abundance (Magurran 2004). Plant species cover, employed in this study as the measure of species abundance, is not directly comparable to the count of individuals per taxon required exclusively for the Simpson index (Magurran 2004).

Species richness (*S*) was determined from the number of species encountered along each transect. Mean estimated total plant species richness (minimum predicted numbers of species based on the sample data; Magurran 2004) at the different sites was estimated using the Chao2 richness estimator (Chao 1984) in the Quadrat Richness module of the Paleontological Statistics Software Package for Education and Data Analysis (PAST; 1000 bootstrap randomisations; Hammer, et al. 2001).

Species evenness was quantified using Buzas and Gibson's evenness index, *EBG*. The *EBG* evenness index shares similarities with Pielou's evenness index (*J*), also known as Shannon's evenness index €, as both incorporate the Shannon-Wiener index (*H*) in their calculations (Magurran 2004). However, there is a distinction in the computation: Pielou's evenness index divides the Shannon-Wiener diversity index (*H*) by the maximum potential value of *H* (*ln*(*S*)) for the given species count (Pielou 1966, Magurran 2004), whereas the *EBG* evenness index is calculated using the formula:

$$EBG = e^{H}/S$$

where e is the base of the natural logarithm, H is the Shannon-Wiener diversity index, and S is the total number of species (Buzas, et al. 1969, Magurran 2004). This difference in computation means that while Pielou's index measures evenness based on the maximum potential diversity, the *EBG* index considers the actual observed diversity (Magurran 2004, Buzas, et al. 2005). Consequently, the *EBG* index is less sensitive to the number of species in a community and takes into account the relative abundance of different species within the community. The Buzas and Gibson's evenness index ranges from 0 for a community dominated by a single species to 1 for communities where all species are equally frequent (Hayek and Buzas 2010).

Similar to species richness, the measures of species diversity and evenness were calculated using PAST (Hammer, et al. 2001).

Inter-annual rainfall variation

Inter-annual rainfall variation plays a significant role in driving vegetation dynamics in Mediterranean ecosystems (Mucina and Rutherford 2006, Esler, et al. 2018). As a result, analyses and interpretations of vegetation dynamics in Mediterranean-type ecosystems should always include an assessment of the effects of inter-annual rainfall variation (Austin, et al. 1981, Foran 1986).

Total annual, summer, winter, autumn, and spring rainfall for the study's duration were calculated using unpublished rainfall data for Robben Island obtained from the South African Weather Service. Total annual rainfall was determined from the sum of the total monthly rainfall for the 12 months that preceded vegetation monitoring. Likewise, total summer (TSUR), winter (TWR), autumn (TAUR) and spring (TSR) rainfall were calculated as sums from months preceding monitoring. On the island, summer occurs between mid-October to March, autumn in April, winter between May and August, and spring in September. We replaced missing monthly rainfall data with the means of non-missing values. Long-term averages of rainfall were calculated over 113 years (1900 – 2013).

Statistical analyses

Change in plant species diversity was determined by assessing differences in mean species diversity, richness, and evenness over the four years following rabbit control. The statistical significance of these inter-annual differences was determined using the Friedman or Wilcoxon two-sample paired tests (Bonferroni-corrected *P* values). The Friedman test, a nonparametric equivalent of repeated-measures Analysis of Variance, was preferred over other non-parametric tests due to its ability to compare related (repeated measures) groups. As the Friedman test cannot be used for comparing fewer than three groups, the Wilcoxon two-sample test, which compares two matched groups, was employed when sites had only two years of diversity, richness, or evenness values exceeding zero. Nonparametric tests were selected because the diversity data remained non-normally distributed even after transformation. Species presence and cover changes driving diversity change were identified through presence-absence matrices (Annex VI Table S1), optimally arranged for analysis using constrained seriation (Brower, et al. 1988). The role of interannual rainfall variation in influencing changes in species diversity, richness, and evenness following rabbit control was evaluated using multiple linear regressions. Total summer rainfall, TAU, and TWR were used as independent variables in all regressions. Total annual rainfall and TSR, which Redundancy Analysis (RDA; McCune, et al. 2002) identified to be collinear and, therefore potentially redundant, were excluded from regressions. Data were transformed using Box-Cox power transformations (Box, et al. 1964, Sakia 1992) after testing for normality using the Shapiro Wilk test (Shapiro, et al. 1965). Regression residuals were tested for serial correlation using Durbin-Watson tests (Durbin, et al. 1951). Regressions, significance and normality tests were carried out using PAST (Hammer, et al. 2001). Analyses were conducted separately for strand, eucalyptus, and inland dune sites to evaluate the effects of landscape variation on species diversity dynamics across the island.

Modelled before-after, control-impact (BACI) design and correlative statistical control

The study, which was based on an attempt to restore vegetation on Robben Island by removing alien invasive European rabbits, was affected by several methodological challenges. As a result of its unplanned nature, the study was initiated a full year after the commencement of rabbit removals. Consequently, it was not possible to adopt the well-established before-after, control-impact (BACI) design (Stewart-Oaten, et al. 1986, Stewart-Oaten, et al. 2001, Smith 2002) commonly used to assess impacts in longitudinal observational studies (Johnson 2002). Furthermore, the unplanned nature of the study prevented the use of planned treatments and randomisation to remove the confounding effects of variation in interannual rainfall. Consequently, the influence of rainfall variation on vegetation response was analysed using correlative statistical control which does not directly demonstrate causality. The remedy for the first methodical challenge was to model island vegetation as a longitudinal time series using data from an earlier vegetation survey. Adamson (1934) surveyed vegetation on Robben Island in 1933-1934 when the island was overrun with rabbits. This survey's results were used as a BACI-like control by assuming that the conditions on the island in 1933-1934 were similar to those just before the rabbit control in 2009 and 2010 (Annex VII). However, this assumption is precarious because the survey was conducted 77 years prior to the present study's sampling, and significant environmental changes have occurred on the island since that time. Additionally, the island was deserted at the time of the 1933-1934 survey (Nankivell, 1934), leading to the complete absence of rainfall records for that period, which constrains the comparability between these periods. Nevertheless, this remains the only detailed vegetation survey on the island that provides a viable baseline. The second methodical challenge was addressed by strengthening, wherever possible, the correlative interpretations of the relationships between rainfall variation and vegetation response in our results by providing plausible mechanisms, demonstrating links between putative causes and outcomes, and sourcing supporting independent evidence from the published literature (Annex VII).

Results

Inter-annual rainfall variation

Inter-annual rainfall varied considerably between the four years following rabbit control (Table 4.1). Total summer rainfall was considerably below the long-term average during the first- and second years following rabbit control and rose to moderately above and equal to the average in the third and fourth (Table 4.1). Total autumn rainfall followed the same pattern as total summer rainfall (Table 4.1). Total winter rainfall was slightly to moderately below the long-term average in the first- and second years following rabbit control and increased substantially to above average in the third and fourth year (Table 4.1).

Table 4-1 Inter-annual rainfall following the control of invasive alien European rabbits on Robben Island. Long-term (1900– 2013) rainfall averages are provided for comparative purposes.

Rainfall (mm)	Year				Long term average
	2010	2011	2012	2013	
Total summer rainfall	22	10	61	51	50
Total autumn rainfall	12	14	42	31	34
Total winter rainfall	238	164	270	354	258

Species diversity change following rabbit control

Strand sites

Species diversity and richness increased significantly following rabbit control at strand sites (Table 4.2). Mean species diversity across the sites decreased moderately between the first- and second years following rabbit control (decrease in mean *H* of 0.48), increased markedly between the second and third (increase in mean *H* of 0.90) and did not change between the third and fourth (Table 4.2). Species richness decreased moderately between the first- and second years following rabbit control (decrease in mean *S* of 3.96, ~4 species Chao2 estimate), increased markedly between the second and third (increase in mean *S* of 12.69, ~13 species Chao2 estimate) and decreased slightly between the third and fourth (decrease in mean *S* of 3.85, ~4 species Chao2 estimate: Table 4.2). Species evenness, in contrast, did not change significantly following rabbit control (Table 4.2). Inter-annual rainfall variation accounted for ~39% and ~41% of the change in diversity and richness (Table 4.3).

However, there was no relationship between diversity and richness change and seasonal inter-annual rainfall variation (Table 4.3).

Eight species emerged following rabbit control – the annual grasses *Ehrharta longiflora* Sm., *Bromus diandrus* Roth. (alien), annual herbs *Anagallis arvensis* L*.*, *Silene cretica* L. (alien), *Euphorbia peplus* L. (alien), *Hypochaeris glabra* L. (alien), perennial herb *Phyllobolus canaliculatus* (Haw.) Bittrich and perennial grass *Ehrharta villosa* Schult.f. *Ehrharta villosa* emerged in the second year following rabbit control while *E. longiflora*, *B. diandrus* and *S. cretica* emerged in the third and *E. peplus*, *A. arvensis*, *H. glabra* and *P. canaliculatus* in the fourth year (Annex VI Table S1). ***One species disappeared following rabbit control*** – the perennial grass *Sporobolus virginicus* (L.) Kunth. disappeared in the second year following rabbit control (Annex VI Table S1). ***Six species occurred transiently following rabbit control*** – the alien annual grass *Vulpia myuros* (L.) C.C.Gmel and annual herbs *Sonchus oleraceus* (L.) L, *Isolepis* sp., *Moraea collina* Thunb., *Spergula arvensis* L. and *Crassula* sp., as well as the alien woody shrub *Atriplex cinerea* Poir. *Vulpia myuros*, *Isolepis* sp., *Moraea collina* Thunb., *Spergula arvensis* L., *Crassula* sp. and *A. cinerea* occurred only once in the third year following rabbit control while *S. oleraceus*, occurred twice - in the first and third year (Annex VI Table S1). ***Two species disappeared temporarily following rabbit control*** - the perennial herb *Zantedeschia aethiopica* (L.) and grass *Cynodon dactylon* (L.) Pers. The species disappeared briefly in the second year following rabbit control (Annex VI Table S1). ***Four species occurred persistently following rabbit control*** - the annual herb *Oncosiphon suffruticosum* (L.) Kallersjo, perennial herb *Conicosia pugioniformis* (L.) N. E. Br. and woody shrubs *Asparagus capensis* L. and *Tetragonia fruticosa* L. *Oncosiphon suffruticosum* and *T. fruticosa* increased in cover following rabbit control while *C. pugioniformis* declined. The cover of *A. capensis* remained constant following rabbit control (Annex VI Table S1). ***Two species dominated species abundance following rabbit control*** – the woody shrub *T. fruticosa* and annual grass *E. longiflora*. *Tetragonia fruticosa* dominated species abundance during the first- and second years following rabbit control and co-dominated with *E. longiflora* during the third and fourth (Annex VI Table S1).

Eucalyptus sites

Species diversity and richness increased slightly following rabbit control at eucalyptus sites (Table 4.2). Mean species diversity and richness across the sites increased slightly from zero between the second- and third years following rabbit control (increase in mean *H* of 0.75 and mean *S* of 2.67, ~6 species Chao2 estimate) and did not change between the third- and fourth (Table 4.2). Species evenness did not change significantly following the increase from zero of species diversity and richness between the second- and third years (Table 4.2). Inter-annual rainfall variation accounted for ~76%, ~91% and ~44% of the change in diversity, richness, and evenness (Table 4.3). At seasonal level, inter-annual variation in TAUR and TWR accounted for ~66% and ~55% of the change in diversity, while TSUR, TAUR and TWR accounted for ~75%, ~79% and ~66% of the change in richness (Table 4.3). There was no relationship between evenness change and seasonal inter-annual rainfall variation (Table 4.3).

Eight species emerged following rabbit control – the annual grass *E. longiflora*, annual herbs *Crassula natans* Thunb., *O. suffruticosum*, *Chenopodium murale* L., *Torilis arvensis* (Huds.) Link, *E. peplus* (alien), perennial herb *C. pugioniformis* and woody shrub *T. fruticosa*. *Ehrharta longiflora*, *C. natans*, *O. suffruticosum*, *C. murale* and *T. fruticosa* emerged in the third year following rabbit control while *T. arvensis*, *E. peplus* and *C. pugioniformis* emerged in the fourth year (Annex VI Table S1). ***One species disappeared temporarily following rabbit control*** - the annual herb *Oxalis pes-caprae* L. The herb disappeared briefly in the second year following rabbit control (Annex VI Table S1). ***One species occurred persistently following rabbit control*** – the perennial herb *P. canaliculatus*. The herb increased in cover following rabbit control (Annex VI Table S1). ***Two species dominated species abundance following rabbit control*** – the woody shrub *T. fruticosa* and perennial herb *P. canaliculatus*. *Tetragonia fruticosa* and *P. canaliculatus* dominated species abundance during the third- and fourth years following rabbit control (Annex VI Table S1).

Inland dune sites

Species diversity, richness and evenness did not change significantly following rabbit control at inland dune sites (Table 4.2). There were no significant relationships between diversity, richness and evenness dynamics and inter-annual rainfall variation (Table 4.3).

Three species emerged following rabbit control – the alien annual grasses *B. diandrus*, *Avena fatua* L. and annual herb *Capnophyllum africanum* (L.) Gaertn. *Bromus diandrus* emerged in the third year following rabbit control while *A. fatua* and *C. africanum* emerged in the fourth year (Annex VI Table S1). ***Six species disappeared following rabbit control*** – the annual herbs *Wahlenbergia androsacea* A.DC, *Emex australis* Steinh., perennial herbs *Ornithoglossum viride* (L.f.) Dryland. Ex W.T.Aiton, *Trachyandra* sp., *Z. aethiopica* and perennial grass *S. virginicus*. All species disappeared in the second year following rabbit control (Annex VI Table S1). ***Six species occurred transiently following rabbit control*** – the alien annual grass *V. myuros*, annual herbs *Isolepis* sp., *T. arvensis*, *A. arvensis*, perennial herb *P. canaliculatus* and woody shrub *A. capensis*. *Phyllobolus canaliculatus* and *A. capensis* occurred once in the second year following rabbit control while *V. myuros*, *Isolepis* sp., *T. arvensis* and *A. arvensis* occurred once in the third year (Annex VI Table S1). ***One species disappeared temporarily following rabbit control*** - the annual grass *E. longiflora* disappeared briefly in the second year following rabbit control (Annex VI Table S1). ***Five species occurred persistently following rabbit control*** – the annual herb *O. suffruticosum*, perennial herb *C. pugioniformis*, perennial grass *E. villosa* and woody shrubs *T. fruticosa* and *Cissampelos capensis* L.f. *Oncosiphon suffruticosum*, *E. villosa* and *T. fruticosa* increased in cover following rabbit control while *C. pugioniformis* declined. The cover of *C. capensis* remained constant following rabbit control (Annex VI Table S1). ***Five species dominated species abundance following rabbit control*** **–** the alien annual grass *B. diandrus*, perennial grass *E. villosa*, perennial herb *C. pugioniformis* and woody shrubs *T. fruticosa* and *C. capensis*. *Tetragonia fruticosa* and *C. capensis* dominated species abundance during the four years following rabbit control and co-dominated with *C. pugioniformis* during the first and *B. diandrus* and *E. villosa* during the third and fourth, respectively (Annex VI Table S1).

Table 4-2 Mean plant species diversity, richness, evenness (± SE) and estimated Chao2 richness (± SD) following the control of invasive alien European rabbits on Robben Island. Significant differences ($P \leq 0.05$) between years determined using Friedman (Chi^2) and Wilcoxon (W) two-sample paired tests. Diversity and evenness values quantified using the Shannon-Wiener diversity and Buzas and Gibson's evenness indices. Wilcoxon two-sample tests used when sites had only two years of diversity, richness or evenness values above zero.

Site	Index	Year				Chi^2/W	*P*
		2010	2011	2012	2013		
Strand	Diversity	0.93 ± 0.17	0.45 ± 0.20	1.35 ± 0.25	1.35 ± 0.21	14.60	0.002
	Richness	3.83 ± 0.65	2.33 ± 0.61	6.83 ± 1.30	6.00 ± 1.06	13.95	0.002
	Chao2 estimate	8.57 ± 2.35	4.61 ± 0.92	17.30 ± 5.63	13.45 ± 2.91	-	-
	Evenness	0.72 ± 0.03	0.84 ± 0.07	0.64 ± 0.03	0.73 ± 0.06	3.80	0.301
Eucalyptus	Diversity	0	0	0.75 ± 0.17	0.97 ± 0.20	<0.01	1.000
	Richness	0	0	2.67 ± 0.42	3.83 ± 0.65	17.00	0.167
	Chao2 estimate	-	-	6.49 ± 2.25	10.82 ± 4.44	-	-
	Evenness	-	-	0.87 ± 0.04	0.77 ± 0.09	12.00	0.753
Inland dune	Diversity	1.08 ± 0.12	0.88 ± 0.18	1.26 ± 0.27	1.23 ± 0.26	5.55	0.124
	Richness	4.33 ± 0.49	3.33 ± 0.56	6.17 ± 1.14	6.00 ± 1.10	6.90	0.066
	Chao2 estimate	12.03 ± 4.57	6.35 ± 1.17	10.43 ± 1.34	8.92 ± 0.60	-	-
	Evenness	0.71 ± 0.05	0.82 ± 0.06	0.70 ± 0.06	0.70 ± 0.07	4.15	0.254

Table 4-3 Relationship between inter-annual rainfall variation and change in plant species richness, evenness and diversity following the control of invasive alien European rabbits on Robben Island. Significant differences ($P \leq 0.05$; in bold) determined using Rao's F statistic and t-tests.

		Multiple Linear Regressions														
Sites	Index	Overall Rainfall			TSUR				TAUR				TWR			
		Adj. R^2	F	P	R^2	*Coeff*	t	P	R^2	*Coeff*	t	P	R^2	*Coeff*	t	P
Strand	Diversity	**0.39**	**4.20**	**0.019**	0.37	0.341	1.01	0.326	0.23	-0.164	-0.56	0.579	0.34	0.064	0.14	0.888
	Richness	**0.41**	**4.61**	**0.013**	0.40	0.862	1.18	0.253	0.28	-0.274	-0.45	0.657	0.33	-0.166	-0.14	0.887
	Evenness	0.27	2.43	0.095	0.22	-0.238	-1.67	0.110	0.15	0.119	0.96	0.349	0.12	0.189	1.13	0.270
Eucalyptus	Diversity	**0.76**	**20.99**	**< 0.001**	0.63	-0.313	-1.57	0.132	**0.66**	**0.552**	**3.17**	**0.005**	**0.55**	**0.624**	**2.60**	**0.017**
	Richness	**0.91**	**63.59**	**< 0.001**	**0.75**	**-0.758**	**-2.69**	**0.014**	**0.79**	**1.355**	**5.51**	**< 0.001**	**0.66**	**1.541**	**4.45**	**<0.001**
	Evenness	**0.44**	**5.25**	**0.008**	0.44	0.297	1.08	0.293	0.33	-0.064	-0.27	0.793	0.35	-0.040	-0.12	0.908
Inland dune	Diversity	0.05	0.35	0.790	0.04	0.169	0.44	0.663	0.02	-0.104	-0.32	0.754	0.04	-0.048	-0.09	0.926
	Richness	0.11	0.84	0.490	0.11	0.450	0.53	0.599	0.07	-0.205	-0.30	0.770	0.09	-0.039	-0.03	0.978
	Evenness	0.13	0.95	0.434	0.09	-0.125	-0.73	0.473	0.04	0.102	0.03	0.977	0.10	0.006	0.03	0.977

Effects of inter-annual rainfall variation on vegetation species diversity response

Inter-annual rainfall variation had a substantial confounding effect on changes in vegetation species diversity during our study (Annex VII). The effects of this variation included suppressing and delaying species responses (*E. longiflora*, *B. diandrus, S. cretica*, and *O. suffruticosum*), facilitating unusual emergences (*A. arvensis*, *E. peplus*, *H. glabra*, *P. canaliculatus*, *V. myuros*, *S. oleraceus*, *Isolepis* sp., *M. collina*, *S. arvensis*, *Crassula* sp, *C. natans*, *T. fruticosa, T. arvensis*, *C. pugioniformis*, *A. fatua*, and *C. africanum*), and causing transient disappearances (*Z. aethiopica*, *C. dactylon, O. pes-caprae*, and *E. longiflora*) in response to drought conditions during the first two years, and the occurrence of above-average winter, autumn, and summer rainfall in the third and fourth years following rabbit control (Annex VII).

We determined that species diversity across strand sites would have decreased in response to rabbit control, given constant and average inter-annual rainfall (Annex VII). This decline in diversity would have been driven by a decrease in both species' richness and evenness (Annex VII). The decline in species richness would have been caused by the emergence of two species (*E. villosa* and *C. dactylon*), and the disappearance of three others (*A. arvensis, E. peplus*, and *H. glabra*) due to rabbit control (Annex VII). However, eight species (*C. pugioniformis*, *O. suffruticosum, T. fruticosa*, *E. longiflora*, *Z. aethiopica*, *B. diandrus*, *S. cretica* and *A. capensis*) would have maintained their presence before and after rabbit control (Annex VII). Specifically, *T. fruticosa* and *E. longiflora* would have increased from medium and low to high cover, while *C. pugioniformis* and *O. suffruticosum* would have declined from high to low cover (Annex VII). *Zantedeschia aethiopica*, *B. diandrus*, *S. cretica,* and *A. capensis* would have maintained uniformly low cover (Annex VII). *Ehrharta villosa* and *C. dactylon* would have emerged with low cover, while *A. arvensis* and *E. peplus* would have disappeared from high and *H. glabra* low cover following rabbit control (Annex VII). Species evenness would have declined in response to rabbit control, with vegetation cover being dominated by four species (*C. pugioniformis*, *O. suffruticosum*, *E. peplus,* and *A. arvensis*) before, and only two *T. fruticosa* and *E. longiflora*) after rabbit control (Annex VII).

Additionally, we deduced that species diversity across inland dune sites would have similarly decreased in response to rabbit control, given constant and average inter-annual rainfall (Annex VII). Like at strand sites, this decline in diversity would have been driven by a reduction in both species' richness and evenness (Annex VII). The decrease in species richness would have been due to the disappearance of five species (*W. androsacea*, *E. australis*, *O. viride*, *Trachyandra* sp. and *Z. aethiopica*) and the emergence of one species (*E. longiflora*) because of rabbit control (Annex VII). Seven species (*E. villosa*, *T. fruticosa*, *O. suffruticosum*, *C. pugioniformis*, *B. diandrus*, *C. capensis* and *Isolepis* sp.) would have maintained their presence both before and after rabbit control. *Ehrharta villosa* and *T. fruticosa* would have increased from low to high cover, while *O. suffruticosum* and *C. pugioniformis* would have decreased conversely (Annex VII). *Bromus diandrus* would have decreased from high to medium cover, while *C. capensis* and *Isolepis* sp. would have retained their low cover (Annex VII). *Ehrharta longiflora* would have emerged with low cover, while *E. australis*, *O. viride*, and *Trachyandra* sp. would have disappeared from high, *Z. aethiopica* from medium, and *W. androsacea* from low cover following rabbit control (Annex VII). Furthermore, rabbit control would have decreased species evenness across inland dune sites by reducing the number of species dominating vegetation cover from six (*O. viride*, *E. australis*, *Trachyandra* sp., *O. suffruticosum*, *C. pugioniformis,* and *B. diandrus*) before, to only two species *T. fruticosa* and *E. villosa*) after rabbit control (Annex VII).

In contrast, we resolved that species diversity at eucalyptus sites would not have changed in response to rabbit control, given constant and average inter-annual rainfall (Annex VII). This is because the four species present at the sites (*C. natans*, *T. fruticosa*, *O. pes-caprae* and *P. canaliculatus*) would have maintained their low cover before and after rabbit control, with no loss or gain in species numbers (Annex VII). As a result, species evenness would have remained constantly high across eucalyptus sites, as the relative abundances of species would have remained similar before and after rabbit control (Annex VII).

Discussion

Impact of rabbit control on vegetation diversity

Our initial expectation was that rabbit control on Robben Island would increase species diversity by enabling the re-establishment of previously suppressed palatable plant species. Moreover, we hypothesised that countervailing residual non-rabbit herbivory would prevent recovering palatable species from dominating the vegetation and, in turn, completely displacing less competitive unpalatable and less palatable species, leading to even greater species diversity (see Introduction). However, contrary to our predictions, rabbit control resulted in a decline in species diversity across strand and inland dune sites while remaining unchanged at eucalyptus sites. The decline in species diversity across strand and inland dune sites was driven by the loss of seven plant species (*A. arvensis*, *E. peplus*, *H. glabra*, *W. androsacea*, *E. australis*, *O. viride* and *Trachyandra* sp.) which was offset by the emergence of a single species (*C. dactylon*) at strand sites. At eucalyptus sites, species richness remained unchanged, with four species (*C. natans*, *T. fruticosa*, *O. pes-caprae* and *P. canaliculatus*) maintaining low cover before and after rabbit control. Species evenness also declined across strand and inland dune sites in response to rabbit control. Before rabbit control, species cover at strand and inland dune sites was dominated by four species (*C. pugioniformis*, *O. suffruticosum*, *E. peplus,* and *A. arvensis*) and six species (*O. viride*, *E. australis*, *Trachyandra* sp., *O. suffruticosum*, *C. pugioniformis,* and *B. diandrus*), respectively. After rabbit control, it was dominated by two species (*109ruticoseosa* and *E. longiflora*) at strand sites and by two species *T. fruticosa* and *E. villosa*) at inland dune sites. However, species evenness at eucalyptus sites remained consistently high before and after rabbit control.

The degraded condition of vegetation on Robben Island following >350 years of continuous rabbit herbivory is the most likely explanation for our unexpected results at strand and inland dune sites. European rabbits possess a hierarchical diet (Thompson and King 1994), which allows them to switch forage species as preferred ones become unavailable (Donlan, et al. 2002). However, prolonged rabbit herbivory prevents the recruitment of preferred species (Donlan, et al. 2002), resulting in their cumulative depletion from vegetation and seed banks (Hunt 2001). On Robben Island, rabbit herbivory is believed to have eliminated many originally occurring species, leaving behind a few natives and weedy aliens that were either unpalatable or could withstand or escape rabbit herbivory (Adamson 1934). This was evident across our study sites, where most plant species were either unpalatable (e.g., *E. peplus* (Bullock 1952, Gillham 1963, Simmonds, et al. 2000, Germishuizen, et al. 2003), *C. natans* (Gillham 1963, van Breda, et al. 1990, Germishuizen, et al. 2003), *C. murale* (Heneidy 2002), *S. arvensis* (Reader, et al. 1981, Native Plant Trust 2022), *A. arvensis* (Rothwell, et al. 1986, Scott, et al. 1987, Rivero, et al. 2001, Germishuizen, et al. 2003), *Z. aethiopica* (Simmonds, et al. 2000, Germishuizen, et al. 2003, El Mokni, et al. 2012), *O. viride* (Vahrmeijer 1981, Germishuizen, et al. 2003), *M. collina* (van Breda, et al. 1990, Germishuizen, et al. 2003), *B. diandrus* (van Breda, et al. 1990, Germishuizen, et al. 2003, Coetzee 2008) and *O. suffruticosum* (Le Roux 2005)) or of limited palatability (e.g., *C. pugioniformis* (Louw, et al. 1988), *H. glabra* (Cowan 1945, van Dyne, et al. 1965, Struik 1967), *W. androsacea* (du Toit 2002, Germishuizen, et al. 2003), *C. africanum* (Germishuizen, et al. 2003), *E. villosa* (Louw, et al. 1988, Germishuizen, et al. 2003), *V. myuros* (Scott, et al. 1987), *E. australis* (Simmonds, et al. 2000, Germishuizen, et al. 2003), *O. pes-caprae* (Simmonds, et al. 2000, Germishuizen, et al. 2003, Vilà, et al. 2006), *A. cinerea* (Simmonds, et al. 2000, Moore 2001, Western Australian Herbarium 2022a), *P. canaliculatus* (UWC Cape Flats Indigenous Nursery 2020), *A. capensis* (van Breda, et al. 1990), *C. dactylon* (van Breda, et al. 1990, Simmonds, et al. 2000, Germishuizen, et al. 2003), *S. cretica* (Germishuizen, et al. 2003) and *Isolepis* sp. (Germishuizen, et al. 2003)).

The few palatable species that occurred at the sites (*E. longiflora* (van Oudtshoorn 2012), *A. fatua* (van den Berg, et al. 2009, van Oudtshoorn 2012), *S. oleraceus* (Lewin 1948, Simmonds, et al. 2000), *T. arvensis* (Esler 1980), *S. virginicus* (Mfitumukiza 2004) and *T. fruticosa* (van Breda, et al. 1990) were distinguished by their ability to escape or withstand herbivory. For example, the annual grasses *E. longiflora* and *A. fatua* and herbs *S. oleraceus* and *T. arvensis* produce large numbers of persistent soil-stored seeds that enable them to re-establish by mass germination after periods of intense herbivory (Halvorson, et al. 2003a, Fisher, et al. 2009, Hyde, et al. 2014, Winston, et al. 2014, Anon 2017g). Furthermore, the short growing period of the annual grasses and herbs exposes them to rabbit herbivory for short periods of time, resulting in large proportions of adult plants surviving to flower and produce fresh seed (Halvorson and Guertin 2003a, Fisher, et al. 2009, Hyde, et al. 2014, Winston, et al. 2014, Anon 2017g). Although European rabbits can browse succulent-leaved woody-stemmed *T. fruticosa* shrubs to their shoot base, they usually have trouble consuming the entire plant (Adamson 1934). This is the same with the mat-forming perennial grass *S. virginicus* whose extensive creeping stolons and rhizomes are resilient to rabbit herbivory (Knevel 2001). As a result, severely browsed *T. fruticosa* and *S. virginicus* plants can withstand rabbit herbivory by recovering from surviving stems or stolons and rhizomes (Adamson 1934). As periods of high rabbit densities on Robben Island were historically short and intermittent (see Chapter 2), the herbivory-resilient palatable species would have been able to persist in the vegetation and seedbanks over the long-term.

Generally, the more palatable a plant species is to European rabbits, the more competitive it is ecologically (Crawley 1990, Pacala and Crawley 1992, Diaz 2000). This is because many characteristics that make plants vulnerable to rabbit herbivory (such as tall vertical shoots) also make them competitive, whereas those that protect them (such as shoots close to the soil surface) make them less competitive. Due to the degraded vegetation conditions on the island outlined above, herbivory would have maintained a high plant species diversity across our sites before rabbit control by moderating the competitive advantage of palatable species. This would have resulted in a relatively diverse species mix containing co-occurring palatable, less palatable, and unpalatable species.

Consequently, rabbit control would have decreased species diversity at the sites by reducing herbivory pressure on the few occurring palatable species (*T. fruticosa*, *E. longiflora*, *E. villosa* and *C. dactylon*), resulting in the displacement of several less palatable and unpalatable species (*A. arvensis*, *E. peplus*, *H. glabra*, *W. androsacea*, *E. australis*, *O. viride* and *Trachyandra* sp.) through interspecific competition. Indeed, with its well-developed roots and succulent leaves, the highly palatable woody shrub *T. fruticosa*, which provided much of the summer rabbit feed on the island, is a strong competitor for soil moisture (van Breda and Barnard 1991, Hoffman, et al. 2009). Similarly, the palatable annual grass *E. longiflora*, which was favoured by rabbits during winter (Gillham 1963), is a strong competitor for light and space due to its rapidly sprouting erect, vigorously tufted shoots and sprawling rhizomes (Fisher, et al. 2009, DiTomaso, et al. 2013). As a result of its deep root systems, mycorrhizal associations, and long stems (often reaching a height of 2m or more), the less palatable perennial grass *E. villosa* competes aggressively for soil moisture, nutrients, and light (Harrington, et al. 1998). Despite its low growth and shade-intolerance (Guglielmini, et al. 2002), the less palatable perennial grass *C. dactylon* is an effective competitor for soil moisture, nutrients, and space due to its spreading abilities (Kumar, et al. 1982) and allelopathic effects (Horowitz 1996, Halvorson, et al. 2003b). Although rabbit preferences for *E. villosa* and *C. dactylon* are unknown, the abundance of these species on the island has been strongly linked to herbivory pressure in the past (Lloyd, et al. 1986, Sherley 2016). In contrast, the less palatable and unpalatable species that were displaced from our sites following rabbit control were all poor interspecific competitors (e.g., *A. arvensis* (Anon 2017a), *E. peplus* (Christodoulakis 1996, Anon 2017c), *H. glabra* (Anon 2017d), *W. androsacea* (Anon 2017h), *E. australis* (Panetta, et al. 1993, Anon 2017b), *O. viride* (Anon 2022) and *Trachyandra* sp. (Adamson 1934)). This was because most of the displaced species are low-growing and shallow-rooted, while most require disturbed and open spaces for germination and, as a result, cannot compete effectively for light, space, and soil moisture and nutrients.

Effect of landscape variation on vegetation diversity response

As expected, the plant species dynamics that underlay changes in vegetation diversity following rabbit control varied across the landscape. This was particularly evident at strand and inland dune sites, where rabbit control led to a decrease in vegetation diversity driven by distinct species dynamics. The difference in species dynamics between these two sites were largely be attributed to differences in soil depth. Strand sites predominantly had shallow soils ranging from 3 to 5 cm deep, whereas inland dune sites had comparatively deep soil depths ranging from 0 cm (at dune troughs) to 70 cm (at dune crests) (Adamson 1934). As a result, the decline in species diversity at strand sites was caused by the disappearance of the shallow-rooted ephemeral herbs *A. arvensis* (Anon 2017a), *E. peplus* (Esler 1980, Esler 1987, Christodoulakis 1996, Burrows, et al. 1999, Latzel, et al. 2011), and *H. glabra* (Anon 2017d), whereas the decline at inland dune sites was driven by the displacement of the deeper-rooted geophytes *W. androsacea* (Anon 2017h), *E. australis* (Kumar, et al. 2019), *O. viride* (Anon 2017e), *Trachyandra* sp. (Adamson 1934) and *Z. aethiopica* (Zizzo, et al. 2002). The deep-rooted geophytes exclusively occurred at inland dune sites, where the soil was deep enough to support their root systems, whereas the shallow-rooted ephemerals were restricted to strand sites where they could establish without being outcompeted for soil moisture and nutrients by the deeper-rooted geophytes.

The difference in soil depth between strand and inland dune sites also resulted in spatially distinct responses to rabbit control by the grasses *E. longiflora*, *E. villosa* and *B. diandrus*. For example, the shallow-rooted (Moore, et al. 2007) annual grass *E. longiflora* increased from low to high cover at strand sites, while it emerged to low cover at inland dune sites in response to rabbit control. Conversely, the deep-rooted (Harrington, et al. 1998) annual grass *E. villosa* emerged to low cover at strand sites while increasing from low to high cover at inland dune sites in response to rabbit control. Lastly, the deep-rooted (Menke 1992, Jackson, et al. 2006) perennial grass *B. diandrus* maintained low cover at strand sites while decreasing from high to medium cover at inland dune sites. Although *E. longiflora* is a strong competitor for light and space due to its sprawling rhizomes and rapidly sprouting long shoots (Fisher, et al. 2009, DiTomaso, et al. 2013), it requires disturbed open sites for successful germination (Winston, et al. 2014) and is palatable. Therefore, due to the scarcity of suitable open habitats at inland dune sites because of higher vegetation density, *E. longiflora* most likely could not respond fully to reduced herbivory pressure following rabbit control beyond re-establishing at low cover at the few available open sites. However, the shallow-rooted *E. longiflora* was most likely able to fully respond to rabbit control at strand sites due to the greater availability of open habitats and absence of more competitive deeper-rooted species. Inversely, the deep-rooted and less palatable *E. villosa* would have been unable to respond fully to reduced herbivory pressure at strand sites following rabbit control due to limited availability of habitats with soils deep enough to support its roots. However, the tall-stemmed perennial grass, which shades and outcompetes other species for soil moisture and nutrients (Hertling 1997, Harrington, et al. 1998, Coetzee 2008), would have been able to fully respond to rabbit control at inland dune sites due to the greater availability of deep-soil habitats. Similar to *E. villosa*, the deep-rooted *B. diandrus* exhibited varying responses to rabbit control at strand and inland dune sites most likely due to differences in the availability of deep-soil habitats. Before rabbit control, *B. diandrus* occurred at high cover and maintained medium cover after rabbit control at inland dune sites, where deep-soil habitats were abundant. However, at strand sites where suitable deep-soil habitats were limited, *B. diandrus* occurred at low cover both before and after rabbit control. Since *B. diandrus* is unpalatable to herbivores, it would have been able to increase to high cover during rabbit herbivory at inland dune sites, while remaining constrained to low cover at strand sites due to the unavailability of suitable deep-soil habitats. *Bromus diandrus* most likely maintained medium cover at inland dune sites because of its strong interspecific competitive ability for space, light, and soil moisture (Menke 1992, Jackson, et al. 2006), unlike other unpalatable species that declined to low cover or were displaced by recovering and more competitive palatable species.

Finally, the woody shrub *C. capensis*, which has deep roots (de Wet, et al. 2002), was likely restricted to inland dune sites due to the scarcity of suitable deep-soil habitats at strand sites. Despite limited palatability in adult plants (van Breda, et al. 1990, Germishuizen and Meyer 2003), selective and intense browsing by rabbits most likely kept the shrub at low cover at inland dune sites by targeting its highly palatable seedlings and shoots. Research shows that even at low rabbit densities, selective and intense browsing on emerging seedlings and shoots by European rabbits can prevent shrub species recruitment (Cubas, et al. 2018, Cubas, et al. 2019, Strive and Cox 2019). Similarly, non-rabbit herbivory on the shrub's seedlings and shoots would have kept *C. capensis* at low cover following rabbit control, despite the species being a strong interspecific competitor (Schmalzer, et al. 1987). Overall, our findings demonstrated that changes in vegetation diversity in response to rabbit control on the island were strongly influenced by differences in soil depth across the landscape. The results highlight the importance of considering soil depth as a key factor influencing plant community dynamics and diversity in Mediterranean-type South African offshore islands, and the need for landscape-scale management strategies that consider these spatial heterogeneities.

There were some exceptions to the above-mentioned pattern of shallow- and deep-rooted plants occurring exclusively or responding differently to rabbit herbivory and control on strand and inland dune sites. For instance, the deep-rooted perennial grass *C. dactylon* (Corr 1993), annual and perennial herbs *S. cretica* (Arnone II, et al. 1997) and *Z. aethiopica* (El Mokni and Hédi El Aouni 2012), and the woody shrub *A. capensis* (World Flora Online Consortium 2022) persisted or emerged exclusively at shallow-soiled strand sites following rabbit control. This seemingly anomalous distribution may be explained by the relatively weak interspecific competitive abilities of *C. dactylon*, *S. cretica*, and *Z. aethiopica*. In addition to requiring open environments for germination, adult *C. dactylon*, *S. cretica*, and *Z. aethiopica* plants compete poorly for light, soil moisture, and nutrients (Jackson 1986, Burton, et al. 1988, Perry 1989, Corr 1993, Arnone II and Kestenholz 1997, Guglielmini and Satorree 2002, Halvorson and Guertin 2003b) and were therefore likely to have been displaced from inland dune sites by more competitive deep-rooted species both before and after rabbit control.

Cynodon dactylon and *S. cretica* have more fibrous root systems than other deep-rooted species, with masses of dense, slender rootlets distributed evenly throughout the soil. Because of their more adaptable roots, *C. dactylon* and *S. cretica* would have been able to establish and outcompete shallow-rooted plant species on marginal habitats at strand sites where the soil was deep enough to support them rather than their deep-rooted, superior competitors. *Zantedeschia aethiopica*, on the other hand, would have been able to establish and outcompete shallow-rooted plants in areas where the soil was at an appropriate depth for its plants to take advantage of crevices in the bedrock. Shale bedrock formed outcrops over a limited area at strand sites (see Chapter 5). Tubers and roots of *Z. aethiopica* commonly occur in buried rock crevices that keep them cool during the dry season and channel water to them during the rainy season (South African National Biodiversity Institute 2023). However, due to the scarcity of such marginally suitable habitats, *C. dactylon*, *S. cretica*, and *Z. aethiopica* would have only persisted and emerged to low cover at strand sites. The seemingly unusual distribution of *A. capensis* was most likely a result of its specific habitat requirements. *Asparagus capensis* thrives in rocky habitats near the ocean (World Flora Online Consortium 2022). Shale bedrock outcrops exclusively over a small area of the strand site (as mentioned above), providing the only suitable habitat for the woody shrub across our study sites. In fact, Adamson (1934) observed that *A. capensis* shrubs on Robben Island were restricted to such rock outcrops at strand sites when the island was overrun with rabbits. Similarly, the unique habitat requirements of the shallow-rooted annual herb *Isolepis* sp. likely accounted for its seemingly unusual distribution, as it maintained low cover exclusively at inland dune sites. This short-statured and ruderal herb requires waterlogged soils for successful establishment (Tshiila 2012). Consequently, *Isolepis* sp. was most likely restricted to areas of shallow soil, such as troughs at the bases of sand dunes, where there was less competition from larger and more competitive species. Additionally, these low-lying areas would have provided suitable habitat for *Isolepis* sp., as they are prone to flooding with fresh water following rain events and receive fresh seepage water from adjacent sand dunes. Although flooding and waterlogging also occur in some areas of strand sites following rainfall events, these conditions are most likely short-lived due to the rapid evaporation resulting from the shallow soils and lack of recharge from seepage from sand dunes. In summary, the distribution patterns of shallow- and deep-rooted plant species at strand and inland dune sites were also likely influenced by factors other than soil depth, such as interspecific competition and habitat requirements. While some species had a distinct affinity for either shallow or deep soils, others exhibited atypical distributions that could be explained by their unique adaptations and competitive capabilities.

Similarly, the responses of the woody shrub *T. fruticosa*, perennial herb *C. pugioniformis* and annual herb *O. suffruticosum* were not affected by differences in soil depth across strand and inland dune sites. *Tetragonia fruticosa*, highly palatable to herbivores, increased from medium to high cover at strand sites and from low to high cover at inland dune sites. In contrast, *C. pugioniformis* and *O. suffruticosum*, which are less palatable and unpalatable, decreased from high to low cover at both strand and inland dune sites. However, it is the adaptable root systems of these species that most likely allowed them to thrive in both deep and shallow soil. This characteristic explains why soil depth had no significant effect on their distribution and responses. *Tetragonia fruticosa* has a well-developed root system composed of long spreading roots that can be shallow or deep depending on soil depth and hardness (van Breda and Barnard 1991). Similarly, *O. suffruticosum* has a flexible root system consisting of a slender taproot with numerous fibrous branching laterals (Government of South Australia n.d.). *Conicosia pugioniformis* plants have small root systems that expand annually where there is room for expansion (South African National Biodiversity Institute 2022). Therefore, individuals in *C. pugioniformis* populations can maintain small roots in shallow soil or develop large roots in deep soil (South African National Biodiversity Institute 2022). *Tetragonia fruticosa* exhibited an increase in cover from medium to high levels in strand sites, whereas low cover was observed in inland dune sites. This difference could be attributed to heavier browsing of woody shrubs by rabbits in the inland sites, owing to the greater amount of vegetation cover. Caravaggi (2018) reported that rabbit herbivory is more severe in areas with greater vegetation cover, as these areas are used by the animals for concealment and cover. Furthermore, the felled wood from a cleared *Eucalyptus* trees that had previously covered part of the inland dune sites had been piled on site for a period before rabbit control, which may have provided additional shelter for rabbits (see Chapter 5).

Vegetation diversity response under *Eucalyptus* plantations

In contrast to the differences in species dynamics between strand and inland dune sites, which were primarily caused by differences in soil depth, the lack of change in vegetation diversity at eucalyptus sites was most likely caused by the inhibitory effects of the alien *Eucalyptus* trees on understory vegetation dynamics. Eucalyptus plantations suppress understory vegetation through shading (Loumeto, et al. 1997), allelopathy (Sasikumar, et al. 2001, Khan, et al. 2008 , Zhang, et al. 2010), accumulation of slow-decomposing litter (Bacon, et al. 1993 , Barbier, et al. 2008), and alteration of nutrient cycling regimes (Bernhard-Reversat 1996, Guo, et al. 2001, Marchante, et al. 2008), resulting in lower soil nutrient content, pH and base saturation (Alexander 1989, Guo and Sims 2001, Marchante, et al. 2008 , Zhang, et al. 2010). Furthermore, *Eucalyptus* trees rapidly deplete soil moisture after rainfall events (Le Maitre, et al. 2002, Dye, et al. 2004, Dye, et al. 2007) due to their high-water consumption rates and dense near-surface roots (del Moral, et al. 1969).

In the case of our sites, *Eucalyptus* trees appear to have inhibited the response of the four species (*C. natans*, *T. fruticosa*, *O. pes-caprae* and *P. canaliculatus*,) which maintained low cover before and after rabbit control by creating drier-than-normal soil moisture conditions and shading understory vegetation. The ephemeral herb *C. natans* and woody shrub *T. fruticosa* require high soil moisture conditions to germinate (Toelken 1981, van Breda and Barnard 1991), while the perennial herbs *O. pes-caprae* and *P. canaliculatus* perform poorly under shade (Verdaguer, et al. 2010, UWC Cape Flats Indigenous Nursery 2021). *Crassula natans*, *T. fruticosa*, *O. pes-caprae* and *P. canaliculatus* may have established at the eucalyptus sites due to unique adaptations to the environmental conditions at the sites, such the ability to tolerate low light levels, dry soil conditions, acidic soils, and the presence of terpenes in the soil. However, the limited ability of the annual herbs *C. natans* and *O. pes-caprae* to compete with other plant species for essential soil resources, due to their relatively shallow root systems, likely led to their exclusion from more diverse plant communities at strand and inland dune sites.

Impact of residual non-rabbit herbivory on vegetation diversity response

Unlike our hypothesis that rabbit control would increase species diversity, the results, however, supported our prediction that residual non-rabbit herbivory would maintain vegetation diversity following rabbit control by preventing less competitive species from being completely displaced by re-establishing more competitive palatable species. This is because, even though recovering palatable species displaced several unpalatable and less palatable species from strand and inland dune sites following rabbit control, many of the latter species (*C. pugioniformis*, *O. suffruticosum*, *B. diandrus*, *Z. aethiopica*, *S. cretica*, *A. capensis*, *C. capensis* and *Isolepis sp.*) persisted. The less palatable and unpalatable species that persisted after rabbit control were all poor inter-specific competitors that need disturbed and open conditions to germinate and establish (e.g., *C. pugioniformis* (Schmalzer and Hinkle 1987), *O. suffruticosum* (Anon 2014), *B. diandrus* ((Jackson, et al. 2006), *Z. aethiopica* (Adamson 1934), *S. cretica* (Vural and Dönmez 2002, Blasi, et al. 2014), *A. capensis* (Adamson 1934), *C. capensis* (Adamson 1934) and *Isolepis sp.* (Tshiila 2012)), just like the species that were displaced. However, remnant non-rabbit herbivory on the island appears to have moderated the recovery of more competitive palatable species, resulting in the existence of residual open habitats in which less competitive species could persist. It is likely that the persistent species then outcompeted and displaced other less competitive unpalatable and less palatable species to occupy these residual open habitats. Indeed, when compared with displaced species, the species that persisted after rabbit control were better interspecific competitors. For instance, the perennial herb *C. pugioniformis* forms dense mats of vegetation that prevent other plants from growing and can survive extreme environmental conditions such as high temperatures, low water availability, and high salinity by switching between Crassulacean acid metabolism (CAM) and C3 photosynthesis (California Invasive Plant Council 2022). In addition, the annual herb *O. suffruticosum*, grows well in dry conditions and releases chemicals that inhibit the growth of competitors (Anon 2014). The annual herb *S. cretica* has large, fibrous, and fast-growing roots that give it a competitive advantage over other species when competing for soil moisture and nutrients (Arnone II and Kestenholz 1997). Finally, the annual and perennial herbs *Isolepis* sp. and *Z. aethiopica* would have benefited from low inter-specific competition in their specialised habitats of waterlogged depressions and shallow standing water (Jackson 1986, Tshiila 2012).

Further research using experimental exclosure plots could provide a more direct assessment of the impact of residual non-rabbit herbivory on the island's vegetation species diversity. A short-term increase in species diversity within exclosure plots would indicate residual herbivory pressure still above the optimal intermediate level, while a decline would indicate herbivory pressure below the intermediate level (see discussion on the intermediate disturbance hypothesis (IDH) in the Introduction). This is because, in the short term, exclusion of vegetation under the former condition would add re-established formerly suppressed palatable species to the vegetation, whereas exclusion under the latter would only facilitate further displacement of less competitive species by more competitive palatable species (see Introduction). A lack of change in species diversity in exclosure plots in the short term would imply that the island's residual herbivory pressure was currently at an appropriate intensity for biodiversity promotion, i.e., at the optimal intermediate level. However, species diversity in the exclosure plots under all the above initial conditions would eventually decline as more competitive palatable species progressively displace less competitive species from enclosed vegetation as time elapses (see Introduction).

Effect of rabbit control on alien plant species richness and abundance

Reducing the richness and abundance of alien plant species is an important goal of many invasive European rabbit eradication programs. This is because invasive European rabbits often increase the number and abundance of alien plant species by creating environmental conditions that facilitate their invasion (Tiver, et al. 1997, Eldridge, et al. 2002, Denham, et al. 2004, Eldridge, et al. 2006, Parker, et al. 2006 , Williams 2011, Schweizer, et al. 2016). Consequently, controlling or removing European rabbits typically results in a decrease in the richness and cover of alien plant species, as the beneficial effects of rabbit activity on their establishment diminish or cease. This was evident across our study sites, where many of the plant species that disappeared after rabbit control (*A. arvensis*, *E. peplus*, *H. glabra*) were alien. Overall, the number of alien plant species across our sites decreased from five (*A. arvensis*, *E. peplus*, *H. glabra*, *B. diandrus* and *S. cretica*) to two (*B. diandrus* and *S. cretica*) species because of rabbit control.

The mechanism underlying the decrease in the richness and cover of alien plant species at our sites was clearly linked to the effects of reduced herbivory pressure on interspecific competition between alien and recovering native species. Except for *B. diandrus* and, to a lesser extent, *S. cretica*, most of the alien species that were present at our sites prior to rabbit control were less palatable or unpalatable low-growing shallow-rooted small annual herbs that require or prefer full sunlight for establishment and growth (e.g., *A. arvensis* (Anon 2017a, Rothwell and Marshall 1986, Rivero, et al. 2001), *E. peplus* (Bullock 1952, Gillham 1963, Esler 1980, Simmonds, et al. 2000), *H. glabra* (Cowan 1945, van Dyne and Heady 1965, Struik 1967, Anon 2017b, Global Biodiversity Information Facility (GBIF) 2022)).

Plant species that emerged or increased in cover following rabbit control (*T. fruticosa*, *E. longiflora*, *E. villosa* and *C. dactylon*), on the other hand, were all native and, in general, strong interspecific competitors for light, space, soil nutrients and moisture (Gillham 1963, Kumar and Abrol 1982, van Breda and Barnard 1991, Horowitz 1996, Harrington, et al. 1998, Halvorson and Guertin 2003b, Hoffman, et al. 2009). Rabbit herbivory would have allowed the less competitive and unpalatable or less palatable alien species to establish and persist on herbivory-created open habitats across our study sites by reducing competition from the more competitive and palatable native species. As a result, the recovery of the more competitive palatable native species following rabbit control would have resulted in the displacement of less competitive alien species due to interspecific competition.

However, not all invasive species were displaced by the recovery of more competitive palatable native species after rabbit control. The alien annual grass *B. diandrus* decreased from high to medium cover at inland dune sites while maintaining low cover at strand sites following rabbit control, while the annual herb *S. cretica* maintained low cover at strand sites before and after rabbit control. This was most likely because *B. diandrus* and *S. cretica* are stronger interspecific competitors than the other displaced alien species and would have been able to withstand competition from recovering native palatable species. *Bromus diandrus* is tall and can compete with native species for space and soil moisture due to its early germination, high density and deep roots (Menke 1992, Jackson, et al. 2006), whereas *S. cretica* is short (Anon 2017f), but has large fast-growing fibrous root systems that inhibit positive biomass response in other species (Arnone II and Kestenholz 1997).

In summary, our results demonstrated that controlling European rabbit herbivory effectively reduced the richness and cover of alien plant species at our sites. This decrease was attributed to reduced herbivory pressure, allowing recovering native palatable species to outcompete less competitive alien species. However, some invasive species, such as *B. diandrus* and *S. cretica*, displayed resilience, likely due to their strong competitive abilities, leading to ongoing coexistence with recovering native species. Our results underscore the crucial role of managing rabbit populations in preserving native plant diversity and curbing the proliferation of invasive alien species.

Future research needs

Our research has revealed that efforts to control rabbit herbivory on Robben Island did not lead to an increase in vegetation species diversity but rather resulted in a decline. This decline was a consequence of over 370 years of European rabbit herbivory, which had degraded the island's vegetation by eliminating many original species, leaving behind only a few palatable native species capable of withstanding or escaping rabbit herbivory, along with numerous unpalatable weedy species. Consequently, attempts to control rabbit herbivory led to reduced vegetation species diversity, as several less ecologically competitive unpalatable species were outcompeted and displaced by the few recovering palatable species.

However, the robustness of these findings remains uncertain, as they might have been influenced by the time gap between the implementation of rabbit control on the island and our assessment of vegetation response (see Schweizer, et al. 2016). Generally, longer intervals between rabbit control and vegetation assessment offer greater opportunities for eliminated species to disperse back to affected areas. Given the degraded state of vegetation on Robben Island, the four-year monitoring period of vegetation diversity response following rabbit control might have been insufficient for previously eliminated palatable species to re-establish at our sites through natural dispersal from refugia on the island or from the mainland. Consequently, it is reasonable to assume that our results would have varied if species diversity response had been assessed at later times after rabbit control. Therefore, further monitoring of vegetation species diversity response on the island is necessary to assess the robustness of our results. Such monitoring would clarify, among other aspects, whether the removal of European rabbits can be considered sufficient or insufficient in facilitating the complete recovery of plant species diversity on the island. It would also determine whether additional restoration measures, such as replanting or reseeding missing native palatable species, are necessary to ensure the full recovery of plant species diversity.

While our results indicate that palatable species less resilient to heavy rabbit herbivory have been removed from our study sites due to prolonged rabbit herbivory, it remains uncertain whether these species have been locally eliminated from the sites or from the entire island. The former scenario is highly unlikely given the island’s small size and the absence of previously non-existent palatable species at our sites following rabbit control. Although species that spread vegetatively will take a long time to reach affected areas, many other palatable species that spread through seed and wind dispersal would have quickly recolonised the sites. Robben Island is roughly 7 km away from the mainland, separated by the South Atlantic Ocean, making it likely that options for the dispersal of palatable species from the mainland are limited. Thus, our results likely represent the permanent response of vegetation species diversity to rabbit control.

Conclusion

Despite expectations, rabbit control did not lead to an increase in vegetation species diversity on Robben Island. In fact, species diversity either remained the same or decreased across all study sites. Rabbit control resulted in a reduction in species diversity at strand and inland dune sites due to the disappearance of seven less palatable and unpalatable species (*A. arvensis*, *E. peplus*, *H. glabra*, *W. androsacea*, *E. australis*, *O. viride* and *Trachyandra* sp.) as they were outcompeted by four recovering palatable species (*T. fruticosa*, *E. longiflora*, *E. villosa* and *C. dactylon*). At eucalyptus sites, species diversity did not change as four species (*C. natans*, *T. fruticosa*, *O. pes-caprae* and *P. canaliculatus*) maintained low coverage before and after rabbit control. Species evenness declined across strand and inland dune sites in response to rabbit control. Following rabbit control, species cover at strand and inland dune sites shifted from being dominated by four species (*C. pugioniformis*, *O. suffruticosum*, *E. peplus*, and *A. arvensis*), and six species (*O. viride*, *E. australis*, *Trachyandra* sp., *O. suffruticosum*, *C. pugioniformis*, and *B. diandrus*) respectively, to being dominated by two species (*T. fruticosa* and *E. longiflora*) at strand sites, and two species (*T. fruticosa* and *E. villosa*) at inland dune sites. The unexpected results at strand and inland dune sites may be due to the degraded condition of vegetation on the island, caused by more than 350 years of continuous rabbit herbivory. During this period, rabbit herbivory eliminated many palatable species from the vegetation, leaving only a few palatable species that could withstand or escape rabbit herbivory and numerous less palatable and unpalatable species. Since the palatability of a plant species to European rabbits is positively related to its competitive ability, the recovery of the four palatable species across the sites in response to reduced herbivory pressure probably resulted in the displacement of seven less competitive, unpalatable species through increased interspecific competition. Some of the less palatable and unpalatable plant species that were displaced from strand and inland dune sites were alien (i.e., *A. arvensis*, *E. peplus*, *H. glabra*). The lack of change in vegetation diversity at eucalyptus sites was most likely due to the inhibitory effects of the alien *Eucalyptus* trees on understory vegetation dynamics.

While South African offshore islands exhibit diverse geology, sizes, distances from the mainland, and climatic conditions, we predict that species diversity across these islands will respond similarly to rabbit control as observed on Robben Island. This is because they have faced similar durations and intensities of rabbit herbivory (Cooper, et al. 1982). Consequently, we expect an initial decline in species diversity across the islands due to the loss of some unpalatable species, outcompeted by resurgent palatable ones. However, as on Robben Island, this initial decline would be followed by a long-term increase in diversity as extirpated palatable and late-successional species recolonise from the seed bank or mainland. However, although Robben Island and other distant invaded islands might experience a long-term decline in diversity after rabbit control, islands closer to the mainland – such as Jutten, Schaapen, and Vondeling – might see faster recolonisation by extirpated species, potentially mitigating the decline. While the general pattern of species diversity response to rabbit control may be similar across the islands, the specific plant species involved and their roles will differ due to each island's unique composition (see, for example, Gillham 1963). Similarly, as on Robben Island, species responses to rabbit control will also vary across the landscapes of those islands with sufficient habitat heterogeneity, influenced by environmental factors such as soil depth and vegetation structure.

References

Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

Alexander JM. 1989. The long-term effect of *Eucalyptus* plantations on tin-mine spoil and its implication for reclamation. *Landscape and Urban Planning* 17: 413–433.

Anon. 2014. Declared Plant Policy under the Natural Resources Management Act 2004. Calomba daisy (*Oncosiphon suffruticosum*). Government of South Australia.

Anon. 2017a. *Anagallis arvensis* (scarlet pimpernel). CABI Invasive Species Compendium. Available at http://www.cabi.org/isc/datasheet/5352. [accessed 15 September 2017]

Anon. 2017b. *Emex australis* (Doublegee). CABI Invasive Species Compendium. Available at http://www.cabi.org/isc/datasheet/20826. [accessed 15 September 2017]

Anon. 2017c. *Euphorbia peplus*. Identic Pty Ltd. Available at https://keyserver.lucidcentral.org/weeds/data/media/Html/euphorbia_peplus.htm. [accessed 15 September 2017]

Anon. 2017d. Flora of North America. *Hypochaeris glabra* Linnaeus. eFlora.org. Available at http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=250005015. [accessed 15 September 2017]

Anon. 2017e. *Ornithoglossum*. Pacific Bulb Society. Available at http://pacificbulbsociety.org/pbswiki/index.php/Ornithoglossum. [accessed 15 September 2017]

Anon. 2017f. *Silene cretica*. Hortipedia. The GardenInfoPortal. Available at http://en.hortipedia.com/wiki/Silene_cretica#Characteristics. [accessed 15 September 2017]

Anon. 2017g. *Sonchus oleraceus* (common sowthistle). CABI Invasive Species Compendium. Available at http://www.cabi.org/isc/datasheet/50584. [accessed 15 September 2017]

Anon. 2017h. *Wahlenbergia androsacea* A. DC.: Encyclopedia of Life. Available at http://www.eol.org/pages/5134842/overview. [accessed 15 September 2017]

Anon. 2022. Bihrmann's Caudiforms: *Ornithoglossum viride*. Available at http://www.bihrmann.com/caudiciforms/subs/orn-vir-sub.asp. [accessed 20 June 2022]

Apps P. 1984. Cats on Dassen Island. *Acta Zoologica Fennica* 172: 115-116.

Arnone II JA, Kestenholz C. 1997. Root competition and elevated CO_2: effects on seedling growth in *Linum usitatissimum* populations and *Linum–Silene cretica* mixtures. *Functional Ecology* 11: 209-214.

Austin MP, Williams OB, Belbin L. 1981. Grassland dynamics under sheep grazing in an Australian Mediterranean type climate. *Vegetatio* 47: 201-211.

Bacon PE, Stone C, Binns DL, Leslie DJ, Edwards DW. 1993 Relationships between water availability and *Eucalyptus camaldulensis* growth in a riparian forest *Journal of Hydrology* 150: 541-561.

Barbier S, Gosselin F, Balandier P. 2008 Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests. *Forest Ecology and Management* 254 1-15.

Barbraud C, Delord K, Le Bouard F, Harivel R, Demay J, Chaigne A, Micol T. 2021. Seabird population changes following mammal eradication at oceanic Saint-Paul Island, Indian Ocean. *Journal for Nature Conservation* 63: 126049.

Bello-Rodríguez V, Mateo RG, Pellissier L, Cubas J, Cooke B, González-Mancebo JM. 2021. Forecast increase in invasive rabbit spread into ecosystems of an oceanic island (Tenerife) under climate change. *Ecological Applications* 31: e02206.

Bernhard-Reversat F. 1996. Nitrogen cycling in tree plantations grown on a poor sandy savanna soil in Congo. *Applied Soil Ecology* 4: 161–172.

Blasi C, Capotorti G, Copiz R, Guida D, Mollo B, Smiraglia D, Zavattero L. 2014. Classification and mapping of the ecoregions of Italy. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* 148: 1255-1345.

Box G, Cox D. 1964. An analysis of transformations. *Journal of the Royal Statistical Society* 26: 211-234.

Brooke RK, Crowe TM. 1982. Variation in species richness among the offshore islands of the southwestern Cape. *South African Journal of Zoology* 17: 49-58.

Brooke RK, Prins AJ. 1986. Review of alien species on South African offshore islands. *South African Journal of Antarctic Research* 16: 102-109.

Brower JC, Kile KM. 1988. Seriation of an original data matrix as applied to palaeoecology. *Lethaia* 21: 79-93.

Bullock AA. 1952. South African poisonous plants. *Kew Bulletin* 7: 117-129.

Burrows CJ, Wilson HD, Meurk CD. 1999. The ecological restoration of Otamahua/Quail Island 2. The vascular land flora and vegetation. *New Zealand Natural Sciences* 24: 127-150.

Burton GW, Hook JE, Butler JL, Hellwig R. 1988. Effect of temperature, daylength and solar radiation on production of coastal bermuda grass. *Agronomy Journal* 80: 557–560.

Buzas MA, Gibson TG. 1969. Species diversity: benthonic foraminifera in western North Atlantic. *Science* 163: 72-75.

Buzas MA, Hayek L-AC. 2005. On richness and evenness within and between communities. *Paleobiology* 31: 199-220.

California Invasive Plant Council. 2022. *Conicosia pugioniformis*. Available at https://www.cal-ipc.org/resources/library/publications/ipcw/report31/. [accessed 2 November 2022]

Caravaggi A. 2018. Lagomorpha Navigation. In: Vonk J, Shackelford T editors. *Encyclopedia of Animal Cognition and Behavior*. Cham: Springer International Publishing. p. 1-5.

Carro F, Ortega M, Soriguer RC. 2019. Is restocking a useful tool for increasing rabbit densities? *Global Ecology and Conservation* 17: e00560.

Chao A. 1984. Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11: 265-270.

Christodoulakis D. 1996. The Flora of Ikaria (Greece, E. Aegean Islands). *Phyton (Horn, Austria)* 36: 63-91.

Coetzee K. 2008. Blaauwberg Conservation Area: management guidelines for larger wildlife and their habitats. *Report prepared for the Biodiversity Management Branch, City of Cape Town*.

Cooke BD. 1991. Rabbits: indefensible on any grounds. *Search* 22: 193–194.

Cooper J, Brooke RK. 1982. Past and present distribution of the feral European rabbit *Oryctolagus cuniculus* on southern African offshore islands. *South African Journal of Wildlife Research* 12: 5-71.

Corr BE. 1993. *Zantedeschia* research in the United States: past, present and future. *Acta Horticulturae* 337: 177-188.

Courchamp F, Chapouis JL, Pascual M. 2003. Mammal invaders on islands: impacts, control and control impact. *Biological Reviews* 78: 347-383.

Cowan IA. 1945. The ecological relationship of the food of the Columbian black-tailed deer, *Odocoileus hemionus columbianus* (Richardson), in the coast forest region of Southern Vancouver Island, British Columbia. *Ecological Monographs* 15: 109-139.

Crawford R, Dyer B. 2000. Wildlife of Robben Island. In: Underhill L editor. *Bright Continent Guide*. Cape Town: Avian Demography Unit.

Crawley MJ. 1990. Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology* 27: 803-820.

Cubas J, Martín-Esquivel JL, Nogales M, Irl SDH, Hernández-Hernández R, López-Darias M, Marrero-Gómez M, del Arco MJ, González-Mancebo JM. 2018. Contrasting effects of invasive rabbits on endemic plants driving vegetation change in a subtropical alpine insular environment. *Biological Invasions* 20: 793-807.

Cubas J, Severin DH, Villafuerte R, Bello-Rodríguez V, Rodríguez-Luengo JL, del Arco M, Martín-Esquivel JL, González-Mancebo JM. 2019. Endemic plant species are more palatable to introduced herbivores than non-endemics. *Proceedings of the Royal Society B: Biological Sciences* 286: 20190136.

Davies S, Jordaan M, Karsten M, Terblanche J, Turner A, van Wilgen N, Veldtman R, Zengeya T, Measey J. 2020. Experience and lessons from alien and invasive animal control projects in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology*. Cham: SpringerOpen. p. 1302-1381.

Dawson TJ, Ellis BA. 1979. Comparison of the diets of yellow-footed rock-wallabies and sympatric herbivores in western New South Wales. *Wildlife Research* 6: 245-254.

de Villiers MS, Mecenero S, Sherley RB, Heinze E, Kieser J, Leshoro TM, Merbold L, Nordt A, Parsons NJ, Peter HU. 2010. Introduced European rabbits (*Oryctolagus cuniculus*) and domestic cats (*Felis catus*) on Robben Island: Population trends and management recommendations. *South African Journal of Wildlife Research* 40: 139-148.

de Villiers SA. 1971. *Robben Island: Out of reach, out of mind. A history of Robben Island*. Cape Town: Struik.

de Vos A, Manville RH, Van Gelder RG. 1956. Introduced mammals and their influence on native biota. *Zoologica (New York)* 41: 163-194.

de Wet H, Tilney PM, van Wyk BE. 2002. Vegetative morphology and anatomy of *Cissampelos* in South Africa. *South African Journal of Botany* 68: 181-190.

del Moral R, Muller CH. 1969. The allelopathic effect of *Eucalyptus camaldulensis American Midland Naturalist* 83: 254–282.

Delibes-Mateos M, Farfán MÁ, Rouco C, Olivero J, Márquez AL, Fa JE, Vargas JM, Villafuerte R. 2018. A large-scale assessment of European rabbit damage to agriculture in Spain: Agricultural damage by rabbits in Spain. *Pest Management Science* 74: 111-119.

Delibes M, Redpath SM, Angulo E, Ferreras P, Villafuerte R. 2007. Rabbits as a keystone species in southern Europe. *Biological Conservation* 13: 149-156.

Denham AJ, Auld TD. 2004. Survival and recruitment of seedlings and suckers of trees and shrubs of the Australian arid zone following habitat management and the outbreak of rabbit calicivirus disease (RCD). *Austral Ecology* 29: 585-599.

Diaz A. 2000. Can plant palatability trials be used to predict the effect of rabbit grazing on the flora of ex-arable land? *Agriculture, Ecosystems & Environment* 78: 249-259.

DiTomaso JM, Kyser GB, Oneto SR, Wilson RG, Orloff SB, Anderson LW, Wright SD, Roncoroni JA, Miller TL, Prather TS (eds). 2013. *Weed control in natural areas in the Western United States*. Weed Research and Information Center, University of California. Davis.

Donlan JC, Tershy BR, Croll DA. 2002. Islands and introduced herbivores: conservation action as ecosystem experimentation *Journal of Applied Ecology* 39: 235-246.

du Toit PCV. 2002. Objektiewe weidingswaardes van Nama-Karooplantegroei, grasse en bossies van die Karoo. *Grootfontein Agric* 4: 8-18.

Durbin J, Watson GS. 1951. Testing for serial correlation in least squares regression. *Biometrika* 37: 409-428.

Dye P, Jacobs S, Drew D. 2004. Verification of 3-PG growth and water-use predictions in twelve *Eucalyptus* plantation stands in Zululand, South Africa *Forest Ecology and Management* 193: 197-218.

Dye P, Versfeld D. 2007. Managing the hydrological impacts of South African plantation forests: An overview. *Forest Ecology and Management* 251: 121-128.

El-Lakany MH. 2002. Guest editorial - Special issue: Forestry and small island developing states. *International Forestry Review* 4: ii-iii.

El Mokni R, Hédi El Aouni M. 2012. *Zantedeschia aethiopica* (Araceae) a new species naturalized in the Northwest of Tunisia. *Flora Mediterranea* 22: 191-196.

Eldridge DJ, Costantinides C, Vine A. 2006. Short-term vegetation and soil responses to mechanical destruction of rabbit (*Oryctolagus cuniculus* L.) warrens in an Australian box woodland. *Restoration Ecology* 14: 50-59.

Eldridge DJ, Simpson R. 2002. Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands. *Basic and Applied Ecology* 3: 19-29.

Esler AE. 1980. Botanical features of Motutapu, Motuihe, and Motukorea, Hauraki Gulf, New Zealand. *New Zealand Journal of Botany* 18: 15-36.

Esler AE. 1987. The naturalisation of plants in urban Auckland, New Zealand 3. Catalogue of naturalised species. *New Zealand Journal of Botany* 25: 539-558.

Esler KJ, Jacobsen AL, Pratt RB. 2018. *The biology of Mediterranean-type ecosystems*. Oxford University Press.

Farrow EP. 1917. On the ecology of the vegetation of Breckland. III. General effects of rabbits on the vegetation. *Journal of Ecology* 5: 1-18.

Fehmi JS. 2010. Confusion among three common plant cover definitions may result in data unsuited for comparison. *Journal of Vegetation Science* 21: 273-279.

Fenton EW. 1940. The influence of rabbits on the vegetation of certain hill-grazing districts of Scotland. *Journal of Ecology* 28: 438-449.

Finlayson G, Taggart P, Cooke B. 2021. Recovering Australia's arid-zone ecosystems: learning from continental-scale rabbit control experiments. *Restoration Ecology* 30: e13552.

Fisher JL, Loneragan WA, Dixon K, Veneklaas EJ. 2009. Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. *Biological Conservation* 142: 256-269.

Foran BD. 1986. The impact of rabbits and cattle on an arid calcareous shrubby grassland in central Australia. *Vegetatio* 66: 49-59.

Foran BD, Low WA, Strong BW. 1985. The response of rabbit populations and vegetation to rabbit control on a calcareous shrubby grassland in central Australia. *Wildlife Research* 12: 237-247.

Friedel MH. 1985. The population structure and density of central Australian trees and shrubs, and relationships to range condition, rabbit abundance and soil. *Australian Journal of Wildlife Research* 7: 130-139.

Germishuizen G, Meyer NL. 2003. *Plants of southern Africa: an annotated checklist*. Pretoria: National Botanical Institute.

Gillham EM. 1955. Ecology of the Pembrokeshire Islands. III. The effect of grazing on the vegetation. *Journal of Ecology* 43: 172-207.

Gillham ME. 1963. Some interactions of plants, rabbits and sea-birds on South African islands. *Journal of Ecology* 51: 275-294.

Gillison AN, Brewer KR. 1985. The use of gradient directed transects or gradsects in natural resource surveys. *Journal of Environmental Management* 20: 103-127.

Global Biodiversity Information Facility (GBIF). 2022. *Hypochaeris glabra* L. Available at https://www.gbif.org [accessed 12 January 2022]

Government of South Australia (ed). n.d. *Declared Weed Sheet: Calomba Daisy (Oncosiphon suffruticosum)*. South Australian Murray-Darling Basin Natural Resources Management Board. Murray Bridge, South Australia.

Guglielmini AC, Satorree H. 2002. Shading effects on spatial growth and biomass partitioning of *Cynodon dactylon*. *Weed Research* 42: 123-134.

Guo LB, Sims REH. 2001. Effects of light, temperature, water and meat works effluent irrigation on eucalypt leaf litter decomposition under controlled environmental conditions. *Applied Soil Ecology* 17: 229–237.

Halvorson WL, Guertin P. 2003a. Factsheet for: *Avena fatua* L. . *USGS Weeds in the West project: status of introduced plants in Southern Arizona parks*. Tucson: U.S. Geological Survey / Southwest Biological Center.

Halvorson WL, Guertin P (eds). 2003b. *Factsheet for: Cynodon dactylon (L.) Pers.* U.S. Geological Survey / Southwest Biological Center. Tucson.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Palaeontological Statistics Software Package for Education and Data Analysis. *Available at http://palaeo-electronica.org/2001/past/issue101.htm [Accessed 24 August 2010]*.

Harrington KC, Hodder LM, Outred HA. 1998. Biology and control of pypgrass. Paper presented at the Proceedings of the 51st New Zealand Plant Protection Conference.

Hayek L-AC, Buzas MA. 2010. *Surveying natural populations; quantitative tools for assessing biodiversity*. New York: Columbia University Press.

Heneidy SZ. 2002. Role of indicator range species as browsing forage and effective nutritive source in Matruth, a Mediterranean coastal region, NW-Egypt. *Online Journal of Biological Sciences* 2: 136-142.

Herrick JE, van Zee JW, Havstad KM, Burkett LM, Whitford WG. 2005. *Monitoring manual for grassland, shrubland and savanna ecosystems: Volume 1 Quickstart*. Las Cruces: USDA-ARS Jornada Experimental Range.

Hertling UM. 1997. *Ammophila arenaria* (l.) Link (Marram grass) in South Africa and its potential invasiveness. DPhil, Rhodes University, Grahamstown.

Hobbs RJ, Grace J. 1981. A study of pattern and process in coastal vegetation using principle components analysis. *Vegetatio* 44: 137-153.

Hoffman MT, Carrick PJ, Gillson L, West AG. 2009. Drought, climate change and vegetation response in the succulent karoo, South Africa. *South African Journal of Science* 105: 54-61.

Horowitz M. 1996. Bermuda grass (*Cynodon dactylon*): a history of the weed and its control in Israel. *Phytoparasitica* 24: 305-320.

Hunt LP. 2001. Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. *Journal of Applied Ecology* 38: 238–252.

Hyde IIA, Wursten BT, Ballings P. 2014. *Torilis arvensis* (Huds.) Link Available at http://www.zimbabweflora.co.zw/speciesdata/species.php?speciesid=143050 [accessed 22 January 2023]

Jackson N, Cudney D, DiTomaso J, C. B, Lee V, Drewitz J, Bossard S, Randall L, Hansen-Winter B, Faber P*, et al.* 2006. *Invasive plants of California's wildland*. California Invasive Plant Council.

Jackson WPU. 1986. The Cape white arum lily, *Zantedeschia aethiopica*. *Veld & Flora* 72: 44-45.

Johnson DH. 2002. The importance of replication in wildlife research. *The Journal of Wildlife Management* 66: 919-932.

Jost L. 2006. Entropy and diversity. *Oikos* 113: 363-375.

Khan MA, Hussain I, Khan EA. 2008 Allelopathic effects of *Eucalyptus* (*Eucalyptus camaldulensis* L.) on germination and seedling growth of wheat (*Tricum aestivum* L.). *Pakistan Journal of Weed Science Research* 14: 9-18.

Kier G, Kreft H, Ming Lee T, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W. 2009. A global assessment of endemism and species richness across island and main land regions. . *Proceedings of the National Academy of Sciences of the United States of America* 106: 9322-9327.

Knevel IC. 2001. The life history of selected coastal foredune species of South Africa. DPhil, Rhodes University.

Kumar A, Abrol IP. 1982. Relative tolerance of grasses to sodic soils. *Indian Farming* 32: 41-43.

Kumar V, Kumari E. 2019. A report on *Emex australis* Steinh.- An emerging weed problem of wheat at Faridabad region of Haryana. *Journal of Crop and Weed* 15: 144-147.

Lange RT, Graham CR. 1983. Rabbits and the failure of regeneration in Australian arid zone *Acacia*. *Australian Journal of Ecology* 8: 377-381.

Latham ADM, Latham MC, Norbury GL, Forsyth DM, Warburton B. 2020. A review of the damage caused by invasive wild mammalian herbivores to primary production in New Zealand. *New Zealand Journal of Zoology* 47: 20-52.

Latzel V, Malíková L, Klimešová J. 2011. Compensatory growth of *Euphorbia peplus* regenerating from a bud bank. *Botany* 89: 313-321.

Le Maitre DC, van Wilgen BW, Gelderblom C, Bailey C, Chapman R, Nel J. 2002. Invasive alien trees and water resources in South Africa: case studies of the costs and benefits of management *Forest Ecology Management* 160: 143-159.

Le Roux A. 2005. *Namaqualand – South African Wild Flower Guide 1*. Cape Town: Botanical Society of South Africa.

Leigh JH, Wood DH, Holgate MC, Slee A, Stanger MG. 1989. Effects of rabbit and kangaroo grazing on two semi-arid grass- land communities in central-western New South Wales. *Australian Journal of Botany* 37: 375-396.

Lever C. 1985. *Naturalised mammals of the world*. London: Longman.

Lewin RA. 1948. Biological flora of the British Isles: Sonchus L. (*S. oleraceus L.* and *S. asper* (L.) Hill). *Journal of Ecology* 36 203-223.

Lloyd JW, Linger MT. 1986. Report on the vegetation of Robben Island. *'n Natuurbewaringsondersoek van Robbeneiland*. Cape Town: Cape Nature

Long JL. 2003. *Introduced mammals of the world: their history, distribution and influence*. Collingwood: CSIRO Publishing.

Loumeto JJ, Huttel C. 1997. Understory vegetation in fast-growing tree plantations on savanna soils in Congo. *Forest Ecology and Management* 99: 65–81.

Louw G, Beukes T. 1988. Ken ons veldplante. *Die Noordwester*: 6-12.

Mace G, K N, Fitter A. 2012. Biodiversity and ecosystem services: a multilayered relationship. *Trends in Ecology & Evolution* 27: 19-26.

Magurran AE. 2004. *Measuring biological diversity*. Oxford: Blackwell Publishing.

Marchante E, Kjoller A, Struwe S, Freitas H. 2008 Short- and long- term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. *Applied Soil Ecology* 40: 210–217.

Marín-García PJ, Llobat L. 2021. What are the keys to the adaptive success of European Wild Rabbit (*Oryctolagus cuniculus*) in the Iberian Peninsula? *Animals* 11: 2453.

McCune B, Grace JB, Urban DL. 2002. *Analysis of ecological communities* Gleneden Beach: MjM Software Design.

McGill BJ, Dornelas M, Gotelli NJ, Magurran AE. 2015. Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology & Evolution* 30: 104-113.

Measey J, Hui C, Somers MJ. 2020. Terrestrial vertebrate invasions in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology* No. 14. Cham, Swtzerland: Springer Open. p. 115-151.

Menke JW. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia* 20: 22-25.

Mfitumukiza D. 2004. Evaluating rangeland potentials for cattle grazing in a mixed farming system. MSc, International Institute for Geo-Information Science and Earth Observation, Enschede.

Moore CB, Moore JH. 2007. Annual veldgrass: *Ehrarta longiflora* Smith. HerbiGuide - The Pesticide Expert on a Disk Available at http://www.herbiguide.com.au/Descriptions/hg_Annual_Veldtgrass.htm. [accessed 25 September 2017]

Moore G. 2001. Soil guide. A handbook for understanding and managing agricultural soils. *Agriculture Western Australia Bulletin No. 4343*.

Mucina L, Adams JB, Knevel IC, Rutherford MC, Powrie LW, Bolton JJ, van der Merwe JH, Anderson RJ, Bornman TG, le Roux A*, et al.* 2006. Coastal vegetation of South Africa. In: Mucina L, Rutherford MC editors. *The vegetation of South Africa, Lesotho and Swaziland*. *Strelitzia 19*. Pretoria: South African National Biodiversity Institute.

Mucina L, Rutherford M (eds). 2006. *Vegetation map of South Africa, Lesotho, and Swaziland*. Pretoria: South African National Biodiversity Institute.

Myers JH, Simberloff D, Kuris AM, Carey JR. 2000. Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution* 15: 316-320.

Myers K, Poole WE. 1963. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations IV. The effects of rabbit grazing on sown pastures. *Journal of Ecology* 51: 435-451.

Nankivell JW. 1934. Robben Island. *The South African Geographical Journal* 17: 29-34.

Native Plant Trust. 2022. *Spergula arvensis* (corn spurry): Go Botany. Available at https://gobotany.nativeplanttrust.org/species/spergula/arvensis/ [accessed 13 January 2022]

Norbury D. 1996. *The effect of rabbits on conservation values*. Wellington, New Zealand: Department of Conservation.

Norbury DC, Norbury GL. 1996. Short-term effects of rabbit grazing on a degraded short-tussock grassland in Central Otago. *New Zealand Journal of Ecology* 20: 285-288.

Pacala SW, Crawley MJ. 1992. Herbivores and plant diversity. *American Naturalist* 40: 243-260.

Panetta F, Randall R. 1993. *Emex australis* and the competitive hierarchy of a grazed annual pasture *Journal of Applied Ecology* 30: 373-379.

Parker JD, Burkepile DE, Hay ME. 2006 Opposing effects of native and exotic herbivores on plant invasions *Science* 311 1459–1461.

Pennell CGL, Rolston MP, Latham ADM, Mace WJ, Vlaming B, van Koten C, Latham MC, Brown S, Card SD. 2016. Novel grass–endophyte associations reduce the feeding behaviour of invasive European rabbits (*Oryctolagus cuniculus*). *Wildlife Research* 43: 681.

Perry PL. 1989. A new species of *Zantedeschia* (Araceae) from the western Cape. *South African Journal of Botany* 55: 447-451.

Pielou EC. 1966. The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* 13: 131-144.

Prada LM, Guerrero-Casado J, Tortosa FS. 2018. European rabbits recognise conspecifics in their predators' diets. *Acta ethologica* 21: 163-168.

Ranwell DS. 1960. Newborough Warren, Anglesey, Ill. Changes in vegetation on parts of the dune system after the loss of rabbits by myxomatosis. *Journal of Ecology* 48: 385-397.

Reader PM, Southwood TRE. 1981. The relationship between palatability to invertebrates and the successional status of a plant. *Oecologia (Berl)* 51: 271-275.

Rebelo AG, Holmes PM, Dorse C, Wood J. 2011. Impacts of urbanization in a biodiversity hotspot: conservation challenges in Metropolitan Cape Town *South African Journal of Botany* 77: 20–35.

Rivero R, Zabala A, Gianneechini R, Gil J, Moraes J. 2001. *Anagallis arvensis* poisoning in cattle and sheep in Uruguay. *Veterinary and Human Toxicology* 43: 27–30.

Robben Island Museum (ed). 2006. *Integrated Conservation Management Plan (ICMP) for the Robben Island World Heritage Site*. Robben Island Museum Cape Town.

Roets F, Pryke JS. 2012. The rehabilitation value of a small culturally significant island based on the arthropod natural capital. *Journal of Insect Conservation* 17: 53-65.

Rothwell JT, Marshall DJ. 1986. Suspected poisoning of sheep by *Anagallis arvensis* (scarlet pimpernel). *Australian Veterinary Journal* 63: 316–316.

Ruiz-Aizpurua L, Tortosa FS. 2018. When more is less: the negative effect of European rabbit release upon local warren occupancy. *Acta ethologica* 21: 101-107.

Russell JC, Kueffer C. 2019. Island biodiversity in the Anthropocene. *Annual Review of Environment and Resources* 44: 31-60.

Sakia RM. 1992. The Box-Cox transformation technique: A review. *The Statistician* 41: 169-178.

SANBI. 2011. Threatened terrestrial ecosystems for South Africa, Cape Flats Dune Strandveld (FS6). Available at http://bgis.sanbi.org/ecosystems/showecosystem.asp?id=63 [accessed 18 October 2017].

Sasikumar K, Vijayalakshmi C, Parthiban KT. 2001. Allelopathic effects of *Eucalyptus* on Redgram (*Cajanus cajan* L.). *Journal of Tropical Agriculture* 39: 134-138.

Schmalzer PA, Hinkle CR (eds). 1987. *Species biology and potential for controlling four exotic plants (Ammophila arenaria, Carpobrotus edulis, Cortaderia jubata, and Gasoul crystallinum) on Vandenberg Air Force Base, California*. National Aeronautics and Space Administration, John F. Kennedy Space Center. Florida.

Schweizer D, Jones HP, Holmes ND. 2016. Literature review and meta-analysis of vegetation responses to goat and European rabbit eradications on islands. *Pacific Science* 70: 55-71.

Scott JM, Blair GJ. 1987. Competition from *Vulpia myuros* (L.) C.C. Gmelin in pastures, and its control by coating seeds with herbicides. *Australian Journal of Experimental Agriculture* 27: 367-375.

Shannon CE. 1948. A mathematical theory of communication. *Bell System Technical Journal* 27: 379-423, 623-656.

Shapiro SS, Wilk MB. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52: 591-611.

Sherley RB. 2016. Unusual foraging behaviour in two introduced mammals following degradation of their island habitat. *Biodiversity Observations* 7: 1-10.

Simmonds H, Holst P, Bourke C. 2000. *The palatability, and potential toxicity of Australian weeds to goats*. Kingston: Rural Industries Research and Development Corporation.

Skead CJ. 2011. Historical incidence of the larger land mammals in the broader Western and Northern Cape In: Boshoff AF, Kerley GIH, Lloyd PH editors. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.

Smith EP. 2002. BACI design In: El-Shaarawi AH, Piegorsch WW editors. *Encyclopedia of environmetrics*. Chichester: Wiley p. 141-148.

South African National Biodiversity Institute. 2022. *Conicosia pugioniformis* (L) N.E.Br subsp. *pugioniformis*. SANBI. Available at http://pza.sanbi.org/. [accessed 12 January 2022]

South African National Biodiversity Institute. 2023. *Zantedeschia* Spreng. SANBI. Available at https://pza.sanbi.org/zantedeschia. [accessed 22 March 2023]

Stewart-Oaten A, Bence JR. 2001. Temporal and spatial variation in environmental impact assessment. *Ecological Monographs* 71: 305-339.

Stewart-Oaten A, Murdoch WW, Parker KR. 1986. Environmental impact assessment: "pseudoreplication" in time? *Ecology* 67: 929-940.

Strive T, Cox TE. 2019. Lethal biological control of rabbits – the most powerful tools for landscape-scale mitigation of rabbit impacts in Australia. *Australian Zoologist* 40: 118-128.

Struik GJ. 1967. Growth habits of dandelion, daisy, catsear, and hawkbit in some New Zealand grasslands. *New Zealand Journal of Agricultural Research* 10: 331-344.

Suzuki M, Miyashita T, Kabaya H, Ochiai K, Asada M, Kikvidze Z. 2013. Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests. *Oikos* 122: 104-110.

Tansley AG, Adamson RS. 1925. Studies of the vegetation of the English chalk. III. The chalk grasslands of the Hampshire-Sussex border. *Journal of Ecology* 13: 177-223.

Thompson HV, King CM. 1994. *The European rabbit: the history and biology of a successful colonizer*. New York: Oxford University Press.

Thresher AC. 2020. When extinction is warranted: Invasive species, suppression-drives and the worst-case scenario. *Ethics, Policy & Environment* 25: 132-152.

Tiver F, Andrew MH. 1997. Relative effects of herbivory by sheep, rabbits, goats and kangaroos on recruitment and regeneration of shrubs and trees in eastern South Australia. *Journal of Applied Ecology* 34: 903-914.

Toelken HR. 1981. The species of *Crassula* L. in Australia. *Journal of the Adelaide Botanic Garden* 3: 57-90.

Travers T, Lea MA, Alderman R, Terauds A, Shaw J. 2021. Bottom-up effect of eradications: The unintended consequences for top-order predators when eradicating invasive prey. *Journal of Applied Ecology* 58: 801-811.

Tshiila AA. 2012. Systematics of *Finicia* clade (Cyperaceae). MSc, University of Cape Town, Cape Town.

Tuomisto H. 2012. An updated consumer's guide to evenness and related indices. *Oikos* 121: 1203-1218.

UWC Cape Flats Indigenous Nursery. 2020. UWC Nature Reserve: *Phyllobolus canaliculatus*. Available at https://uwccfnursery.blogspot.com/2020/05/phyllobolus-canaliculatus [accessed 13 January 2022]

UWC Cape Flats Indigenous Nursery. 2021. Propagating *Phyllobolus canaliculatus* (Vingerkanna). Available at https://www.pinterest.co.uk/pin/593490057135262691/ [accessed 22 March 2021]

Vahrmeijer J. 1981. *Gifplante van Suider-Afrika wat veeverliese veroorsaak*. Kaapstad: Tafelberg Uitgewers Beperk.

van Breda PAB, Barnard SA. 1991. *100 veld plants of the winter rainfall region: A guide to the use of veld plants for grazing*. Pretoria: Department of Agricultural Development.

van Breda PAB, Nel EJ, Bayer MB (eds). 1990. *Palatability of plant species – winter rainfall region: Little Karoo and Ceres Karoo* Elsenburg Agricultural Development Institute

van den Berg L, van Lingen M (eds). 2009. *Weidingswaardes (WIW) vir Karoo plantspesies – Hersiene weergawe*. Grootfontein Agricultural Development Institute. Middelburg.

van Dyne GM, Heady HF. 1965. Botanical composition of sheep and cattle diets on a mature annual range. *Hilgardia* 36: 465-492.

van Oudtshoorn F. 2012. *Guide to grasses of southern Africa*. Pretoria: Briza Publications.

Verdaguer D, Sala A, Vilà M. 2010. Effect of environmental factors and bulb mass on the invasive geophyte *Oxalis pes-caprae* development *Acta Oecologica* 36: 92–99.

Vilà M, Bartomeus I, Gimeno I, Traveset A, Moragues E. 2006. Demography of the invasive geophyte *Oxalis pes-caprae* across a Mediterranean island. *Annals of Botany* 97: 1055–1062.

Villafuerte R, Castro F, Ramírez E, Cotilla I, Parra F, Delibes-Mateos M, Recuerda P, Rouco C. 2017. Large-scale assessment of myxomatosis prevalence in European wild rabbits (*Oryctolagus cuniculus*) 60 years after first outbreak in Spain. *Research in Veterinary Science* 114: 281-286.

Vosloo E. 2008. Eco-xenophobia' for island's deer 'Available at' https://www.iol.co.za/news/south-africa/eco-xenophobia-for-islands-deer--403624 [accessed 8 February 2017]

Vural M, Dönmez AA. 2002. Two new taxa of *Silene* (Caryophyllaceae) from Turkey. *Annales Botanici Fennici* 39: 153-158.

Watt AS. 1957. The effect of excluding rabbits from grassland B (mesobrometum) in Breckland. *Journal of Ecology* 45: 861-879.

Watt AS. 1981. A comparison of grazed and ungrazed Grassland A in East Anglian Breckland. *Journal of Ecology* 69: 499–508.

Western Australian Herbarium. 2022a. *Atriplex cinerea* Poir. Available at https://florabase.dpaw.wa.gov.au [accessed 12 January 2022]

Western Australian Herbarium. 2022b. *Chenopodium murale* L. Available at https://florabase.dpaw.wa.gov.au [accessed 12 January 2022]

Williams AJ, Klages NTW, Crawford RJM. 2000. Functional ecosystems: Coastal islands. In: Durham BD, Pauw JC editors. *Summary Marine Biodiversity Status Report for South Africa*. Pretoria: National Research Foundation.

Williams K (ed). 2011. *Managing Rabbits in Canberra Nature Park*. Office of the Commissioner for Sustainability and the Environment. Canberra.

Williams K, Parer I, Coman B, Burley J, Braysher M. 1995. *Managing vertebrate pests: rabbits*. Canberra: Australian Government Publishing Service

Winston R, DesCamp W, Andreas J, Randall CB, Milan J, Schwarzländer M. 2014. *New invaders of the Southwest*. Washington, DC: Forest Health Technology Enterprise Team, United States Department of Agriculture.

World Flora Online Consortium. 2022. *Asparagus capensis* L. Available at http://www.theworldflora.org/taxon/wfo-0000631836;jsessionid=9C5F2FB7DE63230736B1908A25B0BC98. [accessed 4 November 2022]

Yeld J. 2008. Robben Island conservation 'in a shambles'. 'Available at' http://www.iol.co.za/news/south-africa/robben-island-conservation-in-a-shambles-1.398514#.Utf_RYWRa1s [accessed 8 February 2017]

Zeevalking HJ, Fresco LFM. 1977. Rabbit grazing and species diversity in a dune area. *Vegetatio* 35: 193-196.

Zhang D, Zhang J, Yang W, Wu F. 2010. Potential allelopathic effect of *Eucalyptus grandis* across a range of plantation ages *Ecological Research* 25: 13-23.

Zizzo G, Costantino G, Fascella G. 2002. Influence of rhizome sizes and substrates on calla lily (*Zantedeschia aethiopica* Spreng) grown as pot plants [Sicily]. *Atti VI Giornate Scientifiche SOI (Italy)*.

CHAPTER 5

Grazing capacity change on a small Mediterranean-type South African offshore island following the control of invasive alien European rabbits (*Oryctolagus cuniculus*)

Thabisisani Ndhlovu[1], Zivanai Tsvuura[2] and Karen J Esler[3]

[1]School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa.

[2]Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa.

[3]Centre for Invasion Biology and Department of Conservation Ecology and Entomology, Stellenbosch University, Stellenbosch, South Africa.

Version of chapter published in the African Journal of Range and Forage Science
Ndhlovu, T., Tsvuura, Z. and Esler, K.J., 2022. Grazing capacity change on a small Mediterranean-type South African offshore island following the control of invasive alien European rabbits (Oryctolagus cuniculus). African Journal of Range & Forage Science 40: 359-372.
DOI: 10.2989/10220119.2022.2125577

Abstract

Invasive alien species, such as introduced mammals like the European rabbit (*Oryctolagus cuniculus*), significantly impact native biodiversity and ecological functioning. Introduced to five continents and over 800 islands, European rabbits pose a substantial threat to both biodiversity and human livelihoods. Their impacts had been well-documented globally; however, the effects on the offshore islands along Africa's southern coast have been less studied. Our study examined changes in grazing capacity on Robben Island, the largest and most degraded of the offshore islands along the South African coast, from 2010 to 2013, following an attempted eradication of European rabbits between 2008 and 2009. After the eradication attempt, there was an increase in grazing capacity at both strand and inland dune sites, which was attributed to the recovery of palatable forage species that had previously been suppressed by rabbit herbivory. Conversely, grazing capacity at eucalyptus sites remained unchanged, likely due to the inhibitory effects of alien *Eucalyptus* trees on understory vegetation dynamics. These findings suggest that changes in rabbit populations might similarly affect vegetation on other southern African offshore islands.

Keywords: European rabbits; invasive alien species; ecological restoration; vegetation grazing capacity; Robben Island; South Africa

Introduction

Biological invasions are one of the most important threats to global biodiversity (Travers, et al. 2021). It is estimated that over 100 extinctions have occurred globally during the 20th century, driven mainly by habitat loss, invasive alien species and disease (Pereira, et al. 2012). Biodiversity loss has been especially severe on island ecosystems (Nunes, et al. 2021) which have experienced ~61% of all global extinctions (Travers, et al. 2021). Most of the biodiversity loss on islands has been caused by invasive alien mammals (Cubas, et al. 2018, Cleeland, et al. 2020, Barbraud, et al. 2021, Travers, et al. 2021) with the impacts of the European rabbit (*Oryctolagus cuniculus*) commonly considered to have been the most problematic (Flux, et al. 1992, Schweizer, et al. 2016, Cubas, et al. 2019, Bello-Rodríguez, et al. 2021). European rabbits, which are medium sized herbivores from the order Lagomorpha that originate from the Iberian Peninsula in southwestern Europe, have been introduced to at least 800 islands islands around the world where they have had devastating consequences for native flora and fauna and agricultural systems (Delibes-Mateos 2017, Cubas, et al. 2019). Among many other impacts, European rabbits have been shown to reduce grazing capacity (Farrow 1917, Friedel 1985, Foran 1986, Williams, et al. 1995, Williams 2011, Pennell, et al. 2016), change vegetation species composition, diversity and structure (Farrow 1917, Gillham 1955, Hobbs, et al. 1981, Lange, et al. 1983, Foran, et al. 1985, Foran 1986, Cubas, et al. 2018) and increase landscape degradation (Cooke 1991, Strive, et al. 2019).

Although European rabbits have not established on the South African mainland, they have been introduced to 13 of the 24 offshore islands that occur along its coast (de Vos, et al. 1956, Cooper, et al. 1982, Lever 1985, Long 2003, Skead 2011, Bruton 2021). Feral rabbit populations have since become naturally extinct from seven of the islands (de Vos, et al. 1956, Cooper and Brooke 1982, Lever 1985, Long 2003, Skead 2011) and are currently present on six (i.e. Jutten, Dassen, Vondeling, Schaapen, Robben and Seal Islands, Davies, et al. 2020, Measey, et al. 2020). European rabbits on

South African offshore islands have been formally assessed as having had massive environmental impacts through their negative effects on vegetation resulting in moderate socio-economic losses (Bruton 2021). As a result, European rabbits are considered under South Africa's National Environment Management: Biodiversity Act 10 of 2004 as Category 1b invasive species that need to be controlled. Since the 1990s, European rabbits have been targeted globally by a growing number of island restoration projects aimed at their control or eradication (Nunes, et al. 2021). However, this has not been the case on South African offshore islands, where there have been few historical attempts to manage invasive European rabbit populations. As a result, although there is some understanding of how herbivory by rabbits has affected vegetation on the islands (see, for e.g., Adamson 1934, Nankivell 1934, Gillham 1963), very little is known about how the vegetation may respond to rabbit control or removal.

In this study, we monitored change in grazing capacity on a South African offshore island, Robben Island, following an attempt to eradicate invasive alien European rabbits between 2008 and 2009 (Anon 2008a, b, de Villiers, et al. 2010, Sherley 2016). Robben Island is the largest and most degraded of the offshore islands that occur along the South African coast (Brooke, et al. 1986, Smith 1997, Crawford, et al. 2000). Our objectives were to (1) determine the effect of rabbit control on grazing capacity on the island and (2) identify the changes in plant species cover that underlay the observed change. In addition to European rabbits, Robben Island hosts a variety of other herbivores such as introduced helmeted guinea fowl (*Numida meleagris*), chukar partridge (*Alectoris chukar*), Indian peafowl (Pavo cristatus), springbok (*Antidorcas marsupials*), fallow deer (*Dama dama*) and steenbok (*Raphicerus campestris*). These organisms depend on the island's vegetation for forage and thus their persistence and populations are directly affected by its grazing capacity (Crawford and Dyer 2000, Sherley 2016, Philander 2017). South African offshore islands vary in their geology, size, distance offshore and climatic conditions (Williams, et al. 2000). However, we believe that an understanding of vegetation dynamics on Robben Island following rabbit control could provide valuable insights into the potential response of vegetation on other South African Mediterranean-type offshore islands.

Grazing capacity refers to the productivity of an area of vegetation and is expressed as the area of land required to maintain a single animal unit over an extended period without deterioration to vegetation or soil (Booysen 1967). On semi-natural ecosystems such as Robben Island, this refers to the area of vegetation required to sustainably support an equivalent unit of the various wild herbivores (e.g., guinea fowl, chukar partridges, Indian peafowl, springbok, fallow deer and steenbok) that occur on the island**.** Herbivory by European rabbits reduces grazing capacity by selectively removing palatable plant species and favouring the survival and growth of less palatable and unpalatable species (Friedel 1985, Foran 1986, Williams, et al. 1995, Williams 2011, Cubas, et al. 2019). European rabbits preferably consume soft, low-fibre, highly nutritious plants such as grasses, succulents and forbs (Friedel 1985, Foran 1986, Duffy, et al. 1996, Mátrai, et al. 1998), while shrubs are of minor importance as rabbit forage (Myers, et al. 1963, Hall, et al. 1964) and are largely affected by rabbit herbivory through its effects on their regeneration. Even at very low densities, rabbits have been shown to prevent the recruitment of palatable shrub species, particularly in arid regions (Cubas, et al. 2018, Cubas, et al. 2019, Strive and Cox 2019). Control of rabbit abundance commonly leads to recovery in grazing capacity as palatable plants re-establish in response to release from herbivory pressure (Schweizer, et al. 2016). Plant species subject to intense rabbit herbivory tend to have a more robust positive response to rabbit control (Donlan, et al. 2002, Eijzenga 2011, Schweizer, et al. 2016). The strong positive correlation between a species' competitive ability and its palatability to rabbits (Crawley 1990, Pacala, et al. 1992, Diaz 2000) suggests that control of rabbit herbivory not only allows the re-establishment of palatable plants, but also leads to a decline in annuals and unpalatable forbs and grasses through inter-specific competition.

The expectation behind the attempt by Robben Island Management (RIM) to eradicate European rabbits from the Island was that control of their herbivory would lead to a recovery in grazing capacity as palatable forage species re-established in response to release from herbivory pressure. Likewise, we expected grazing capacity on Robben Island to increase following the attempt to eradicate invasive alien rabbits. Our postulation was that, as expected by RIM and suggested in the literature, release of the island's vegetation from rabbit herbivory pressure would have led to the re-establishment of palatable plant species that were constrained by rabbit herbivory, resulting in an increase in grazing capacity. However, grazing capacity in areas subjected to long-term intense rabbit herbivory and with limited options for dispersal from outside such as Robben Island may not respond to rabbit control. This is because prolonged rabbit herbivory may result in complete loss of edible or preferred plant species from plant communities and seed banks (Hobbs and Grace 1981, Hunt 2001, Williams 2011). In such cases, seed banks would have been destroyed, and hence no change in species composition occurs when vegetation is protected from rabbit herbivory (Leigh, et al. 1989, Norbury, et al. 1996, Latham, et al. 2020, Finlayson, et al. 2021). European rabbits had been present on Robben Island for ~350 years at the time of the eradication attempt. Therefore, it was also possible that grazing capacity on the island would not change following rabbit control as there would be no palatable forage species left in the vegetation and seedbanks to respond to the reduction in herbivory pressure.

Materials and Methods

Study site

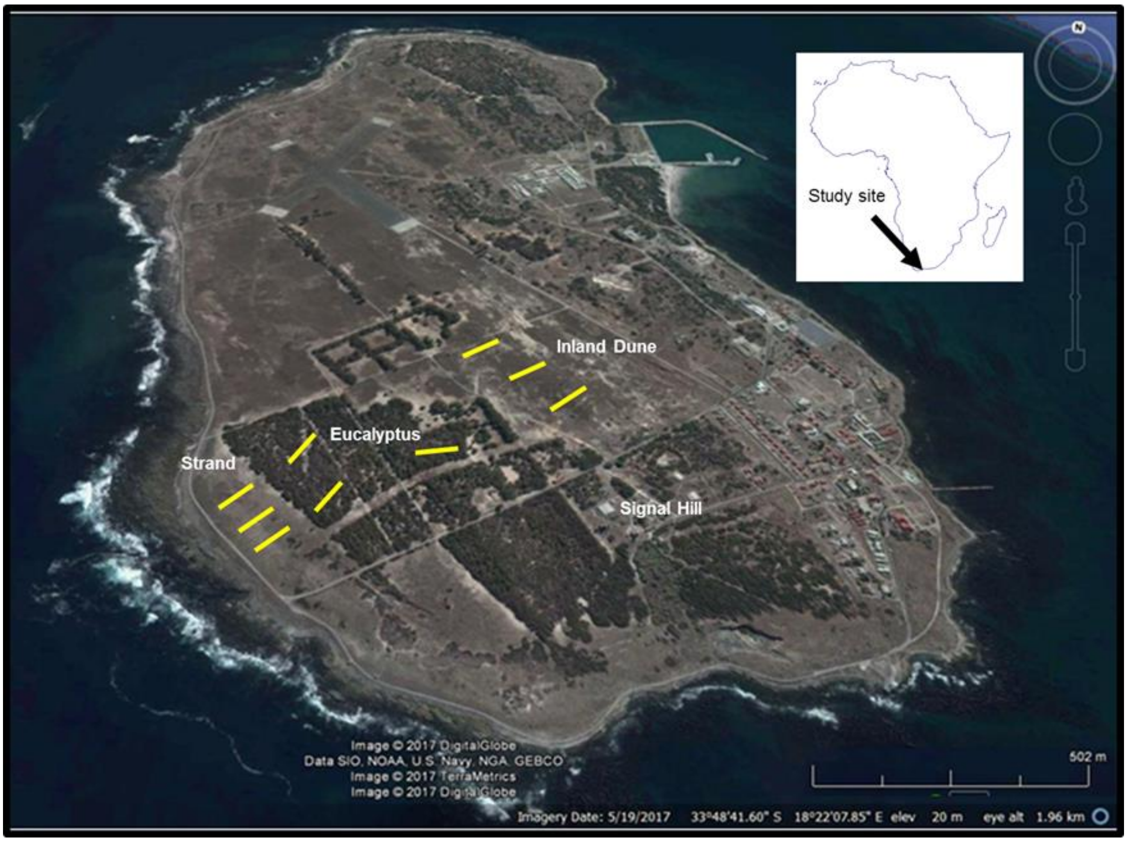


Figure 5-1 Location of the study site and the placement of sampling transects. Satellite image obtained from Google Earth (Version 5.1.3533.1731). Mountain View, CA: Google Inc. (2009).

Robben Island (33° 48’S, 18° 22’E; Figure 5.1) is the largest (~507 ha) of a chain of offshore islands that lie along South Africa’s southern coast (Crawford and Dyer 2000). It lies in Table Bay, approximately 11 km north of Cape Town and 7 km from the nearest mainland (Crawford and Dyer 2000). The island is low lying and gently undulating to flat. It is roughly oval with a north-south axis length of ~3.4 km and a width of just over 2 km (Adamson 1934, Miller 1991). The soils are sandy or have an admixture of sand (Adamson 1934). The island experiences a temperate Mediterranean-type climate of hot, dry summers and cool, wet winters, similar to that of the adjacent mainland

(Adamson 1934, Crawford and Dyer 2000, Robben Island Museum 2006). Robben Island was part of the mainland during the last Pleistocene glaciation (c. 17 000 YA) (Tankard 1976, Brooke, et al. 1982) when the sea level was lower than present (Miller 1991). The island was subsequently cut off from the mainland by the South Atlantic Ocean at the end of the glacial period (c. 12 000 YA) when the sea level rose to present levels (Dingle, et al. 1972, Tankard 1976). The environment on Robben Island has undergone considerable change since it was first occupied by humans in the 17th century (Robben Island Museum 2006). Although it is now impossible to determine the original nature of vegetation on Robben Island, the close similarities in climate and soil between the island and adjacent parts of the mainland have led researchers to believe the vegetation was historically contiguous (Adamson 1934, Nankivell 1934, Mucina, et al. 2006, Robben Island Museum 2006). The current view is that pre-human settlement vegetation on the island resembled present-day Cape Flats Dune Strandveld (CFDS) and Cape Seashore Vegetation (CSV; Crawford and Dyer 2000, Mucina and Rutherford 2006, Robben Island Museum 2006). Cape Flats Dune Strandveld is a shrubland that is dominated by evergreen, sclerophyllous shrubs in its southern range, and drought-deciduous shrubs and succulents in the north (Liengme 1987, Robben Island Museum 2006). Cape Seashore Vegetation is open grassy to dwarf-shrubby (sometimes succulent) and occurs on beaches and coastal dunes and cliffs in the Western and Eastern Cape Provinces. Cape Flats Dune Strandveld is constricted by habitat transformation to a narrow band along South Africa’s southwestern coast while nearly half of the CSV is conserved in protected areas (Mucina, et al. 2006, Mucina and Rutherford 2006, Rebelo, et al. 2011). As a result, CFDS is classified as 'endangered' (SANBI 2011) while CSV is considered to be 'least threatened' (Rebelo, et al. 2011). While the island's vegetation has been affected by many factors, including several large herbivores introduced since the 17th century, it is prolonged rabbit herbivory that is believed to have had the most profound impact on the island's environment (Adamson 1934, Nankivell 1934, Robben Island Museum 2006).

European rabbits were introduced to Robben Island by the Dutch colonial governor Jan van Riebeeck in 1654 (Measey, et al. 2020). Rabbit numbers on the island are thought to have been historically low because of trapping, hunting and predation by human inhabitants and feral cat populations (Apps 1984, Crawford and Dyer 2000, Sherley 2016). However, rabbit numbers appear to have periodically exploded during periods when the island became uninhabited by humans and predation by feral cats was reduced or precluded (Adamson 1934, Nankivell 1934, de Villiers, et al. 2010, Sherley 2016). One such explosion in rabbit numbers appears to have occurred in 1931 following its desertion by humans after the closure of the General Infirmary. The General Infirmary had operated on the island for 88 years, during which period ~500 hospital staff had lived on the island at any given time and cared for hundreds of persons with Hansen's disease (leprosy). Feral cats are believed to have been absent from the island during the period. A more recent explosion in rabbit numbers occurred in 2008 following the abandonment of the island by humans after the closure of the island prison in 1998 and culmination in 2008 of a series of cat removal exercises begun in 1998. The population of rabbits on the island during the period is estimated to have increased from ~31 individuals in 1998 to ~100 in 1999, ~2100 in 2003, and ~4100 in 2006, culminating in ~24100 individuals in 2008 (Crawford and Dyer 2000, de Villiers, et al. 2010, Sherley 2016). The explosion in rabbit numbers in 2008 caused an environmental crisis on the island that generated negative press coverage (Anon 2008a, b, Yeld 2008). The crisis included massive die-offs of rabbits and other introduced mammalian herbivores such as fallow deer, bontebok, and springbok due to reduced vegetation grazing capacity (Vosloo 2008, Yeld 2008, Sherley 2016). In response, Robben Island management (RIM) conducted a significant rabbit control exercise from November 2008 to May 2009, culling ~4790 rabbits (de Villiers et al. 2010; Sherley 2016). Concurrently, about 18000 rabbits died from starvation, attributed to a sharp decline in summer rainfall, significantly below the long-term average (see Chapter 2). The control efforts targeting the remaining 1,200 rabbits continued into 2010, leading to further reductions in the population. By November 2010, rabbit sightings had become extremely rare, with only three observed in March and none thereafter. No rabbits were detected during field sampling from November 2010 until the study concluded in 2013. Further efforts to remove rabbits from the island beyond the initial 2009-2010 cull have resulted in the cumulative removal of an estimated 13600 animals (Davies, et al. 2020, Measey, et al. 2020). At the time of writing, European rabbits had reportedly not been seen on the island since 2019 (Davies, et al. 2020, Measey, et al. 2020), although it is not yet certain whether they have been extirpated (Bruton 2021).

Field sampling

We monitored plant cover change at nine sites (strand (n=3), eucalyptus (n=3), and inland dune (n=3)) on the south-eastern portion of Robben Island over four years (2010-2013) following rabbit control (see Figure 5.1 for the location of sites). The sites were positioned along a deliberately selected transect that extended across major ecological land units on the island, utilising the gradsect method (Gillison and Brewer 1985), which is designed to capture ecological variability across the entire study site along a gradient.

Species cover at each site was determined annually in early summer (November) using line point intercepts (see Herrick, et al. 2005) along three sets of two fixed head-to-head 50-metre transects, each separated by 50 metres. This 50-metre spacing was chosen to enhance data quality and representativeness by ensuring the independence of data points and capturing ecological variability across sites. The point intercept method involved placing points at 1-metre intervals along each transect, resulting in 100 points per transect and a total of 300 recordings per site.

Strand sites were located nearest to the seashore on sand over shale, while eucalyptus and inland dune sites occurred further inland on sand over limestone. Sand over shale at strand sites is shallow (3-5 cm; Adamson 1934), while sand over limestone at eucalyptus and inland dune sites is deeper (0-70 cm; Adamson 1934). Shale bedrock outcropped over a limited area at strand sites. Eucalyptus sites were covered by a mature plantation (>65 years old; Brooke and Prins 1986, Smith 1997) of *Eucalyptu*s (57% cover) and pine (7% cover) trees. Plantation trees had been recently cleared from parts of the inland dune sites before the commencement of sampling. Felled wood from cleared plantation trees at inland dune sites was piled onsite and removed during the second year following rabbit control. Dead standing trees and woody debris were removed from eucalyptus sites during the study as part of routine fire prevention measures. Plant nomenclature followed The Plant List (2013), Version 1.1 (http://www.theplantlist.org).

Data analysis

Grazing capacity

Grazing capacity values per transect were calculated using the Bayer method of rangeland condition assessment (Bayer 1990). The technique determines grazing capacity using plant species cover estimates, plant utilisation indices, long-term mean annual rainfall and a generalised rain-use efficiency index. Plant utilisation indices, which indicate the amount of the plant consumed by animals, are assigned to species according to their palatability to domestic livestock (Bayer 1990, van Breda, et al. 1990). Plant species are grouped into four palatability classes, viz. highly palatable, palatable, less palatable, and unpalatable for utilisation indices. Highly palatable species have an index value of 90%, palatable species 50% and less palatable species 20% (Bayer 1990). Unpalatable species, which have no forage value, have an index value of 0%. Palatability classes for species encountered during our study were determined from published sources (Annex VIII Table S1). Rain-use efficiency (RUE) is an expression of annual primary production (kg DM ha^{-1} y^{-1}) as a sole function of annual rainfall (mm y^{-1}), which is defined as "the number of kilograms of aerial dry matter phytomass (DM) produced over 1 ha in 1 year per millimetre of total rain fallen" (Le Houérou 1984). The RUE used in the Bayer method (4 kg DM ha^{-1} y^{-1} mm^{-1} rain) is adopted from the mean value obtained by Le Houérou et al. (1988) for arid zones across the globe. Multiplying RUE with the long-term mean total annual rainfall (in mm) at a site provides its potential forage production (kg DM ha^{-1} y^{-1}; Bayer 1990).

Each 1% of plant species cover represents 1% of potential production (Bayer 1990). Multiplying plant species cover scores by the appropriate utilisation indices provides an assessment of the proportion of usable forage available at a site (Bayer 1990). Dividing the proportion of available usable forage by 100 to scale it as a percentage and multiplying it with potential forage production gives the actual forage production (AFP, kg DM ha^{-1} y^{-1}) at the site (Bayer 1990). Grazing capacity (ha LSU^{-1} y^{-1}) is then obtained by dividing actual production into 650 and multiplying by 6.67 (Bayer 1990). The dividend 650 is equivalent to the annual DM requirement (in kg) of a 60 kg Dorper sheep based on an estimated daily intake of 3% of body weight (Bayer 1990), and 6.67 is the factor used to convert small stock units (SSU) to large stock units (1 LSU = 6.67 SSU; Meissner, et al. 1983). Grazing capacity, which refers to the productivity of an area of vegetation in terms of the size of land required to maintain a single animal unit over an extended period without deterioration to vegetation or soil (Booysen 1967), is typically expressed as ha LSU^{-1} y^{-1}. In this study, we expressed grazing capacity as the number of LSUs that can be supported by 100 ha of vegetation for a year without deterioration to vegetation or soil (i.e. LSU 100 ha^{-1} y^{-1}) for ease of presentation.

A major weakness of the Bayer method is that precise forage and intake values of many plants for different herbivore species are not known (Bayer 1990). Also, forage and intake values vary for the same plant species from site to site and season (Bayer 1990). In addition, the basing of potential forage production on mean annual rainfall by the method is problematic as plant growth is not only affected by the quantity of rainfall but also its temporal distribution (Bayer 1990). Despite these weaknesses, the Bayer method has been used to evaluate grazing capacity in several published studies (e.g. Hoffman, et al. 2009, Saayman, et al. 2009). The method, however, is not used to make recommendations on stocking rates (Pauw 2011). Reservations have also been expressed (see Hoffman, et al. 2010, Kerley, et al. 2010) about the suitability of using assessments based on foraging preferences of domestic livestock to assess impacts of non-domesticated herbivores on rangeland grazing capacity. We concur with Kerley and Landman (2010) that, in such situations, standard agricultural-based methods for assessing rangeland condition need to be replaced by alternative approaches that take into account the different ways in which non-domesticated herbivores forage and use the landscape. However, in agreement with Hoffman, et al. (2010), we also believe that the use of agricultural-based methods can provide useful approximations of grazing capacity where alternative non-agricultural methods are not readily available. We were not aware at the time we conducted this study of an alternative non-agricultural method we could have used to evaluate grazing capacity change cost-effectively and accurately at our study sites.

Inter-annual rainfall variation

Inter-annual rainfall variation significantly influences vegetation dynamics in Mediterranean-type ecosystems (Mucina and Rutherford 2006, Esler, et al. 2018). Inter-annual variation in season and amount of rainfall, soil factors and rabbit density have all been shown to play a dominant role in driving vegetation dynamics in Mediterranean ecosystems under rabbit herbivory (Austin, et al. 1981, Foran 1986).

We used unpublished rainfall data for Robben Island obtained from the South African Weather Service to calculate total annual, summer, winter, autumn, and spring rainfall for the study's four-year duration. We calculated total annual rainfall (TAR) as the sum of the total monthly rainfall for the 12 months that preceded vegetation monitoring. Likewise, we calculated total summer (TSUR), winter (TWR), autumn (TAUR) and spring (TSR) rainfall from months preceding monitoring. On the island, summer occurs between mid-October to March, autumn in April, winter between May and August, and spring in September. We replaced missing monthly rainfall data with the means of non-missing values. Long-term averages of rainfall were calculated over 113 years (1900 – 2013).

Statistical analyses

The change in grazing capacity was determined from differences in mean grazing capacity between the four years that proceeded rabbit control. Inter-annual grazing capacity change was assessed within the strand, eucalyptus and inland dune sites using repeated-measures ANOVA tests. Species cover changes that drove grazing capacity change were identified and ranked using inter-annual differences in mean species contributions to AFP between the four years proceeding rabbit control.

Actual forage production values for individual species were calculated using the Bayer method. To focus our analysis on the most important vegetation changes, only plant species that contributed ≥ 5 kg DM ha^{-1} y^{-1} to AFP change after rabbit control were considered. Significant differences in individual plant species contributions to AFP within the sites were determined using Friedman's test. For species with only two years of mean actual production values above zero, the Exact Wilcoxon two-sample paired test was used. The non-parametric tests were used when no suitable transformation of the data satisfied the assumptions of ANOVA. Normality was tested using the Shapiro–Wilk test (Shapiro, et al. 1965). Adjustments for multiple comparisons were made using a false discovery rate (FDR) based method (classical one-stage method, maximum acceptable FDR ≤ 0.05) (Pike 2011). Principal Components Analysis (PCA) biplots were used to graphically portray changes in individual plant species contributions to AFP following rabbit removal.

The role of interannual rainfall variation in influencing changes in grazing capacity in the years following rabbit control was evaluated using multiple linear regressions. Multivariate multiple regressions were used to evaluate the influence of inter-annual rainfall variation on changes in mean individual species contributions to AFP. Total summer rainfall, TAU and TWR were used as independent variables in all regressions. Total annual rainfall and TSR, which Redundancy Analysis (RDA; McCune, et al. 2002) identified to be collinear and, therefore potentially redundant, were excluded from regressions. Rao's F statistic was used to test for overall multivariate significance, while t-tests were used to determine the significance of separate combinations of independent and dependent variables. Data were transformed using Box-Cox power transformation (Box, et al. 1964, Sakia 1992) prior to regression analysis where necessary. Tests for multivariate normality and homoscedasticity were conducted using the Doornik and Hansen omnibus test (Doornik, et al. 1994). Regression residuals were tested for serial correlation using Durbin-Watson tests (Durbin, et al. 1951). Redundancy Analysis (RDA) tri-plots (ter Braak, et al. 1994) were used to graphically represent species AFP-rainfall relationships.

Significance, normality, regression and serial correlation tests were carried out using the Paleontological Statistics Software Package for Education and Data Analysis (Hammer, et al. 2001). Principal Components Analysis and RDA were conducted using vegan (Oksanen, et al. 2015) in R (R Core Team 2020). We used PCA and RDA because Detrended Correspondence Analysis confirmed species cover data underlying grazing capacity calculations conformed to the linear model (Annex VIII Figure S1). False discovery rate-based adjustments were made using the spreadsheet provided by Pike (2011). Analyses were conducted separately for strand, eucalyptus and inland dune sites to evaluate the effects of landscape variation on vegetation grazing capacity dynamics across the island (see section on field sampling above for a description of the environmental differences between the sites).

Multiple comparison and serial correlation

We ignored the effects of multiple comparison and serial correlation in our interpretation of statistical results. Our approach to the study was exploratory, and as a result, we were more worried about making Type II errors (false negatives) than Type I errors (false positives; see Nakagawa 2004). Multiple comparisons lead to inflated rates of Type I error. While adjustments for multiple comparison, such as the Bonferroni correction, effectively limit Type I errors, they inevitably increase the number of Type II errors. Likewise, serial correlation may lead to over-optimistically low *P*-values (Type I error; Weissgerber, et al. 2016, Forstmeier, et al. 2017). However, adjusting for serial correlation – like adjusting for multiple comparison – leads to inflated Type II error rates. We provided multiple comparison-adjusted *P* values for comparisons of inter-annual species forage production (Annex VIII Table S2) and serial correlation evaluations for the relationships between inter-annual rainfall variation, grazing capacity change and species forage production (Annex VIII Table S4) for reference.

Modelled before-after, control-impact (BACI) design and correlative statistical control

Ecological restoration interventions – such as the control of invasive alien rabbits in this study – can provide experimental manipulations that research ecologists can use to elucidate environmental patterns and processes and test ecological theory (Donlan, et al. 2002). However, in many cases, the utility of restoration interventions as ecological experiments is limited by methodological weaknesses (e.g. lack of valid controls, randomisation and insufficient replication) arising from their usually unplanned nature (Michener 1997, Donlan, et al. 2002). Our study, which was opportunistically based on an unplanned attempt to restore vegetation on Robben Island by removing alien invasive European rabbits, was affected by several such methodological challenges.

Firstly, due to its unplanned nature, our study was initiated a full year after the commencement of rabbit removals. Consequently, we could not adopt the well-established before-after, control-impact (BACI) design (Stewart-Oaten, et al. 1986, Stewart-Oaten, et al. 2001, Smith 2002) commonly used for assessing impacts in longitudinal observational studies (Johnson 2002). Longitudinal observational studies, with measurements taken before and after some treatment, generally are more informative than cross-sectional observational studies, in which measurements are taken only after the treatment (Johnson 2002). A significant drawback of adopting a cross-sectional approach is the difficulty in determining whether variables (e.g., species contribution to forage production) have changed after an intervention or impact without measurements collected before treatment to use for comparison. In our case, the study's cross-sectional nature made it difficult to determine whether the absence of species during the first and second years of data collection represented long-standing phenomena (and therefore linked to rabbit herbivory) or were artefacts caused by the drought conditions that prevailed during the period. Our approach to resolving this methodical challenge was to model island vegetation as a longitudinal time series using data from an earlier vegetation survey by Adamson (1934) as a pseudo BACI control (Annex IX). Adamson (1934) surveyed vegetation on Robben Island in 1933-1934 when the island was overrun with rabbits. We used this survey’s results as a BACI-like control by assuming that the conditions on the island in 1933-1934 were like those in the period preceding the rabbit control in 2009 and 2010 (Annex IX). However, this assumption is precarious because the Adamson (1934) survey occurred 77 years before the present study's sampling, and the island has experienced significant environmental transformations since then. Moreover, the island was uninhabited during the 1933-1934 survey (Nankivell 1934), resulting in a lack of rainfall data for that period, which limits the comparison between these times. Nonetheless, the Adamson (1934) study remains the sole detailed vegetation survey on the island that offers a potentially reliable baseline.

Secondly, the study's opportunistic nature precluded us from using planned treatments and randomisation to cancel out effects of confounding variables such as variation in interannual rainfall. As a result, we were constrained to evaluating and cancelling out the influence of rainfall variation on vegetation response using correlative statistical control and thus could not demonstrate causality. However, confidence can be placed on correlative relationships if they can be shown to be consistent with mechanisms that are both reasonable and supported by independent evidence (Johnson 2002). Romesburg (1981) contends that causation may even be invoked if correlational evidence is accompanied by, for example, the elimination of other possible causes, demonstration that the correlation occurs under a wide variety of circumstances, and the existence of a plausible dependence between the putative cause and the outcome. To this end, whenever possible, we strengthened the correlative interpretations of the relationships between rainfall variation and vegetation response in our results by providing plausible mechanisms, demonstrating links between putative causes and outcomes and sourcing supporting independent evidence from the published literature (Annex IX).

Results

Inter-annual rainfall variation

Inter-annual rainfall varied considerably between the four years following rabbit control (Table 5.1). Total summer rainfall was considerably below the long-term average during the first- and second years following rabbit control and rose to moderately above and equal to the average in the third and fourth (Table 5.1). Total autumn rainfall followed the same pattern as total summer rainfall (Table 5.1). Total winter rainfall was slightly to moderately below the long-term average in the first- and second year following rabbit control and increased substantially to above average in the third and fourth year (Table 5.1).

Table 5-1 Inter-annual rainfall following the control of invasive alien European rabbits on Robben Island. Long-term (1900– 2013) rainfall averages are provided for comparative purposes.

Rainfall (mm)	Year				Long term average
	2010	2011	2012	2013	
Total summer rainfall	22	10	61	51	50
Total autumn rainfall	12	14	42	31	34
Total winter rainfall	238	164	270	354	258

Grazing capacity change following rabbit control

Strand sites

Grazing capacity increased significantly following rabbit control at strand sites (Table 5.2). Mean grazing capacity across the sites increased moderately between the first- and second years following rabbit control (increased by 3.45 LSU 100 $ha^{-1}y^{-1}$), slightly more markedly between the second- and third years (increased by 4.35 LSU 100 $ha^{-1}y^{-1}$) and decreased slightly between the third- and fourth years (decreased by 0.38 LSU 100 $ha^{-1}y^{-1}$; Table 5.2). The increase in cover of the highly palatable woody shrub *Tetragonia fruticosa* Linn and emergence of the palatable annual grass *Ehrharta* *longiflora* Sm between the second- and third years mainly drove grazing capacity increase following rabbit control (Figure 5.2; Annex VIII Table S2 and S5). Emergence of the less palatable perennial grass *Ehrharta villosa* Schult.f. and decline in cover of the less palatable perennial herb *Conicosia pugioniformis* (L.) N. E. Br. between the first- and second years were of intermediate importance (Figure 5.2; Annex VIII Table S2 and S5). Emergence of the less palatable annual herb *Silene cretica* L. between the second- and third years and disappearance of the palatable perennial grass *Sporobolus virginicus* (L.) Kunth between the first- and second years were of minor importance (Figure 5.2; Annex VIII Table S2 and S5).

Inter-annual rainfall variation accounted for ~36% of grazing capacity change, with TAUR accounting for ~35% (Table 5.3). At the species level, inter-annual rainfall variation accounted for 100% and ~33% of the forage production change by *E. longiflora* and *S. cretica*, respectively, following rabbit control (Annex VIII Table S3). Increase in TAUR and TWR accounted for ~95% and ~65%, respectively, of the increase in forage production by *E. longiflora* between the second- and third years following rabbit control (Figure 5.3; Annex VIII Table S3). In contrast, increase in TSUR suppressed forage production by the annual grass by ~79% during the same period (Figure 5.3; Annex VIII Table S3). Although inter-annual rainfall variation accounted for ~33% of the change in forage production by *S. cretica*, there was no significant relationship at the seasonal level (Annex VIII Table S3). Inter-annual rainfall variation had no significant influence on forage production by *T. fruticosa*, *C. pugioniformis*, *E. villosa* and *S. virginicus* (Annex VIII Table S3).

A decline in the contribution to grazing capacity of *C. pugioniformis* was correlated with increased contribution of *T. fruticosa* (strongly) and *E. longiflora* (weakly; Figure 5.2). A decline in contribution to grazing capacity of *S. virginicus* was correlated with an increa se in the contribution of *T. fruticosa* (strongly), *E. longiflora* (moderately), *E. villosa* (weakly) and *S. cretica* (very weakly; Figure 5.2). An increase in contribution to the grazing capacity of *E. villosa* and *S. cretica* was weakly correlated with the decline in contribution of *T. fruticosa* (Figure 5.2).

Eucalyptus sites

Grazing capacity did not change significantly following rabbit control at eucalyptus sites (Table 5.2). However, there were minor changes in forage production (Annex VIII Supplementary Material 1 Table S2), which were driven by fluctuations in the cover of the highly palatable woody shrub *T. fruticosa*, palatable annual grass *E. longiflora* and less palatable annual herb *Oxalis pes-caprae* L. and perennial herb *Phyllobolus canaliculatus* (Haw.) Bittrich. (Figure 5.2; Annex VIII Table S2 and Table S4).

Inter-annual rainfall variation accounted for ~49% of grazing capacity change, with TAUR and TWR accounting for ~36% and ~43%, respectively (Table 5.3). At the species level, inter-annual rainfall variation accounted for ~61%, ~39% and ~47% of the forage production by *T. fruticosa*, *O. pes-caprae* and *P. canaliculatus*, respectively, following rabbit control (Annex VIII Table S3). An increase in TAUR accounted for ~53% of the increase in forage production of *T. fruticosa* between the second- and third years following rabbit control (Annex VIII Table S3). Increase in TWR accounted for ~29% of the increase in forage production by *O. pes-caprae* between the third- and fourth years following rabbit control (Annex VIII Table S3). Although inter-annual rainfall variation accounted for ~47% of the change in forage production by *P. canaliculatus*, there was no significant relationship at the seasonal level (Annex VIII Table S3). Inter-annual rainfall variation had no significant influence on the change in forage production by *E. longiflora* (Annex VIII Table S3).

A decline in contribution to grazing capacity of *P. canaliculatus* was moderately correlated with an increase in contribution of *O. pes-caprae* (Figure 5.2).

Inland dune sites

Grazing capacity increased significantly following rabbit control at inland dune sites (Table 5.2). Mean grazing capacity across the sites increased markedly between the first- and second years (increased by 6.03 LSU 100 ha^{-1}y^{-1}) following rabbit control, then increased moderately between the second- and third years (increased by 4.97 LSU 100 ha^{-1} y^{-1}) and decreased slightly between the third- and fourth years (decreased by 0.57 LSU 100 ha^{-1} y^{-1}; Table 5.2). The increase in cover of the highly palatable woody shrub *T. fruticosa* and less palatable perennial grass *E. villosa* mainly drove grazing capacity change following rabbit control (Figure 5.2; Annex VIII Table S2 and S5). Decline in cover of the less palatable perennial herb *C. pugioniformis* was of intermediate importance (Figure 5.2; Annex VIII Table S2 and S5). Increase in cover and emergence between the third- and fourth years of the palatable annual grasses *E. longiflora* and *Avena fatua* L. (alien) were of minor importance (Figure 5.2; Annex VIII Table S2 and S5).

Inter-annual rainfall variation accounted for ~39% of grazing capacity change, with TAUR accounting for ~36% (Table 5.3). At the species level, inter-annual rainfall variation accounted for ~39%, ~33% and ~42% of the change in contribution to grazing capacity of *C. pugioniformis*, *E. longiflora* and *A. fatua* following rabbit control (Annex VIII Table S3). Increase in TAUR suppressed forage production by *C. pugioniformis* by ~14% between the second- and third years following rabbit control (Figure 5.3; Annex VIII Table S3). Increase in TWR accounted for ~25% and ~22% of the increase in forage production by *E. longiflora* and *A. fatua* between the third- and fourth years, respectively, following rabbit control (Figure 5.3; Annex VIII Table S3). Inter-annual rainfall variation had no significant influence on change in forage production by *T. fruticosa* and *E. villosa* (Annex VIII Table S3).

Decline in contribution to grazing capacity of *C. pugioniformis* was correlated with increase in contribution of *T. fruticosa* (strongly), *A. fatua* (moderately) and *E. villosa* (weakly; Figure 5.2). Increase in contribution to grazing capacity of *E. longiflora* was correlated weakly with a decline in the contribution of *T. fruticosa* (Figure 5.2).

Table 5-2 Mean grazing capacity (LSU 100 ha^{-1}y^{-1} ± SE) following the control of invasive alien European rabbits on Robben Island. Significant differences ($P < 0.05$) between years determined using repeated-measures ANOVA.

Site	Year				*F*	*P*
	2010	2011	2012	2013		
Strand	8.19 ± 0.90	11.64 ± 1.90	15.99 ± 1.93	15.61 ± 2.51	6.41	0.005
Eucalyptus	0.07 ± 0.03	0.05 ± 0.05	2.64 ± 1.01	5.31 ± 2.51	3.07	0.060
Inland dune	8.29 ± 1.67	14.32 ± 2.76	19.29 ± 2.31	18.72 ± 2.45	18.69	<0.001

Table 5-3 Relationship between inter-annual rainfall variation and grazing capacity change following the control of invasive alien European rabbits on Robben Island. Significant differences ($\mathrm{P} < 0.05$) determined using Rao's *F* statistic and *t*-tests.

Site	Multiple Linear Regressions														
	Overall rainfall			TSUR				TAUR				TWR			
	Adj. R^2	*F*	*P*	R^2	*Coeff*	*t*	*P*	R^2	*Coeff*	*t*	*P*	R^2	*Coeff*	*t*	*P*
Strand	0.36	4.54	0.014	0.15	-0.471	-0.95	0.353	0.35	0.964	2.72	0.013	0.08	0.666	0.38	0.709
Eucalyptus	0.49	8.43	< 0.001	0.44	-0.891	-1.29	0.213	0.44	1.264	2.08	0.050	0.43	1.726	2.07	0.050
Inland dune	0.39	5.90	0.005	0.13	-0.994	-1.65	0.114	0.36	1.518	3.42	0.003	0.07	1.611	0.89	0.384

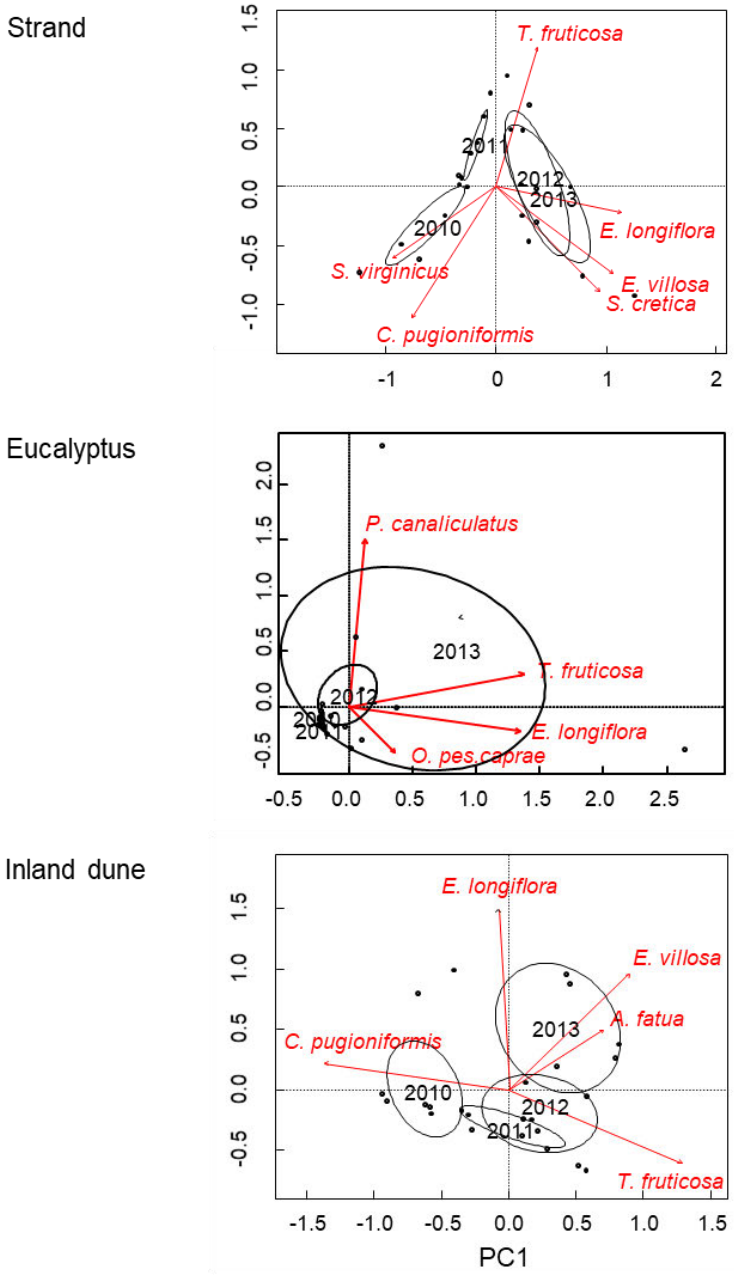


Figure 5-2 Principal components analysis plots showing change in plant species contribution to forage production (kg DM ha^{-1} y^{-1}) following the control of European rabbits on Robben Island.Arrows point towards directions of maximum change, length of arrows indicate rates of change and angles between arrows represent correlations between changes (<90° = positively correlated, 90° = uncorrelated, > 90° = negatively correlated). Only species that contributed ≥ 4 kg DM ha^{-1} y^{-1}to change in forage production shown. Also shown are 95% confidence ellipses for annual forage production. PCA axes 1 (T = 0.60, p < 0.001) and 2 (T = 0.48, p = 0.002) with eigenvalues of 1.993 and 1.621 represented 33.2% and 27% of the total variance, respectively, at strand sites, while the axes (PCA 1 T = 0.71, p < 0.001 and PCA2 T =

0.86, $p < 0.001$) had eigenvalues of 1.807 and 1.327 and represented 45.2% and 33.2% of the total variance at eucalyptus sites. At inland dune sites, eigenvalues for PCA axes 1 ($T = 0.53$, $p = 0.002$) and 2 ($T = 0.69$, $p < 0.001$) were 2.049 and 1.178, and represented 51.2% and 29.5% of the total variance, respectively. The significance of PCA axes was tested using a simple parametric bootstrap method (999 bootstraps, unscaled variables, Hellinger transformed data) (see Forkman, et al. 2019).

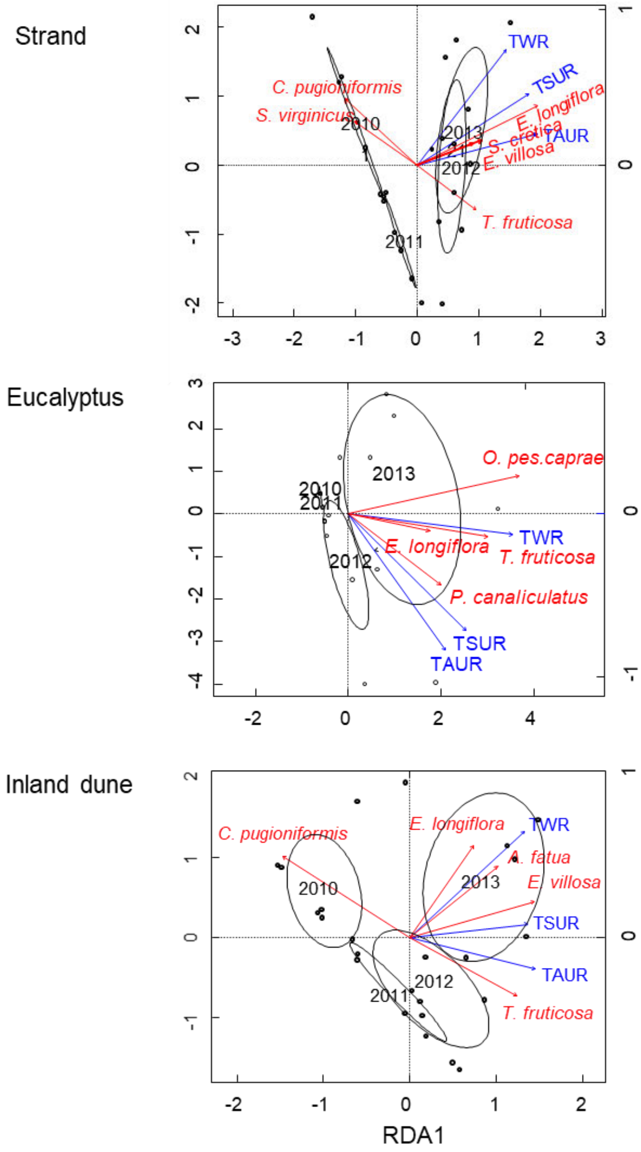


Figure 5-3 Redundancy Analysis plots showing relationships between inter-annual rainfall and change in plant species contribution to forage production (kg DM ha^{-1} y^{-1}) following the control of European rabbits on Robben Island. Arrows point towards directions of maximum change, length of arrows indicate rates of change and angles between arrows represent correlations (<90° = positively correlated, 90° = uncorrelated, > 90° = negatively correlated). Only species that contributed ≥ 4 kg DM ha^{-1} y^{-1} to change in forage production shown. Also shown are 95% confidence ellipses for annual forage

production. The Monte Carlo permutation test showed evidence of non-randomness of the ordination for the strand ($F = 3.52$, $p = 0.001$) and inland dune sites ($F = 4.0$, $p = 0.002$) but not the Eucalyptus sites ($F = 0.87$, $p = 0.491$), based on 999 permutations. RDA axes 1 and 2 with eigenvalues of 1.573 and 0.469 represented 26.2% and 7.8% of the total variance, respectively, at strand sites, while eigenvalues of 0.61 and 0.103 represented 15.3% and 2.6% of the total variance, respectively, at Eucalyptus sites. At inland dune sites, eigenvalues for RDA axes 1 and 2 were 1.194 and 0.279, which represented 29.9% and 7% of the total variance, respectively. Values for species–rainfall correlations are shown in Annex VIII Table S3.

Effects of inter-annual rainfall variation on grazing capacity

Inter-annual rainfall variation substantially confounded the vegetation dynamics that occurred during our study (Annex IX). The confounding effects consisted mainly of suppressed and delayed responses by the woody shrub *T. fruticosa*, perennial herbs *C. pugioniformis* and *P. canaliculatus*, perennial grass *E. villosa*, annual herb *O. pes-caprae* and annual grasses *E. longiflora* and *A. fatua* in response to years of below and above average autumn, winter and summer rainfall (Annex IX).

We determined that grazing capacity would have increased across strand sites following rabbit control given average and constant inter-annual rainfall (Annex IX). Mean grazing capacity across the sites would have increased between the first- and second years and remained stable (possibly at ~16 LSU 100 $ha^{-1}y^{-1}$) in the proceeding years (Annex IX). The increase in grazing capacity would have been driven by increased cover of *T. fruticosa* and *E. longiflora* and the emergence of *E. villosa* between first- and second years (Annex IX). These increases would have been accompanied by a decline in the cover of *C. pugioniformis* (Annex IX). The increase in the cover of *T. fruticosa* would have been of major, *E. longiflora* intermediate and emergence of *E. villosa* minor importance in driving grazing capacity change while the decline in the cover of *C. pugioniformis* would have been of intermediate importance (Annex IX).

Additionally, we surmised that grazing capacity would have also increased across inland dune sites in response to rabbit control (Annex IX). Mean grazing capacity across the sites would have increased between the first- and second years following rabbit control and increased slightly across the second, third and fourth (possibly to ~19 LSU 100 $ha^{-1}y^{-1}$; Annex IX). The increase in grazing capacity would have been driven by the increased coverage of *T. fruticosa*, *E. villosa*, and the emergence of *E.*

longiflora and *A. fatua* between the first- and second years (Annex IX). The increases would have been accompanied by a decline in cover of *C. pugioniformis* (Annex IX). The increase in cover of *T. fruticosa* and *E. villosa* would have been of major importance in driving grazing capacity (Annex IX). The decline in cover of *C. pugioniformis* would have been of intermediate while the emergence of *E. longiflora* and *A. fatua* minor importance (Annex IX).

Lastly, we deduced that grazing capacity would still have not changed at eucalyptus sites following rabbit control in the absence of inter-annual rainfall variation (Annex IX). The lack of change in grazing capacity was caused by subdued responses of *T. fruticosa*, *E. longiflora, O. pes-caprae* and *P. canaliculatus* to rabbit control (Annex IX).

Discussion

Impact of rabbit control on grazing capacity

As we expected, grazing capacity on Robben Island increased across strand and inland dune sites, driven by the recovery and re-establishment of palatable forage species in response to release from herbivory pressure. The woody shrub *T. fruticosa*, perennial grass *E. villosa* and annual grasses *E. longiflora* and *A. fatua,* which drove most of the grazing capacity increase following rabbit control, are palatable to herbivores (Louw, et al. 1988, van Breda, et al. 1990, van den Berg, et al. 2009, van Oudtshoorn 2012). All species are favoured rabbit browse and graze on Robben Island (Adamson 1934, Gillham 1963, Lloyd, et al. 1986, Sherley 2016). Control of European rabbits would have allowed these palatable species to recover from adverse effects of intensive herbivory and contribute to increased grazing capacity. For example, European rabbits browse succulent-leaved *T. fruticosa* shrubs to the base of their shoots (Adamson 1934) and negatively affect *E. longiflora* plants by pulling up their entire roots and rhizomes when feeding (Moore and Moore 2007). Likewise, rabbit herbivory strongly affects *E. villosa* and *A. fatua* plants, resulting in their abundance declining considerably under heavy herbivory (Adamson 1934, Tainton, et al. 1990, van den Berg and van Lingen 2009, van Oudtshoorn 2012). Reduced rabbit browsing and grazing following rabbit control would have enabled the plants to recover from browsed stems, rhizomes (Hodder 1997) and seed (Stubbendieck, et al. 1992, Winston, et al. 2014), leading to the increase in grazing capacity at strand and inland dune sites.

The lack of change in grazing capacity at eucalyptus sites may have resulted from the inhibitory effects of the alien trees on understory vegetation dynamics. With their elevated water consumption rate and dense near surface roots (del Moral, et al. 1969), *Eucalyptus* trees rapidly deplete soil moisture from upper soil layers (Le Maitre, et al. 2002, Dye, et al. 2004, Dye, et al. 2007). This may have led to drier than average plant growth conditions at eucalyptus sites and limited plant species response to rabbit control. *Eucalyptus* plantations have also been shown to inhibit understory vegetation through shading (Loumeto, et al. 1997), allelopathy (del Moral, et al. 1969, Bernhard-Reversat 1988, May, et al. 1990 , Toky, et al. 1993, Sasikumar, et al. 2001, Khan, et al. 2008 , Zhang, et al. 2010), production of thick slow-decomposing litter (Bernhard-Reversat 1988, Bacon, et al. 1993 , Bernhard-Reversat 1996, Barbier, et al. 2008) and alteration of nutrient cycling regimes (del Moral and Muller 1969, Adams, et al. 1986, Gaertner, et al. 2011) resulting in reduced soil nutrient content (Bernhard-Reversat 1996, Guo, et al. 2001, Marchante, et al. 2008) and decreased soil pH and base saturation (Alexander 1989, Zhang, et al. 2010). In particular, the drier conditions under *Eucalyptus* trees would have suppressed the response of the woody shrub *T. fruticosa* and annual grass *E. longiflora* to the removal of rabbit herbivory, while those of the perennial and annual herbs *P. canaliculatus* and *O. pes-caprae* would have been subdued by low amounts of soil nutrients and shading. Germination in *T. fruticosa* and *E. longiflora*, which reproduce solely from seed, is controlled by soil moisture (van Breda and Barnard 1991, Western Australian Herbarium 1998, Bossard, et al. 2000, Winston, et al. 2014), while the more drought-tolerant *P. canaliculatus* and *O. pes-caprae* perform poorly under conditions of low soil fertility and shade (Verdaguer, et al. 2010, UWC Cape Flats Indigenous Nursery 2021).

Control of rabbit herbivory not only results in the re-establishment of palatable plant species but also commonly leads to a simultaneous decline in the abundance of unpalatable plants through inter-specific competition (see, for e.g., Finlayson, et al. 2021). This is because of the strong correlation between a species competitive ability and its palatability to rabbits. In general, the more palatable a plant species, the greater its competitive ability (Crawley 1990, Pacala and Crawley 1992, Diaz 2000). Characteristics that expose plant species to rabbit herbivory (e.g., tall vertical shoots) generally confer competitive advantage, while those that protect them (e.g., shoots that grow close to the soil surface) reduce competitive ability. Such vegetation dynamics most likely explain the decline in cover of the less palatable perennial herb *C. pugioniformis* at our study sites. *Conicosia pugioniformis* would have been outcompeted for light by the taller *E. longiflora*, *E. villosa* and *A. fatua* following rabbit control. Furthermore, the decline in cover of *C. pugioniformis* following rabbit control may have also been partly in response to increased competition for soil moisture from the recovering highly palatable woody shrub *T. fruticosa*. Although both species have taproots that can penetrate the soil to reasonable depths, the root system in *T. fruticosa* is morphologically more versatile in that the species develops long spreading roots in shallow soil and deeper roots in deep or harder soil (Schmalzer and Hinkle 1987, van Breda and Barnard 1991). Herbivory by European rabbits would have favoured the survival and growth of the less competitive *C. pugioniformis* by selectively removing the more palatable and competitive *E. longiflora*, *E. villosa*, *A. fatua* and *T. fruticosa*. European rabbits prefer to browse on plants with tall vertical shoots and inflorescences such as *E. longiflora*, *E. villosa* and *A. fatua* than species that grow close to the soil surface, such as *C. pugioniformis* (Farrow 1917, Crawley 1990). Although both *T. fruticosa* and *C. pugioniformis* are succulents, the latter has an astringent taste and is often salty (Louw and Beukes 1988, de Villiers, et al. 2001) so that it is less favoured browse by rabbits.

Plant species subject to intense rabbit herbivory tend to have a robust positive growth response to cessation of rabbit herbivory (see review in Introduction). This was borne out by vegetation changes at strand sites following rabbit control. The highly palatable *T. fruticosa* mainly drove grazing capacity increase across the sites while the palatable *E. longiflora* was of intermediate and the less palatable *E. villosa* minor importance. However, this seems to have not been the case at inland dune sites where *E. villosa* was of greater importance in driving grazing capacity increase than *E. longiflora* and the palatable *A. fatua*. This discrepancy is, however, of no import as it is rather the competitive advantage of *E. villosa* on dune environments (Hertling 1997, Harrington, et al. 1998, Coetzee 2008) that most likely accounted for its significant role in vegetation change at inland dune sites following rabbit control. *Ehrharta villosa* reacts positively to sand burial by rapidly extending its upright stems from subterranean rhizomes (Hertling 1997, Harrington, et al. 1998). Furthermore, it has a deep rhizome system that helps with competition on dunes for moisture by allowing access to water from deep below the soil surface (Harrington, et al. 1998). *Ehrharta villosa* roots also have higher levels of mycorrhizal infection than most other species with which it competes (Harrington, et al. 1998). Mycorrhizae enable plants to draw more nutrients and water from the soil than their roots would otherwise access. The perennial grass also has long stems – often to a height of two metres or more – which enable it to grow over surrounding vegetation and outcompete co-occurring species for light (Harrington, et al. 1998). In contrast, the annual grasses *E. longiflora* and *A. fatua* grow to a metre in height (Halvorson and Guertin 2003, Winston, et al. 2014). The annual grasses also reproduce from seeds that require sunny, moist open areas for successful germination (Parker, et al. 1982, Halvorson and Guertin 2003, Muhl 2008, Winston, et al. 2014) while *E. villosa* regenerates through rhizome growth, spreading rapidly by between 34 and 75 cm per month (Hodder 1997). Plants that regenerate from rhizomes can withstand drier conditions than those that depend on seed germination. As a result of these competitive advantages, *E. villosa* occurs in abundance and is often the only grass in dune areas within Strandveld vegetation (Coetzee 2008). Thus, *E. longiflora* responded with greater robustness to rabbit control when freed from overwhelming *E. villosa* competition at strand sites where soils were shallower and conferred less competitive advantage to the latter species. Likewise, the minor importance of *A. fatua* in driving species response at inland dune sites was clearly an artifact of competition with *E. villosa*. However, unlike *E. longiflora*, *A. fatua* was unable to escape competition with *E. villosa* at inland dune sites as it could not successfully establish itself at strand sites because of their shallow and seasonally waterlogged soils. This was because, although *A. fatua* seeds can persist for extended periods (up to 7-10 years) when buried >5 cm under the soil surface, they are much less durable under shallow burial and rapidly (in 1-2 months) lose their viability when deposited in standing water or waterlogged soils (Halvorson and Guertin 2003). Due to the occurrence of deep soils and the resulting greater availability of suitable habitat for recovering palatable species, grazing capacity across inland dune sites increased to a higher-level than at strand sites following rabbit control.

Although our results indicate that long-term rabbit herbivory on Robben Island has not resulted in complete loss of palatable plant species from the vegetation and seedbanks, there are indications that several such species may have been lost through the process. Strandveld vegetation, to which Cape Flats Dune Strandveld on Robben Island belongs, is generally used for stock-farming (cattle and sheep) because of its high grazing capacity and a large proportion of palatable species (Liengme 1987). However, the increase in grazing capacity observed during this study was driven by only four palatable species — *T. fruticosa*, *E. villosa*, *E. longiflora* and *A. fatua*. This may be an indication that many palatable species have indeed disappeared from the island vegetation and seedbanks because of prolonged rabbit herbivory, with the four species above remaining only because of their comparatively higher resilience to the adverse effects of rabbit browsing and grazing. For example, although European rabbits can browse *T. fruticosa* shrubs to their shoot base, they usually have trouble consuming the entire plant (Adamson 1934). As a result, severely browsed plants can later recover (Adamson 1934). Furthermore, *T. fruticosa* has long-lived seed borne in rigid envelopes that require extended periods to allow soil moisture to penetrate for germination (van Breda and Barnard 1991). *Tetragonia fruticosa* plants can therefore withstand heavy herbivory as long-lived seed. Similarly, the annual grasses *E. longiflora* and *A. fatua* produce large numbers of persistent soil-stored seeds that enable them to re-establish by mass germination (Halvorson and Guertin 2003, Fisher, et al. 2009, Winston, et al. 2014). A single *A. fatua* plant can produce up to 500 seeds that can stay dormant in the soil for seven to ten years (Halvorson and Guertin 2003). Furthermore, the short annual period of growth of *E. longiflora* and *A. fatua* exposes them to rabbit grazing for a considerably lesser period than most other plants such that a proportion of their adult plants manage to survive even during episodes of heavy rabbit herbivory to flower and produce fresh seed (Halvorson and Guertin 2003, Fisher, et al. 2009, Winston, et al. 2014). Periods of heavy rabbit herbivory appear to have occurred intermittently and over short timespans on the island. The short periods of high rabbit densities may have allowed palatable species that could withstand heavy rabbit herbivory such as *T. fruticosa*, *E. villosa*, *E. longiflora* and *A. fatua* to recover and persist in the vegetation and seedbanks.

Future research needs

As noted above, the prolonged occurrence (>300 years) of rabbits on Robben Island may have led to the progressive extirpation of palatable plant species other than relic *T. fruticosa*, *E. villosa*, *E. longiflora* and *A. fatua*. Such an outcome would have been possible even though rabbit numbers were low for most of their history on the island. Herbivory by even a few rabbits has been shown to have a considerable cumulative effect on vegetation over time (Farrow 1917, Cooke 2017, Cooke 2021). Furthermore, periods of heavy rabbit herbivory appear to have occurred intermittently and over short timespans on the island. The short periods of high rabbit densities may have allowed more resilient palatable species that could withstand heavy rabbit herbivory such as *T. fruticosa*, *E. villosa*, *E. longiflora* and *A. fatua* to recover and persist. However, other palatable species less resilient to heavy rabbit herbivory would have instead been wholly removed. It is, however, unclear if these less resilient palatable species have been eliminated locally from our study sites or the entire island. In either case, the chances and timing of the eliminated species return to affected areas will depend on their dispersal range, barriers to dispersal, and refugia distance. There is, therefore, a need for further monitoring of vegetation change on the island to determine if other palatable species additional to *T. fruticosa*, *E. villosa*, *E. longiflora* and *A. fatua* will return to the study sites in later years, including their timing and, if possible, source areas (e.g., refugia sites on the island or mainland populations across the Atlantic Ocean). Such information could clarify, among other things, whether the removal of European rabbits can be regarded as being sufficient in facilitating full recovery of grazing capacity on the island or inadequate due to the island's vegetation having been degraded by prolonged rabbit herbivory to such an extent that it is now trapped in an alternative quasi-stable depauperate state from which it cannot transition without the application of additional active restoration interventions (see Holmes, et al. 2020 for a discussion on degradation thresholds, alternative ecological states, and passive and active restoration). In the latter case, eradication of rabbits would need to be coupled with additional restoration actions, such as the replanting or reseeding of missing native palatable species, to ensure the complete recovery of grazing capacity. Indeed, there is speculation in the literature (see, for e.g., Adamson 1934, Nankivell 1934, Cooper and Brooke 1982, Brooke and Prins 1986) that long-standing rabbit herbivory on invaded South African offshore islands may have driven ecosystems past critical ecological thresholds such that simply removing rabbits may no longer lead to unaided restoration back to the original vegetation. Under this scenario, the removal of invasive European rabbits from Robben Island would then be best regarded as a baseline activity towards the overall goal of restoring or rehabilitating vegetation grazing capacity on the island.

Conclusion

Our study showed that control of European rabbits resulted in recovery of grazing capacity on Robben Island. The increase in grazing capacity was driven by the re-establishment of a highly palatable shrub (*T. fruticosa*) and palatable grasses (*E. villosa*, *E. longiflora* and *A. fatua*) in response to release from rabbit herbivory. This was accompanied by a decline in the abundance of the less palatable perennial herb *C. pugioniformis* through increased inter-specific competition with the re-establishing palatable species. These dynamics were in accordance with findings in the literature that control of rabbit abundance commonly leads to recovery in grazing capacity due to the re-establishment of palatable plants in response to release from herbivory pressure (see references in the Introduction). Furthermore, the changes in plant species cover were in accordance with observations in the literature that recovery of grazing capacity following rabbit control is commonly driven by palatable species that are subject to the most intense rabbit herbivory and is frequently accompanied by a decline in abundance of less palatable and unpalatable species. The latter species, which increase in abundance during rabbit herbivory, decline in response to inter-specific competition with recovering palatable species. Lastly, the results of the study disproved the supposition that long-term rabbit herbivory had caused complete loss of palatable plant species from the island vegetation and seedbanks although some palatable species may have been lost from localised sites or the island. Plant species that drove grazing capacity increase following rabbit control — *T. fruticosa, E. villosa*, *E. longiflora* and *A. fatua* — were most likely a subset of the full complement of palatable species that occurred on the island before the introduction of rabbit herbivory. The four species are highly resilient to heavy rabbit herbivory as they can either escape or withstand its effects (see discussion on impact of rabbit control on grazing capacity above).

Although South African offshore islands vary in geology, size, distance offshore and climatic conditions, we believe that grazing capacity across the islands would respond similarly to rabbit invasion and control as on Robben Island. This would be particularly the case with other Mediterranean-type offshore islands (e.g., Bird, Dassen, Dyer and Seal) on which rainfall, like on Robben Island, is confined to the winter months. However, the actual plant species involved, and the nature of their roles would differ between the islands due to their different species composition (see Gillham 1963 for a discussion on the different forage species that occur on, for e.g., Jutten, Robben, Meeuw and Schaapen islands). Furthermore, species responses to rabbit control would also vary within islands in tandem with spatial variation in environmental factors such as soil depth, underlying substrate and drainage regimes (see discussion on impact of rabbit control on grazing capacity above for an example of the influence of landscape variation in vegetation overstory, soil depth and drainage regime on vegetation species response to rabbit control).

References

Adams MA, Attiwill PM. 1986. Nutrient cycling and nitrogen mineralization in eucalypt forests of south-eastern Australia. 1. Nutrient cycling and nitrogen turnover. *Plant and Soil* 92: 319–339.

Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

Alexander JM. 1989. The long-term effect of *Eucalyptus* plantations on tin-mine spoil and its implication for reclamation. *Landscape and Urban Planning* 17: 413–433.

Anon. 2008a. Rabbits a threat to Robben Island. 'Available at' https://www.iol.co.za/news/south-africa/rabbits-a-threat-torobben-island-420389 [accessed 8 February 2017]

Anon. 2008b. Robben Island's rabbits to be culled. 'Available at' https://www.iol.co.za/news/south-africa/robben-islands-rabbits-to-be-culled-420363 [accessed 8 February 2017]

Apps P. 1984. Cats on Dassen Island. *Acta Zoologica Fennica* 172: 115-116.

Austin MP, Williams OB, Belbin L. 1981. Grassland dynamics under sheep grazing in an Australian Mediterranean type climate. *Vegetatio* 47: 201-211.

Bacon PE, Stone C, Binns DL, Leslie DJ, Edwards DW. 1993 Relationships between water availability and *Eucalyptus camaldulensis* growth in a riparian forest *Journal of Hydrology* 150: 541-561.

Barbier S, Gosselin F, Balandier P. 2008 Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests. *Forest Ecology and Management* 254: 1-15.

Barbraud C, Delord K, Le Bouard F, Harivel R, Demay J, Chaigne A, Micol T. 2021. Seabird population changes following mammal eradication at oceanic Saint-Paul Island, Indian Ocean. *Journal for Nature Conservation* 63: 126049.

Bayer MB. 1990. A proposed method of veld condition assessment for the winter rainfall region. Unpublished internal research report. *Elsenburg: Elsenburg Agricultural Development Institute (Western Cape Department of Agriculture). Available at http:// www.elsenburg.com/trd/plantprod/downloads/assessveld.pdf [accessed 29 June 2009]*.

Bello-Rodríguez V, Mateo RG, Pellissier L, Cubas J, Cooke B, González-Mancebo JM. 2021. Forecast increase in invasive rabbit spread into ecosystems of an oceanic island (Tenerife) under climate change. *Ecological Applications* 31: e02206.

Bernhard-Reversat F. 1988. Soil nitrogen mineralization under a *Eucalyptus* plantation and a natural *Acacia* forest in Senegal. *Forest Ecology and Management* 23: 233-244.

Bernhard-Reversat F. 1996. Nitrogen cycling in tree plantations grown on a poor sandy savanna soil in Congo. *Applied Soil Ecology* 4: 161–172.

Booysen PDV. 1967. Grazing and grazing management terminology in southern Africa. *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa* 2: 45- 57.

Bossard CC, J.M. R, Hoshovsky MC. 2000. *Invasive plants of California's wildlands*. Berkeley: University of California Press.

Box G, Cox D. 1964. An analysis of transformations. *Journal of the Royal Statistical Society* 26: 211-234.

Brooke RK, Crowe TM. 1982. Variation in species richness among the offshore islands of the southwestern Cape. *South African Journal of Zoology* 17: 49-58.

Brooke RK, Prins AJ. 1986. Review of alien species on South African offshore islands. *South African Journal of Antarctic Research* 16: 102-109.

Bruton M. 2021. Biological invasions in South Africa. *Transactions of the Royal Society of South Africa* 76: 301-305.

Cleeland JB, Pardo D, Raymond B, Terauds A, Alderman R, McMahon CR, Phillips RA, Lea M-A, Hindell MA. 2020. Introduced species and extreme weather as key drivers of reproductive output in three sympatric albatrosses. *Scientific Reports* 10: 8199.

Coetzee K. 2008. Blaauwberg Conservation Area: management guidelines for larger wildlife and their habitats. *Report prepared for the Biodiversity Management Branch, City of Cape Town*.

Cooke B. 2017. Effects of pastoralism and rabbits on the economy and culture of the Diyari people of north-eastern South Australia. *Australian Economic History Review* 57: 65-83.

Cooke BD. 1991. Rabbits: indefensible on any grounds. *Search* 22: 193–194.

Cooke BD. 2021. Pasture plant biomass increase following introduction of European rabbit fleas, *Spilopsyllus cuniculi*, into Australia to facilitate myxomatosis transmission. *Biological Control* 155: 104536.

Cooper J, Brooke RK. 1982. Past and present distribution of the feral European rabbit *Oryctolagus cuniculus* on southern African offshore islands. *South African Journal of Wildlife Research* 12: 5-71.

Crawford R, Dyer B. 2000. Wildlife of Robben Island. In: Underhill L editor. *Bright Continent Guide*. Cape Town: Avian Demography Unit.

Crawley MJ. 1990. Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology* 27: 803-820.

Cubas J, Martín-Esquivel JL, Nogales M, Irl SDH, Hernández-Hernández R, López-Darias M, Marrero-Gómez M, del Arco MJ, González-Mancebo JM. 2018. Contrasting effects of invasive rabbits on endemic plants driving vegetation change in a subtropical alpine insular environment. *Biological Invasions* 20: 793-807.

Cubas J, Severin DH, Villafuerte R, Bello-Rodríguez V, Rodríguez-Luengo JL, del Arco M, Martín-Esquivel JL, González-Mancebo JM. 2019. Endemic plant species are more palatable to introduced herbivores than non-endemics. *Proceedings of the Royal Society B: Biological Sciences* 286: 20190136.

Davies S, Jordaan M, Karsten M, Terblanche J, Turner A, van Wilgen N, Veldtman R, Zengeya T, Measey J. 2020. Experience and lessons from alien and invasive animal control projects in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology*. Cham: SpringerOpen. p. 1302-1381.

de Villiers AJ, van Rooyen MW, Theron GK. 2001. Seedbank phytosociology of the Strandveld Succulent Karoo, South Africa: a pre-mining benchmark survey for rehabilitation. *Land Degradation and Development* 12: 119-130.

de Villiers MS, Mecenero S, Sherley RB, Heinze E, Kieser J, Leshoro TM, Merbold L, Nordt A, Parsons NJ, Peter HU. 2010. Introduced European rabbits (*Oryctolagus cuniculus*) and domestic cats (*Felis catus*) on Robben Island: Population trends and management recommendations. *South African Journal of Wildlife Research* 40: 139-148.

de Vos A, Manville RH, Van Gelder RG. 1956. Introduced mammals and their influence on native biota. *Zoologica (New York)* 41: 163-194.

del Moral R, Muller CH. 1969. The allelopathic effect of *Eucalyptus camaldulensis American Midland Naturalist* 83: 254–282.

Delibes-Mateos M. 2017. Rumours about wildlife pest introductions: European rabbits in Spain. *Ambio* 46: 237-249.

Diaz A. 2000. Can plant palatability trials be used to predict the effect of rabbit grazing on the flora of ex-arable land? *Agriculture, Ecosystems & Environment* 78: 249-259.

Dingle RV, Rogers J. 1972. Pleistocene palaeogeography of the Agulhas Bank. *Transactions of the Royal Society of South Africa* 40: 155–165.

Donlan JC, Tershy BR, Croll DA. 2002. Islands and introduced herbivores: conservation action as ecosystem experimentation *Journal of Applied Ecology* 39: 235-246.

Doornik JA, Hansen H. 1994. An omnibus test for univariate and multivariate normality. *W4&91 in Nuffield Economics Working Papers*.

Duffy S, Fairley J, O'Donnell G. 1996. Food of rabbits *Oryctolagus cuniculus* on upland grasslands in Connemara. *Biology and Environment: Proceedings of the Royal Irish Academy* 96B: 69-75.

Durbin J, Watson GS. 1951. Testing for serial correlation in least squares regression. *Biometrika* 37: 409-428.

Dye P, Jacobs S, Drew D. 2004. Verification of 3-PG growth and water-use predictions in twelve *Eucalyptus* plantation stands in Zululand, South Africa *Forest Ecology and Management* 193: 197-218.

Dye P, Versfeld D. 2007. Managing the hydrological impacts of South African plantation forests: An overview. *Forest Ecology and Management* 251: 121-128.

Eijzenga H. 2011. Vegetation change following rabbit eradication on Lehua Island, Hawaiian Islands. Paper presented at the International Conference on Island Invasives, Gland, Switzerland and Auckland, New Zealand.

Esler KJ, Jacobsen AL, Pratt RB. 2018. *The biology of Mediterranean-type ecosystems*. Oxford University Press.

Farrow EP. 1917. On the ecology of the vegetation of Breckland. III. General effects of rabbits on the vegetation. *Journal of Ecology* 5: 1-18.

Finlayson G, Taggart P, Cooke B. 2021. Recovering Australia's arid-zone ecosystems: learning from continental-scale rabbit control experiments. *Restoration Ecology* 30: e13552.

Fisher JL, Loneragan WA, Dixon K, Veneklaas EJ. 2009. Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. *Biological Conservation* 142: 256-269.

Flux J, Fullagar P. 1992. World distribution of the rabbit *Oryctolagus cuniculus* on islands. *Mammal Review* 22: 151-205.

Foran BD. 1986. The impact of rabbits and cattle on an arid calcareous shrubby grassland in central Australia. *Vegetatio* 66: 49-59.

Foran BD, Low WA, Strong BW. 1985. The response of rabbit populations and vegetation to rabbit control on a calcareous shrubby grassland in central Australia. *Wildlife Research* 12: 237-247.

Forkman J, Josse J, Piepho H. 2019. Hypothesis tests for Principal Component Analysis when variables are standardized. *Journal of Agricultural, Biological, and Environmental Statistics* 24: 289-308.

Forstmeier W, Wagenmakers E-J, Parker TH. 2017. Detecting and avoiding likely false-positive findings - a practical guide. *Biological Reviews* 92: 1941-1968.

Friedel MH. 1985. The population structure and density of central Australian trees and shrubs, and relationships to range condition, rabbit abundance and soil. *Australian Journal of Wildlife Research* 7: 130-139.

Gaertner M, Richardson DM, Privett SD. 2011. Effects of alien plants on ecosystem structure and functioning and implications for restoration: insights from three degraded sites in South African fynbos. *Environmental Management* 48: 57–69.

Gillham EM. 1955. Ecology of the Pembrokeshire Islands. III. The effect of grazing on the vegetation. *Journal of Ecology* 43: 172-207.

Gillham ME. 1963. Some interactions of plants, rabbits and sea-birds on South African islands. *Journal of Ecology* 51: 275-294.

Gillison AN, Brewer KR. 1985. The use of gradient directed transects or gradsects in natural resource surveys. *Journal of Environmental Management* 20: 103-127.

Guo LB, Sims REH. 2001. Effects of light, temperature, water and meat works effluent irrigation on eucalypt leaf litter decomposition under controlled environmental conditions. *Applied Soil Ecology* 17: 229–237.

Hall EAA, Specht RL, Eardley CM. 1964. Regeneration of the vegetation on Koonamore Vegetation Reserve, 1926-1962. *Australian Journal of Botany* 12: 205-264.

Halvorson WL, Guertin P. 2003. Factsheet for: *Avena fatua* L. . *USGS Weeds in the West project: status of introduced plants in Southern Arizona parks*. Tucson: U.S. Geological Survey / Southwest Biological Center.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Palaeontological Statistics Software Package for Education and Data Analysis. *Available at http://palaeo-electronica.org/2001/past/issue101.htm [Accessed 24 August 2010]*.

Harrington KC, Hodder LM, Outred HA. 1998. Biology and control of pypgrass. Paper presented at the Proceedings of the 51st New Zealand Plant Protection Conference.

Herrick JE, van Zee JW, Havstad KM, Burkett LM, Whitford WG. 2005. *Monitoring manual for grassland, shrubland and savanna ecosystems: Volume 1 Quickstart*. Las Cruces: USDA-ARS Jornada Experimental Range.

Hertling UM. 1997. *Ammophila arenaria* (l.) Link (Marram grass) in South Africa and its potential invasiveness. DPhil, Rhodes University, Grahamstown.

Hobbs RJ, Grace J. 1981. A study of pattern and process in coastal vegetation using principle components analysis. *Vegetatio* 44: 137-153.

Hodder LM. 1997. The biology and control of *Ehrharta villosa*, South African pypgrass. MSc, Massey University, Auckland.

Hoffman MT, Madden CF, Erasmus K, Saayman N, Botha JC. 2009. The impact of indigenous ungulate herbivory over five years (2004–2008) on the vegetation of the Little Karoo, South Africa. *African Journal of Range & Forage Science* 26: 169-179.

Hoffman MT, Madden CF, Erasmus K, Saayman N, Botha JC, Kruger FJ. 2010. Measuring the impact of indigenous herbivores: reply to Kerley and Landman. *African Journal of Range & Forage Science* 27: 181-183.

Holmes PM, Esler KJ, Gaertner M, Geerts S, Hall SA, Nsikani MM, Richardson DM, Ruwanza S. 2020. Biological invasions and ecological restoration in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology*. Cham, Switzerland: Springer Open. p. 665-700.

Hunt LP. 2001. Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. *Journal of Applied Ecology* 38: 238–252.

Johnson DH. 2002. The importance of replication in wildlife research. *The Journal of Wildlife Management* 66: 919-932.

Kerley GI, Landman M. 2010. Measuring the impact of indigenous herbivores: putting Hoffman et al. (2009) into a broader perspective. *African Journal of Range & Forage Science* 27: 179–180.

Khan MA, Hussain I, Khan EA. 2008 Allelopathic effects of *Eucalyptus* (*Eucalyptus camaldulensis* L.) on germination and seedling growth of wheat (*Tricum aestivum* L.). *Pakistan Journal of Weed Science Research* 14: 9-18.

Lange RT, Graham CR. 1983. Rabbits and the failure of regeneration in Australian arid zone *Acacia*. *Australian Journal of Ecology*. 8: 377-381.

Latham ADM, Latham MC, Norbury GL, Forsyth DM, Warburton B. 2020. A review of the damage caused by invasive wild mammalian herbivores to primary production in New Zealand. *New Zealand Journal of Zoology* 47: 20-52.

Le Houérou HN. 1984. Rain use efficiency: a unifying concept in arid-land ecology *Journal of Arid Environments* 7: 213-247.

Le Houérou HN, Bingham RL, Skerbek W. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments* 15: 1-18.

Le Maitre DC, van Wilgen BW, Gelderblom C, Bailey C, Chapman R, Nel J. 2002. Invasive alien trees and water resources in South Africa: case studies of the costs and benefits of management *Forest Ecology Management*. 160: 143-159.

Leigh JH, Wood DH, Holgate MC, Slee A, Stanger MG. 1989. Effects of rabbit and kangaroo grazing on two semi-arid grass- land communities in central-western New South Wales. *Australian Journal of Botany* 37: 375-396.

Lever C. 1985. *Naturalised mammals of the world*. London: Longman.

Liengme CA. 1987. West Coast Strandveld: its utilization and management. MSc. Thesis, University of Cape Town, Cape Town.

Lloyd JW, Linger MT. 1986. Report on the vegetation of Robben Island. *'n Natuurbewaringsondersoek van Robbeneiland*. Cape Town: Cape Nature

Long JL. 2003. *Introduced mammals of the world: their history, distribution and influence*. Collingwood: CSIRO Publishing.

Loumeto JJ, Huttel C. 1997. Understory vegetation in fast-growing tree plantations on savanna soils in Congo. *Forest Ecology and Management* 99: 65–81.

Louw G, Beukes T. 1988. Ken ons veldplante. *Die Noordwester*: 6-12.

Marchante E, Kjoller A, Struwe S, Freitas H. 2008 Short- and long- term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. *Applied Soil Ecology* 40: 210–217.

Mátrai K, Altbäcker V, Hahn I. 1998. Seasonal diet of rabbits and their browsing effect on juniper in Bugac Juniper Forest (Hungary). *Acta Theriologica* 43: 107-112.

May EF, Ash JE. 1990 An assessment of the allelopathic potential of *Eucalyptus*. *Australian Journal of Botany* 38: 245–254.

McCune B, Grace JB, Urban DL. 2002. *Analysis of ecological communities* Gleneden Beach: MjM Software Design.

Measey J, Hui C, Somers MJ. 2020. Terrestrial vertebrate invasions in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology* No. 14. Cham, Swtzerland: Springer Open. p. 115-151.

Meissner HH, Hofmeyr HS, van Rensburg WJJ, Pienaar JP (eds). 1983. *Classification of livestock for realistic prediction of substitution values in terms of a biologically defined large stock unit*. Department of Agriculture. Pretoria.

Michener WK. 1997. Quantitatively evaluating restoration experiments: research design, statistical analysis, and data management consideration. *Restoration Ecology* 5: 324-337.

Miller D. 1991. A geological description of Robben Island. *South African Lapidary Magazine* 23: 5-8.

Moore CB, Moore JH. 2007. Annual veldgrass: *Ehrarta longiflora* Smith. HerbiGuide - The Pesticide Expert on a Disk Available at http://www.herbiguide.com.au/Descriptions/hg_Annual_Veldtgrass.htm. [accessed 25 September 2017]

Mucina L, Adams JB, Knevel IC, Rutherford MC, Powrie LW, Bolton JJ, van der Merwe JH, Anderson RJ, Bornman TG, le Roux A*, et al.* 2006. Coastal vegetation of South Africa. In: Mucina L, Rutherford MC editors. *The vegetation of South Africa, Lesotho and Swaziland*. *Strelitzia 19*. Pretoria: South African National Biodiversity Institute.

Mucina L, Rutherford M (eds). 2006. *Vegetation map of South Africa, Lesotho, and Swaziland*. Pretoria: South African National Biodiversity Institute.

Muhl SA. 2008. Alien grass invasion of Renosterveld: Influence of soil variable gradients. MSc, Stellenbosch University, Stellenbosch.

Myers K, Poole WE. 1963. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations IV. The effects of rabbit grazing on sown pastures. *Journal of Ecology* 51: 435-451.

Nakagawa S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology* 15: 1044-1045.

Nankivell JW. 1934. Robben Island. *The South African Geographical Journal* 17: 29-34.

Norbury DC, Norbury GL. 1996. Short-term effects of rabbit grazing on a degraded short-tussock grassland in Central Otago. *New Zealand Journal of Ecology* 20: 285-288.

Nunes SF, Mota-Ferreira M, Sampaio M, Andrade J, Oliveira N, Rebelo R, Rocha R. 2021. Trophic niche changes associated with the eradication of invasive mammals in an insular lizard: an assessment using isotopes. *Current Zoology* 68: 211-219.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H 2015. vegan: Community Ecology Package. R package version 2.2-1. http://CRAN.R-project.org/package=vegan.

Pacala SW, Crawley MJ. 1992. Herbivores and plant diversity. *American Naturalist* 40: 243-260.

Parker VT, Muller CH. 1982. Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. *American Midland Naturalist* 107: 69-81.

Pauw MJ. 2011. Monitoring ecological rehabilitation on a coastal mineral sands mine in Namaqualand, South Africa. MSc thesis, Stellenbosch University, Stellenbosch.

Pennell CGL, Rolston MP, Latham ADM, Mace WJ, Vlaming B, van Koten C, Latham MC, Brown S, Card SD. 2016. Novel grass–endophyte associations reduce the feeding behaviour of invasive European rabbits (*Oryctolagus cuniculus*). *Wildlife Research* 43: 681.

Pereira HM, Navarro LM, Martins IS. 2012. Global biodiversity change: the bad, the good, and the unknown. *Annual Review of Environment and Resources* 37: 25-50.

Philander R. 2017. Robben Island to cull deer. 'Available at' https://www.iol.co.za/capeargus/news/robben-island-to-cull-deer-9940208 [accessed 26 October 2017]

Pike N. 2011. Using false discovery rates for multiple comparisons in ecology and evolution. *Methods in Ecology and Evolution* 2: 278–282.

R Core Team 2020. R: A Language and Environment for Statistical Computing. Vienna http://www.R-project.org/: R Foundation for Statistical Computing

Rebelo AG, Holmes PM, Dorse C, Wood J. 2011. Impacts of urbanization in a biodiversity hotspot: conservation challenges in Metropolitan Cape Town. *South African Journal of Botany* 77: 20–35.

Robben Island Museum (ed). 2006. *Integrated Conservation Management Plan (ICMP) for the Robben Island World Heritage Site*. Robben Island Museum Cape Town.

Romesburg HC. 1981. Wildlife science: gaining reliable knowledge. *The Journal of Wildlife Management* 45: 293-313.

Saayman N, Morris CD, Hardy MB, Botha JC. 2009. Can brush-cutting of *Pteronia paniculata* improve the composition and productivity of veld in the Succulent Karoo, South Africa? *African Journal of Range & Forage Science* 26: 181–190.

Sakia RM. 1992. The Box-Cox transformation technique: A review. *The Statistician* 41: 169-178.

SANBI. 2011. Threatened terrestrial ecosystems for South Africa, Cape Flats Dune Strandveld (FS6). Available at http://bgis.sanbi.org/ecosystems/showecosystem.asp?id=63 [accessed 18 October 2017].

Sasikumar K, Vijayalakshmi C, Parthiban KT. 2001. Allelopathic effects of *Eucalyptus* on Redgram (*Cajanus cajan* L.). *Journal of Tropical Agriculture* 39: 134-138.

Schmalzer PA, Hinkle CR (eds). 1987. *Species biology and potential for controlling four exotic plants (Ammophila arenaria, Carpobrotus edulis, Cortaderia jubata, and Gasoul crystallinum) on Vandenberg Air Force Base, California*. National Aeronautics and Space Administration, John F. Kennedy Space Center. Florida.

Schweizer D, Jones HP, Holmes ND. 2016. Literature review and meta-analysis of vegetation responses to goat and European rabbit eradications on islands. *Pacific Science* 70: 55-71.

Shapiro SS, Wilk MB. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52: 591-611.

Sherley RB. 2016. Unusual foraging behaviour in two introduced mammals following degradation of their island habitat. *Biodiversity Observations* 7: 1-10.

Skead CJ. 2011. Historical incidence of the larger land mammals in the broader Western and Northern Cape In: Boshoff AF, Kerley GIH, Lloyd PH editors. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.

Smith C. 1997. *Robben Island*. South Africa: Struik Publishers.

Smith EP. 2002. BACI design In: El-Shaarawi AH, Piegorsch WW editors. *Encyclopedia of environmetrics*. Chichester: Wiley p. 141-148.

Stewart-Oaten A, Bence JR. 2001. Temporal and spatial variation in environmental impact assessment. *Ecological Monographs* 71: 305-339.

Stewart-Oaten A, Murdoch WW, Parker KR. 1986. Environmental impact assessment: "pseudoreplication" in time? *Ecology* 67: 929-940.

Strive T, Cox TE. 2019. Lethal biological control of rabbits – the most powerful tools for landscape-scale mitigation of rabbit impacts in Australia. *Australian Zoologist* 40: 118-128.

Stubbendieck J, Hatch SL, Butterfield CH. 1992. *North American Range Plants*. Lincoln, Nebraska: University of Nebraska Press.

Tainton NM, Bransby DI, Booysen Pd. 1990. *Common veld and pasture grasses of Natal* (2nd edn). Pietermaritzburg: Shuter and Shooter.

Tankard AJ. 1976. Cenozoic sea-level changes: a discussion. *Annals of the South African Museum* 71: 1–17.

ter Braak CJF, Looman CWN. 1994. Biplots in reduced-rank regression. *Biometrical Journal* 36: 983-1003.

Toky OP, Singh V. 1993. Litter dynamics in short-rotation high density tree plantations in an arid region of India. *Agriculture, Ecosystems & Environment* 45: 129-145.

Travers T, Lea MA, Alderman R, Terauds A, Shaw J. 2021. Bottom-up effect of eradications: The unintended consequences for top-order predators when eradicating invasive prey. *Journal of Applied Ecology* 58: 801-811.

UWC Cape Flats Indigenous Nursery. 2021. Propagating *Phyllobolus canaliculatus* (Vingerkanna). Available at https://www.pinterest.co.uk/pin/593490057135262691/ [accessed 22 March 2021]

van Breda PAB, Barnard SA. 1991. *100 veld plants of the winter rainfall region: A guide to the use of veld plants for grazing*. Pretoria: Department of Agricultural Development.

van Breda PAB, Nel EJ, Bayer MB (eds). 1990. *Palatability of plant species – winter rainfall region: Little Karoo and Ceres Karoo* Elsenburg Agricultural Development Institute van den Berg L, van Lingen M (eds). 2009. *Weidingswaardes (WIW) vir Karoo plantspesies – Hersiene weergawe*. Grootfontein Agricultural Development Institute. Middelburg.

van Oudtshoorn F. 2012. *Guide to grasses of southern Africa*. Pretoria: Briza Publications.

Verdaguer D, Sala A, Vilà M. 2010. Effect of environmental factors and bulb mass on the invasive geophyte *Oxalis pes-caprae* development *Acta Oecologica* 36: 92–99.

Vosloo E. 2008. Eco-xenophobia' for island's deer 'Available at' https://www.iol.co.za/news/south-africa/eco-xenophobia-for-islands-deer--403624 [accessed 8 February 2017]

Weissgerber TL, Garovic VD, Milin-Lazovic JS, Winham SJ, Obradovic Z, Trzeciakowski JP, Milic NM. 2016. Reinventing biostatistics education for basic scientists. *PLoS Biology 14*: *e1002430*.

Western Australian Herbarium. 1998. FloraBase - the Western Australian Flora. Department of Parks and Wildlife. Available at https://florabase.dpaw.wa.gov.au. [accessed 22 March 2021]

Williams AJ, Klages NTW, Crawford RJM. 2000. Functional ecosystems: Coastal islands. In: Durham BD, Pauw JC editors. *Summary Marine Biodiversity Status Report for South Africa*. Pretoria: National Research Foundation.

Williams K (ed). 2011. *Managing Rabbits in Canberra Nature Park*. Office of the Commissioner for Sustainability and the Environment. Canberra.

Williams K, Parer I, Coman B, Burley J, Braysher M. 1995. *Managing vertebrate pests: rabbits* Canberra: Australian Government Publishing Service

Winston R, DesCamp W, Andreas J, Randall CB, Milan J, Schwarzländer M. 2014. *New invaders of the Southwest*. Washington, DC: Forest Health Technology Enterprise Team, United States Department of Agriculture.

Yeld J. 2008. Robben Island conservation 'in a shambles'. 'Available at' http://www.iol.co.za/news/south-africa/robben-island-conservation-in-a-shambles-1.398514#.Utf_RYWRa1s [accessed 8 February 2017]

Zhang D, Zhang J, Yang W, Wu F. 2010. Potential allelopathic effect of *Eucalyptus grandis* across a range of plantation ages. *Ecological Research* 25: 13-23.

CHAPTER 6

Vegetation response to control of invasive alien European rabbits (*Oryctolagus cuniculatus*) on South African offshore islands. A general theoretic model and island-specific hypotheses

Overview

This chapter is as a culmination of the preceding three data chapters, drawing together the key findings and insights gained from the research on Robben Island. It presents a comprehensive synthesis of the vegetation's responses to rabbit control, develops a general theoretical framework for understanding these responses, and formulates island-specific hypotheses for future research and conservation efforts. The chapter is structured as follows: Section I introduces the chapter's purpose. Section II summarises key findings from each empirical chapter, highlighting significant changes in vegetation composition, diversity, cover, and grazing capacity after rabbit control. Section III examines the ecological factors and vegetation processes driving these changes, providing a mechanistic understanding of the response. Section IV synthesises Sections II and III to develop a conceptual model for Robben Island, serving as a foundation for extrapolation to other South African offshore islands. Section V formulates a theoretical framework to predict vegetation responses on other invaded islands (Dassen, Jutten, Schaapen, Seal, and Vondeling Islands), building on Robben Island insights. Section VI applies the framework to explore potential vegetation responses on specific invaded islands. Section VII discusses the implications for managing vegetation on the other invaded islands, considering ecosystem similarities and differences, and rabbit control's effectiveness as a restoration tool. Section VIII concludes by summarising key takeaways and highlighting the broader implications for conservation and management of invaded island ecosystems globally, including the potential of rabbit control as a powerful restoration tool.

I. Introduction

Invasive alien species (IAS) pose a significant threat to biodiversity, human health, and the economy. They disrupt ecological networks, degrade habitats, compete with native species, and spread diseases (Mazza, et al. 2014, IPBES 2023). Alarmingly, IAS are implicated in 60% of global extinctions, and in 16% of cases, they are the sole cause (Asian Development Bank 2023, IPBES 2023). Beyond biodiversity, they risk human health and result in substantial economic losses. IAS are responsible for 10% of global disease cases (Mazza, et al. 2014), and their cost to the global economy over the past 50 years is estimated at US$1.288 trillion (Diagne, et al. 2021). Currently, their annual global cost is at least US$423 billion (World Economic Forum 2023). These statistics underline the urgent need to address the IAS crisis. The European rabbit (*Oryctolagus cuniculus*) exemplifies the severe consequences of introducing IAS to new environments (Schweizer, et al. 2016, Fontanesi, et al. 2021). Introduced to over 800 islands and island groups worldwide, rabbits now pose significant threats to island biodiversity and human livelihoods (Schweizer, et al. 2016, Cubas, et al. 2019, Bello-Rodríguez, et al. 2021). They, among many other impacts, overgraze vegetation, compete with native animals, and can cause infrastructure damage. Their adverse impact has spurred global initiatives to eradicate them where possible (Schweizer, et al. 2016). Since the 1800s, there have been at least 90 successful rabbit eradications, with ongoing advances in methods (Schweizer, et al. 2016).

Amongst the islands and island groups worldwide afflicted by the introduction of European rabbits are the 33-plus offshore islands fringing the southern African coastline, 24 of which fall within South African borders (Cooper and Brooke 1986). Introduced to 13 South African islands in the 17th century and persisting on six (de Vos, et al. 1956, Skead 2011, Davies, et al. 2020, Measey, et al. 2020), rabbits have been documented to have had a substantial impact on the island vegetation, characterised by sustained selective browsing and grazing (Adamson 1934, Gillham 1963). This has effectively trapped the vegetation in early successional stages, owing to the removal of palatable late successional species (Adamson 1934, Nankivell 1934, Gillham 1963). Recent reviews have affirmed the ongoing detrimental influence of rabbits on offshore island flora, prompting their classification as Category 1b invasive species requiring control measures under South Africa's National Environmental Management: Biodiversity Act (NEM:BA) (Kumschick, et al. 2020, Bruton 2021). This thesis presents the first empirical studies investigating the response of vegetation on Robben Island, South Africa's largest and most ecologically compromised offshore island, to rabbit control. Notably, Robben Island is the only one among South Africa’s offshore islands where a sustained rabbit eradication programme has been implemented. While a qualitative evaluation by Cooper and Brooke (1982) noted enhanced vegetation cover on Meeuw Island five years after rabbits naturally died out, compared to the rabbit populated Schaapen Island, Robben Island offered the first opportunity for quantitative analysis of vegetation response to rabbit control on a South African offshore island. Brooke and Prins (1986) have proposed that rabbit eradication on larger islands like Schaapen, Jutten, Dassen, and Robben might initiate secondary vegetation succession, leading to the re-establishment of late-successional native plant species. However, other literature sources (e.g., Adamson 1934, Nankivell 1934, Cooper and Brooke 1982) suggest that persistent rabbit herbivory may have pushed island ecosystems beyond critical ecological thresholds, such that rabbit removal alone might not guarantee unaided succession back to the original natural vegetation. It is therefore of paramount importance to empirically determine the vegetation response to rabbit control on South African offshore islands to inform effective management strategies and ensure the preservation of these unique ecosystems.

In this chapter, I synthesise the empirical findings derived from Chapters 3 to 5 of this thesis into a cohesive conceptual model and overarching theoretical framework. I then utilise this framework to broaden understanding of vegetation response to rabbit control beyond Robben Island, extracting transferable insights applicable to other invaded South African offshore islands. The data used in these chapters were collected through four years (2010-2013) of monitoring vegetation change at nine sites on Robben Island (strand (n=3), eucalyptus (n=3), and inland dune (n=3)), following an attempted eradication of invasive European rabbits between 2008 and 2009. This study has four primary objectives:

1. To synthesise the key findings from the empirical chapters.
2. To integrate these findings into a coherent conceptual model of vegetation response on Robben Island.
3. To develop a general theoretical framework, drawing upon the consolidated findings and the conceptual model, that is applicable to other invaded islands.
4. To leverage this framework to formulate hypotheses about vegetation response on other invaded islands (Dassen, Jutten, Schaapen, Seal, and Vondeling Islands) following rabbit control or removal.

To achieve these goals, the study addresses the following questions:

1. How did vegetation composition, diversity, and grazing capacity change on Robben Island after rabbit control?

2. What ecological and vegetation processes drove these changes?
3. What are the implications for the potential response of vegetation on other invaded South African offshore islands?

Although South African offshore islands vary in geology, size, distance offshore, and climate, they share enough similarities to be considered a distinct biogeographical unit (Williams, et al. 2000). Therefore, studying vegetation dynamics on Robben Island can provide valuable insights into how vegetation might respond to rabbit control on other invaded offshore islands.

II. Summary of Key Findings from Empirical Chapters

In this section I consolidate the key findings from each of the empirical chapters (Chapters 3 to 5) in this thesis, highlighting the significant changes observed in vegetation composition, diversity, cover, and grazing capacity following rabbit control (Table 6.1).

Table 6-1 Chapter by chapter summary of changes in vegetation composition, diversity, and grazing capacity on Robben Island following rabbit control.

Empirical chapter	Hypotheses	Results
Chapter 3: Vegetation Composition	I had anticipated that vegetation on Robben Island would undergo secondary succession towards its original or projected undisturbed composition in response to rabbit control. Specifically, the hypothesis was that this succession would involve the re-establishment of late-successional perennial grasses, succulents, and herbs, as well as the recolonisation or increase in cover of woody shrubs.	• Contrary to expectations, vegetation on Robben Island did not undergo secondary succession towards its original or projected undisturbed composition in response to rabbit control. • Instead, changes in plant species composition across strand and inland dune sites were primarily driven by increases in the abundance of early successional species, including the woody shrub *Tetragonia fruticosa* and grasses *Ehrharta longiflora, Cynodon dactylon*, and *Ehraharta villosa*. • These changes were accompanied by reductions in the abundance of the early successional annual grass *Bromus diandrus* and perennial herbs *Oncosiphon suffruticosum* and *Conicosia pugioniformis*.

		• Vegetation composition did not change at eucalyptus sites following rabbit control. The lack of change in composition was due to subdued responses of *Phyllobolus canaliculatus*, *Oxalis pes-caprae* and *T. fruticosa* to rabbit control.
Chapter 4: Species Diversity	The expectation was that rabbit control on Robben Island would increase species diversity by enabling the re-establishment of previously suppressed palatable plant species. Moreover, I hypothesised that countervailing residual non-rabbit herbivory would prevent recovering palatable species from dominating the vegetation and, in turn, completely displace less competitive unpalatable and less palatable species, leading to even greater species diversity.	• Contrary to expectations, rabbit control resulted in a decline in species diversity across strand and inland dune sites while remaining unchanged at eucalyptus sites. • The decline in species diversity across strand and inland dune sites was driven by the loss of seven plant species (*Anagallis arvensis*, *Euphorbia peplus*, *Hypochaeris glabra*, *Wahlenbergia androsacea*, *Emex australis*, *Ornithoglossum viride* and *Trachyandra* sp.) which was offset by the emergence of a single species (*C. dactylon*) at strand sites.

		• Species evenness also declined across strand and inland dune sites in response to rabbit control. • Before rabbit control, species cover at strand and inland dune sites was dominated by four species (*Conicosia pugioniformis*, *Oncosiphon suffruticosum*, *E. peplus*, and *A. arvensis*) and six species (*O. viride*, *E. australis*, *Trachyandra* sp., *O. suffruticosum*, *C. pugioniformis*, and *Bromus diandrus*), respectively. • After rabbit control, it was dominated by two species (*T. fruticosa* and *E. longiflora*) at strand sites and by two species (*T. fruticosa* and *E. villosa*) at inland dune sites. • Species evenness at eucalyptus sites remained consistently high before and after rabbit control.
Chapter 5: Grazing Capacity	I expected grazing capacity on Robben Island to increase following rabbit control. My postulation	• As expected, control of rabbit herbivory led to an increase in grazing capacity across

	was that release of the island’s vegetation from rabbit herbivory pressure would have led to the re-establishment of palatable plant species that were constrained by rabbit herbivory, resulting in an increase in grazing capacity.	strand and inland dune sites on Robben Island. • This increase was driven by the recovery and re-establishment of palatable forage species, such as *T. fruticosa*, *E. villosa*, *E. longiflora*, and *Avena fatua*. • The recovery and re-establishment were accompanied by a decline in cover of the less palatable perennial herb *C. pugioniformis.* • Grazing capacity did not change at eucalyptus sites following rabbit control, due to the subdued responses of *T. fruticosa*, *E. longiflora*, *O. pes-caprae*, and *P. canaliculatus* to rabbit control.

III. Ecological Factors and Vegetation Processes Underpinning Vegetation Response

In this section, I present the ecological factors and vegetation processes (Table 6.2) that underpin the changes in composition, diversity, cover, and grazing capacity shown in Section II. The aim is to identify and elucidate the mechanisms driving vegetation response to rabbit control. It is important to note that the ecological factors and vegetation processes discussed below are inferences derived from the interpretation of results in the relevant chapters, not direct observations. While these inferences are based on empirical evidence, they remain theoretical constructs intended to explain observed patterns and trends. Detailed reasoning and evidence supporting these inferences can be found in the annexes and discussion sections of the relevant chapters.

Table 6-2 Inferred ecological factors and vegetation processes underpinning the changes in composition, diversity, cover, and grazing capacity on Robben Island following rabbit control.

Ecological Factors	Vegetation Processes		
	Vegetation Composition	Species Diversity	Grazing Capacity
Prolonged Rabbit Herbivory:	Rabbits have been grazing on Robben Island for over 350 years, eliminating late successional and palatable species from the island's vegetation and seed banks. This has hindered the vegetation's natural progression towards its original or projected undisturbed composition.	Over 350 years of continuous rabbit herbivory has led to the depletion of palatable plant species from both the vegetation and seed banks on Robben Island.	Over 350 years of rabbit habitation led to the systematic elimination of most palatable plant species, reducing the grazing capacity.
Intermittent Nature of Intense Rabbit Herbivory Pressure:	Despite the prolonged herbivory, a few herbivory-resilient early successional palatable species (e.g., *T. fruticosa*, *E. longiflora, C. dactylon*, and *E. villosa*) have managed to persist due to the intermittent nature of high rabbit herbivory pressure.	Periods of high rabbit densities have been short and intermittent, allowing a few herbivory-resilient palatable species to persist.	Short periods of high rabbit density allowed more resilient palatable species (e.g., *T. fruticosa*, *E. villosa*, *E. longiflora*, and A. *fatua*) to recover and persist. However, less resilient palatable species may have been completely eradicated.

Moderation of Interspecific Competition by Rabbit Herbivory:		Rabbit grazing has maintained a relatively high plant species diversity by preventing the dominance of the few ecologically competitive palatable species.	
Release from Rabbit Herbivory Pressure:	The removal of rabbits has significantly reduced herbivory pressure, leading to a resurgence of early successional palatable species.	Following rabbit control, several palatable species recovered and re-established on Robben Island due to the release from herbivory pressure.	The control of rabbit herbivory allowed these resilient palatable species to recover from the adverse effects of intensive herbivory. As a result, the cover of these species increased, enhancing the overall grazing capacity on Robben Island.
Increased Interspecific Competition:	The reduction in herbivory pressure has led to intensified competition, causing a decline in the abundance of unpalatable species (e.g., *B. diandrus*, *O. suffruticosum* and *C. pugioniformis*).	The recovery of palatable species led to increased competition among plant species, displacing several less ecologically competitive, less palatable and unpalatable species (e.g., *A. arvensis*, *E. peplus*, *H. glabra*, *W. androsacea*, *E. australis*, *O. viride* and *Trachyandra* sp.)	The re-establishment of palatable forage species led to a decline in the abundance of unpalatable plants (e.g., *C. pugioniformis*). This was probably due to the increased ability of the more palatable species to compete for resources such as light

			and soil moisture due to reduced herbivory pressure.
Moderation of Interspecific Competition by Residual Non-Rabbit Herbivory:		The persistence of residual non-rabbit herbivory on the island played a role in moderating the recovery of the more competitive palatable species and the displacement of less competitive, less palatable and unpalatable species	
Precluded Seed Dispersal from Mainland:	The island's isolation has limited the chances for the dispersal of extirpated late successional and palatable species from the mainland.	The island's geographical isolation likely limits the options for the dispersal of extirpated plant species from the mainland.	Robben Island's isolation likely limits the options for the dispersal of palatable species from the mainland. Thus, the current vegetation response to rabbit control is likely permanent.
Variation in Soil Depth	Soil depth significantly influenced vegetation composition response to rabbit control. Shallow-rooted species, such as *E. longiflora*, were able to fully respond to rabbit	Soil depth significantly influenced how vegetation diversity responded to rabbit control. Specifically, diversity in shallow-soiled strand sites declined due to the loss of	Following rabbit control, grazing capacity increased in both shallow and deep-soiled strand and inland dune sites. The increase was more pronounced in deep-soiled inland

	control at strand sites where there were more open habitats and less competition from deeper-rooted species. Deep-rooted species, such as *E. villosa*, were unable to fully respond to rabbit control at strand sites due to the limited availability of deep-soil habitats. However, deep-rooted species were able to respond well to rabbit control at inland dune sites where there was more deep soil.	shallow-rooted, less competitive, unpalatable species like *A. arvensis, E. peplus, and H. glabra*. This loss was caused by increased competition with recovering, shallow-rooted, and more competitive palatable species, particularly *E. longiflora*. Conversely, deeper inland dune communities experienced a decline in species diversity due to the loss of deep-rooted unpalatable species like *W. androsacea, E. australis, O. viride, Trachyandra* sp., and *Z. aethiopica*. This decline was driven by increased competition with resurgent, competitive, and deep-rooted palatable species, especially *E. villosa*.	dune sites, likely due to their suitability for the recovery of palatable species. Notably, the resurgence of the deep-rooted perennial grass *E. villosa* led to the enhanced grazing capacity at inland dune sites, while the recovery of the shallow-rooted annual grass *E. longiflora* was responsible for the increase at strand sites.
Inhibition of Vegetation Dynamics by Alien *Eucalyptus* Trees	*Eucalyptus* trees suppressed the response of other plant species to rabbit control, resulting in an	*Eucalyptus* trees at the study sites stifled the response of understory species (including *T. fruticosa*, *C.*	*Eucalyptus* trees impeded the recovery of vegetation grazing capacity following rabbit control.

	unaltered species composition even after the rabbit populations were reduced. This applied to early successional species such as *T. fruticosa*, *C. natans, O. pes-caprae,* and *P. canaliculatus*. These species remain at low coverage both before and after rabbit control, likely because *Eucalyptus* trees create drier soil conditions and cast shade on the understory vegetation.	*natans, O. pes-caprae,* and *P. canaliculatus*) to rabbit control, leading to no significant change in overall species diversity. These species maintained low cover both before and after rabbit control, likely due to the *Eucalyptus* trees creating unusually dry soil conditions and shading the understory vegetation.	Their high water absorption may have created drier understory conditions, suppressing the growth of palatable species like T. *fruticosa* and *E. longiflora*, which rely on high soil moisture for germination and establishment. Additionally, *Eucalyptus* trees deplete soil nutrients, further hindering understory vegetation growth and would have negatively impacted species like *P. canaliculatus* and *O. pes-caprae*, which require fertile soil environments. Furthermore, the shade cast by *Eucalyptus* trees restricted the growth of understory plants, like *P. canaliculatus* and *O. pes-caprae* which require sunny conditions.

IV. Conceptual Model of Vegetation Response to Rabbit Control

In this section I synthesise the findings from Sections II and III to develop a conceptual model of vegetation response to rabbit control on Robben Island (Figure 6.1). The conceptual model illustrates the inferred relationships between rabbit control, ecological factors, and vegetation response.

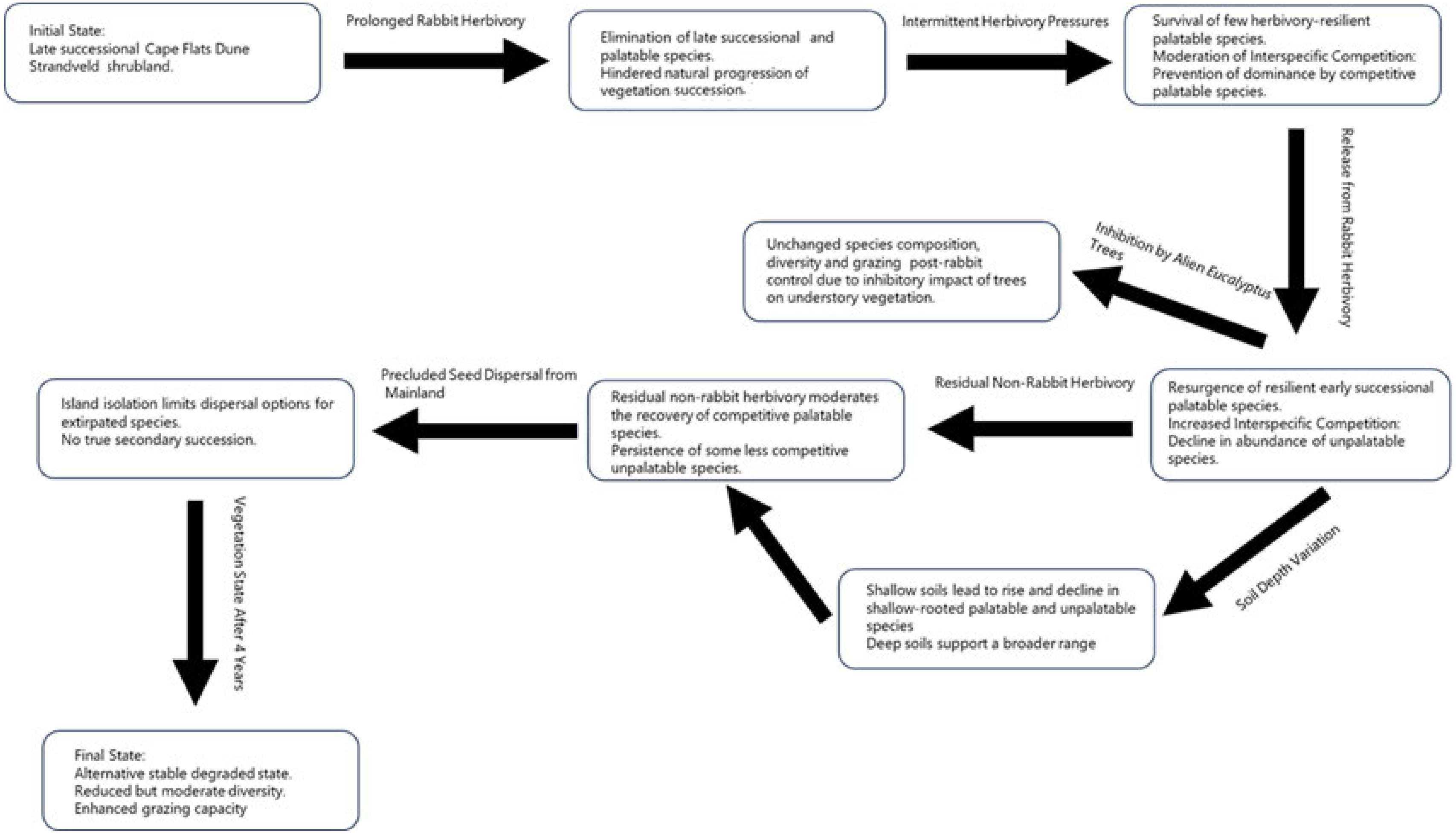
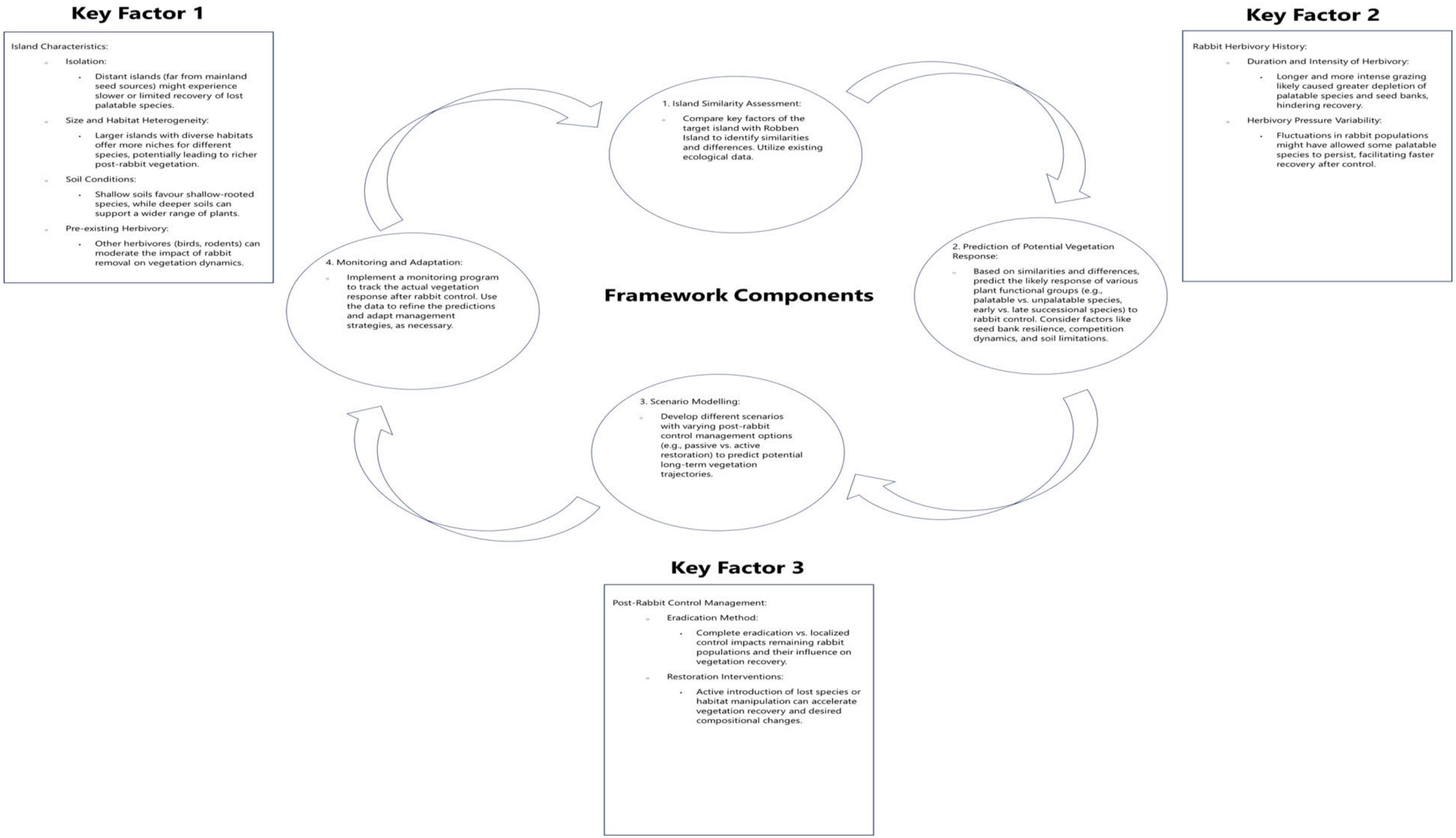


Figure 6-1 Conceptual model of vegetation response to rabbit control on Robben Island.

V. General Theoretical Framework for Predicting Vegetation Responses on Rabbit-Invaded Islands

Building upon insights gleaned from the experience of rabbit control on Robben Island (Sections II, III, and IV), I formulated a theoretical framework to predict vegetation responses on other invaded South African offshore islands (Figure 6.2). This framework underscores the necessity of considering various ecological factors and their interplay when estimating the potential outcomes of rabbit eradication. It provides a flexible tool for predicting and managing vegetation changes on islands following rabbit eradication, considering the unique ecological context of each island.



Key Factor 1

Island Characteristics:

- Isolation:
    - Distant islands (far from mainland seed sources) might experience slower or limited recovery of lost palatable species.
- Size and Habitat Heterogeneity:
    - Larger islands with diverse habitats offer more niches for different species, potentially leading to richer post-rabbit vegetation.
- Soil Conditions:
    - Shallow soils favour shallow-rooted species, while deeper soils can support a wider range of plants.
- Pre-existing Herbivory:
    - Other herbivores (birds, rodents) can moderate the impact of rabbit removal on vegetation dynamics.

Key Factor 2

Rabbit Herbivory History:

- Duration and Intensity of Herbivory:
    - Longer and more intense grazing likely caused greater depletion of palatable species and seed banks, hindering recovery.
- Herbivory Pressure Variability:
    - Fluctuations in rabbit populations might have allowed some palatable species to persist, facilitating faster recovery after control.

Framework Components

1. Island Similarity Assessment:

- Compare key factors of the target island with Robben Island to identify similarities and differences. Utilize existing ecological data.

2. Prediction of Potential Vegetation Response:

- Based on similarities and differences, predict the likely response of various plant functional groups (e.g., palatable vs. unpalatable species, early vs. late successional species) to rabbit control. Consider factors like seed bank resilience, competition dynamics, and soil limitations.

3. Scenario Modelling:

- Develop different scenarios with varying post-rabbit control management options (e.g., passive vs. active restoration) to predict potential long-term vegetation trajectories.

4. Monitoring and Adaptation:

- Implement a monitoring program to track the actual vegetation response after rabbit control. Use the data to refine the predictions and adapt management strategies, as necessary.

Key Factor 3

Post-Rabbit Control Management:

- Eradication Method:
    - Complete eradication vs. localized control impacts remaining rabbit populations and their influence on vegetation recovery.
- Restoration Interventions:
    - Active introduction of lost species or habitat manipulation can accelerate vegetation recovery and desired compositional changes.

Figure 6-2 General theoretical framework for predicting vegetation responses to rabbit control on rabbit-invaded South African offshore Islands.

VI. Island-Specific Hypotheses

In this section I build on the theoretical framework of Section V to explore how vegetation might respond to rabbit control on other islands beyond Robben Island. I formulate hypotheses for Dassen, Jutten, Schaapen, Seal, and Vondeling Islands (Tables 6.3, 6.4, 6.5, 6.6 and 6.7) using available island-specific ecological data collected using Google and Google Scholar (Annex X). The framework allows analysis of each island's unique ecology, comparing it to Robben Island to identify key factors influencing post-rabbit vegetation dynamics. This comparison allows for the generation of island-specific hypotheses for targeted restoration interventions. The specific tables for each island detail predicted changes in vegetation composition, diversity, and grazing capacity based on the framework and available ecological data. By extending the framework to other islands and formulating targeted hypotheses, I hope to pave the way for informed decision-making and successful future restoration initiatives.

A. Dassen Island

Table 6-3 Predicted vegetation response to rabbit control on Dassen Island

Framework Components	Outcomes
1. Island Similarity Assessment:	• Isolation: Dassen Island is slightly further from the mainland (9-11 km) compared to Robben Island (7 km), potentially resulting in slower recolonisation of extirpated species. • Size and Habitat Heterogeneity: Dassen Island is smaller (220 ha) than Robben Island (507 ha) and has less diverse habitats, potentially limiting the range of species that can establish. • Soil Conditions: Both islands have sandy soils, but Dassen Island has patches enriched by guano, potentially offering higher nutrient availability in localised areas. • Pre-existing Herbivory: Both islands have seabirds and rodents, but Dassen Island lacks the abundance of other herbivores present on Robben Island. • Duration and Intensity: The long duration of rabbit presence on Dassen Island (since around 1662-1668) is comparable to Robben Island, suggesting similar potential depletion of palatable species and seed banks. However, the available information on herbivory intensity is limited, hindering precise comparisons. • Herbivory Pressure Variability: Historical declines in the cat population on Dassen Island (e.g., in the 1980s) suggests a possible decrease in rabbit numbers (i.e., through boom–and–bust predator–prey cycles (Berruti 1986)), potentially allowing some palatable species to persist. However, the lack of detailed information about past rabbit populations makes it difficult to assess the magnitude of this variability compared to Robben Island.

2. Prediction of Potential Vegetation Response:

- Species composition:
    - Early successional palatable species: Likely recovery of herbivory-resilient species like *T. fruticosa* and *Trachyandra divaricata* observed on Robben Island.
    - Late successional palatable species: Slower recovery due to the island's isolation and potential limitations in seed dispersal.
    - Unpalatable species: Decline in abundance of species like *Mesembryanthemum crystallinum* and *Preniu pallens* due to increased competition from recovering palatable species.
- Diversity:
    - Initial decline: Similar to Robben Island, a temporary decline due to the loss of unpalatable species and the dominance of a few resilient palatable species.
    - Long-term increase: Potential for increased diversity as other palatable and late successional species recolonize or establish from the seed bank or mainland.
- Grazing capacity:
    - Increase: Overall grazing capacity likely increases due to the recovery of palatable species like *T. fruticosa*.
    - Spatial variation: Areas with higher nutrient availability from guano patches might experience greater increases in grazing capacity.

3. Scenario Modelling:

- Passive vs. Active Restoration: Passive restoration might be sufficient for early successional species recovery, but active interventions like planting or seed bank restoration could accelerate the re-establishment of late successional species and increase diversity.

	• Eradication vs. Control: Complete eradication would eliminate potential future rabbit impacts, while control might be less effective in the long term.
4. Monitoring and Adaptation:	• Monitor vegetation composition, diversity, and grazing capacity to track progress and adjust restoration strategies as needed. • Consider factors like guano patch dynamics and rodent herbivory when interpreting monitoring data.
5. Limitations:	• Lack of detailed data on rabbit populations, vegetation composition, and soil conditions limits the precision of predictions. • Potential for unforeseen interactions between ecological factors on Dassen Island.
6. Overall Prediction:	Rabbit control on Dassen Island is likely to lead to a shift in vegetation composition towards palatable species, an initial decline followed by a potential increase in diversity, and an overall increase in grazing capacity. However, the specific trajectory and pace of these changes will depend on various ecological factors and require ongoing monitoring and adaptation. With more comprehensive data, the predictions can be further refined, and the effectiveness of restoration interventions can be optimised.

B. Jutten Island

Table 6-4 Predicted vegetation response to rabbit control on Jutten Island

Framework Components	Outcomes
1. Island Similarity Assessment:	• Isolation: Jutten Island is significantly closer to the mainland (0.8 km) compared to Robben Island (7 km). This suggests a higher potential for recolonisation of extirpated palatable species from the mainland source. Mainland propagule dispersal may have entirely prevented island species extirpation. • Size and Habitat Heterogeneity: Information about Jutten Island's habitat details is unavailable. However, its smaller size (46 hectares vs. 507 hectares for Robben Island) might limit the diversity of plant communities and niches compared to Robben Island. • Soil Conditions: Data on soil depth and nutrient availability is lacking for Jutten Island. This information is crucial for understanding the potential limitations for plant establishment and growth. • Pre-existing Herbivory: The presence of other herbivores (birds, rodents) is likely, but their impact on vegetation dynamics is unknown. This information gap limits our ability to fully predict the effect of rabbit removal on herbivory pressure. • Rabbit Herbivory History: Duration and Intensity: Both islands have experienced prolonged rabbit herbivory (300+ years), suggesting similar depletion of palatable species and seed banks. • Herbivory Pressure Variability: Information about rabbit population fluctuations on Jutten Island is missing. Fluctuations observed on Robben Island might not directly translate to Jutten.

2. Prediction of Potential Vegetation Response:	• Species Composition: Based on Robben Island's experience, an increase in early successional palatable species like *T. fruticosa* and *Ehrharta* spp. is expected. However, the lack of information about specific functional groups on Jutten Island limits more precise predictions. Early successional species, especially those with resilient seed banks, are more likely to show faster recovery after rabbit control. However, the establishment of late successional species might be limited by factors like dispersal limitations and competition from established early successional species. • Species Diversity: The removal of rabbits might lead to increased competition among plant species, potentially favouring competitive palatable species and displacing less competitive unpalatable species. While Robben Island experienced a decline in diversity after rabbit control, Jutten Island's closer proximity to the mainland might facilitate faster recolonisation by other extirpated palatable species, potentially mitigating the decline. However, the limited information about existing plant communities makes it difficult to predict the specific competitive dynamics. • Grazing Capacity: Similar to Robben Island, an increase in grazing capacity is expected due to the recovery of palatable species. Considering the prolonged rabbit presence (300 years), depletion of palatable species and their seed banks is likely. However, the shorter isolation distance compared to Robben Island suggests a potentially faster recovery of some palatable species, particularly those with good seed dispersal mechanisms. However, the extent and timeline of this increase would depend on the specific composition of palatable species present and their response to rabbit control.
3. Scenario Modelling:	• Passive vs. Active Restoration: Passive restoration relies solely on natural recovery, while active restoration involves interventions like planting native species or habitat manipulation. Active restoration could accelerate and guide desired vegetation composition, especially on a smaller island like Jutten.

	• Eradication vs. Control: The chosen method for rabbit control will significantly impact vegetation response. Complete eradication could lead to faster recovery but also higher uncertainty due to potential ecological imbalances. Control might offer a more cautious approach while still reducing herbivory pressure.
4. Monitoring and Adaptation:	• Regular monitoring of vegetation composition, diversity, and grazing capacity is crucial to track the actual response and adapt restoration strategies as needed. This adaptive approach is crucial for ensuring long-term success of restoration efforts.
5. Limitations:	• The predictions presented here are based on limited information about Jutten Island. Acquiring additional data on soil conditions, habitat characteristics, existing plant communities, and herbivore interactions would significantly improve the accuracy of the predictions. • The chosen rabbit control method and potential post-rabbit control interventions will also influence the vegetation response. Careful consideration of these factors is necessary for developing a successful restoration plan.
6. Overall Prediction:	While the available data limits the precision of the predictions, the theoretical framework provides a valuable starting point for understanding the potential consequences of rabbit control on Jutten Island. By gathering more information and considering the island's specific context, land managers can develop a more informed and effective plan for rabbit removal and post-rabbit control restoration on Jutten Island.

C. Schaapen Island

Table 6-5 Predicted vegetation response to rabbit control on Schaapen Island

Framework Components	Outcomes
1. Island Similarity Assessment:	• Isolation: Compared to Robben Island (7 km), Schaapen Island's much closer proximity to the mainland (0.5 km) suggests a higher potential for recolonisation of extirpated palatable species by propagules dispersing from the mainland. • Size and Habitat Heterogeneity: Information on Schaapen Island's habitat types is lacking, making a direct comparison with Robben Island's diverse habitats (coastal rocky areas, dunes, inland plains) difficult. However, with 41 hectares, it is considerably smaller than Robben Island (507 hectares), potentially limiting the number of niches and diversity of plant communities post-rabbit control. • Soil Conditions: Lack of data on Schaapen Island's soil depth and nutrient availability prevents a direct comparison with Robben Island's variable soil conditions. This information gap limits our understanding of potential limitations for certain plant groups following rabbit control. • Pre-existing Herbivory: No information exists on other herbivores on Schaapen Island, but the presence of seabirds could be a factor influencing vegetation dynamics. The impact of seabirds would need to be considered when interpreting vegetation changes after rabbit control. • Rabbit Herbivory o Duration and Intensity: Rabbits have been present on Schaapen Island since at least 1781, likely for much longer, similar to Robben Island's 370 years of rabbit herbivory. This prolonged and "prodigious" grazing pressure suggests significant depletion of palatable species and seed banks, potentially hindering post-rabbit control recovery.

	o Herbivory Pressure Variability: Records indicate rabbit population fluctuations on Schaapen Island, providing some potential for persistence of remnant palatable species in suitable refuges during low rabbit density periods. This could facilitate faster recovery compared to islands with consistently high rabbit pressure.
2. Prediction of Potential Vegetation Response:	• Vegetation composition: Based on the comparable duration and intensity of rabbit herbivory, we can expect an initial increase in early successional, herbivory-resistant species similar to Robben Island, such as *T. fruticosa* and *Ehrharta* spp. However, the closer proximity to the mainland suggests a higher chance of recolonisation by late successional and palatable species from the mainland source, compared to Robben Island. The overall post-rabbit control composition will depend on the success of recolonisation and competition dynamics among different functional groups. • Species diversity: Initially, diversity might decline due to reduced herbivory pressure leading to increased competition among plant species, resulting in the displacement of some less competitive unpalatable species, as observed on Robben Island. However, long-term diversity could increase if late successional and palatable species successfully recolonise and establish, creating a more complex and diverse plant community. • Grazing capacity: As with Robben Island, grazing capacity is likely to increase following rabbit control due to the recovery of palatable species like *T. fruticosa* and *Ehrharta* grasses. However, the smaller size of Schaapen Island might limit the overall grazing potential compared to Robben Island.
3. Scenario Modelling:	• Passive vs. Active Restoration: Without information on the intended rabbit eradication method or planned restoration interventions, it is difficult to model specific scenarios. However, passive restoration may be sufficient due to the island's proximity to the mainland and potential for natural recolonisation. Active restoration could involve introducing

	extirpated late successional species, but more research is needed to determine their suitability and feasibility. Given the limitations in knowledge about Schaapen Island's habitat and specific plant functional groups, passive restoration with monitoring might be initially preferable. This would allow for natural recolonisation and provide valuable data to inform future interventions, if needed. • Eradication vs. Control Measures: The lack of information about the intended rabbit control method makes it difficult to predict the specific impact on vegetation. However, complete eradication would likely lead to a faster and more pronounced response compared to control measures.
4. Monitoring and Adaptation:	• Implementing a monitoring program to track changes in vegetation composition, diversity, and grazing capacity is crucial. This data can be used to refine predictions and adapt management strategies as needed.
5. Limitations:	• The lack of detailed information on Schaapen Island's habitat characteristics, soil conditions, and specific plant functional groups limits the accuracy of these predictions. • The absence of data on planned rabbit eradication methods and potential restoration interventions hinders the development of specific scenarios. • Recommendations: o Conduct a comprehensive ecological survey of Schaapen Island to gather data on habitat types, soil conditions, and specific plant functional groups. o Develop a detailed plan for rabbit control and potential restoration interventions based on the findings of the ecological survey.

  - Implement a robust monitoring program to track changes in vegetation composition, diversity, and grazing capacity after rabbit control.
  - Adapt management strategies based on the monitoring data to ensure the success of restoration efforts.

6. Overall Prediction: While the lack of detailed information about Schaapen Island presents some challenges, the theoretical framework based on Robben Island can provide a valuable starting point for predicting and managing the potential changes in vegetation after rabbit control. By implementing a monitoring program and adapting management strategies based on real-world data, land managers can increase the success of island restoration efforts and ensure the long-term sustainability of Schaapen Island's ecosystem.

D. Seal Island

Table 6-6 Predicted vegetation response to rabbit control on Seal Island

Framework Components	Outcomes
1. Island Similarity Assessment:	• Isolation: Compared to Robben Island (7 km from mainland), Seal Island is closer (6 km) and might experience faster recolonisation of extirpated palatable species. • Size and Habitat Heterogeneity: Seal Island is much smaller (2 hectares vs. 507 hectares) and likely has limited habitat diversity, potentially leading to a slower and less diverse recovery compared to Robben Island. • Soil Conditions: No information is available on Seal Island's soil depth or nutrient availability, making it difficult to assess their potential impact on vegetation recovery. • Pre-existing Herbivory: Information on other herbivores on Seal Island is lacking. Their presence could influence vegetation dynamics after rabbit control. • Duration and Intensity of Rabbit Herbivory: Robben Island's rabbit herbivory history spans centuries, with documented fluctuations in intensity, while details for Seal Island are lacking. However, Seal Island has a long history (over 3 centuries) of rabbit herbivory.
2. Prediction of Potential Vegetation Response:	• Species Composition: o Early successional palatable species like *T*. fruticosa and *Ehrharta* spp. might recover well due to the release from rabbit herbivory, similar to Robben Island. o Late successional palatable species might recover slowly due to limited seed dispersal and competition from early successional species.

    - Unpalatable species like *C. pugioniformis* might decline due to increased competition from recovering palatable species.
- Diversity:
    - Species diversity might initially decline due to the loss of unpalatable species and dominance of a few early successional palatable species.
    - Long-term diversity could increase if late successional palatable species establish and create a more complex vegetation structure.
- Grazing Capacity:
    - Overall grazing capacity might increase due to the recovery of palatable species.
    - However, the limited size and habitat diversity of Seal Island might constrain the potential for increased grazing compared to Robben Island.

3. Scenario Modelling:

- Passive vs. Active Restoration:
    - Passive restoration might lead to slower recovery due to limited seed dispersal and competition dynamics on the small island.
    - Active restoration, such as planting late successional palatable species, could accelerate recovery and increase diversity.
- Eradication Method:
    - Understanding the chosen eradication method (e.g., poisoning, trapping) is crucial for assessing potential impacts on non-target species and ecosystem dynamics.

4. Monitoring and Adaptation:	• Implement a monitoring program to track actual vegetation changes after rabbit control. • Use the data to refine predictions and adjust management strategies as needed.
5. Limitations:	• The lack of detailed information about Seal Island's ecology significantly limits the accuracy of these predictions. • Additional data collection on habitat, soil, vegetation, and rabbit populations is crucial for more precise predictions and effective management. • The framework relies on assumptions based on Robben Island, which might not fully translate to Seal Island due to its unique characteristics.
6. Overall Prediction:	While the framework provides a valuable starting point for predicting vegetation response on Seal Island, the limited information necessitates further data collection and analysis. A comprehensive understanding of the island's ecology is essential for making informed decisions about rabbit control and potential restoration interventions.

E. Vondeling Island

Table 6-7 Predicted vegetation response to rabbit control on Vondeling Island

Framework Components	Outcomes
1. Island Similarity Assessment:	• Isolation: Compared to Robben Island (7 km), Vondeling Island is much closer to the mainland (0.8 km). This suggests higher potential for recolonisation of extirpated palatable species by propagules from the mainland. • Size and Habitat Heterogeneity: Vondeling Island is much smaller (21 hectares) compared to Robben Island (507 hectares). This suggests it likely has fewer and less diverse habitats, potentially limiting the range of plant species that can establish after rabbit control. • Soil Conditions: Lacking data on soil depth and nutrient availability hinders a detailed comparison with Robben Island. • Pre-existing Herbivory: Information about other herbivores on Vondeling Island is unavailable, making it difficult to assess their potential impact on vegetation dynamics after rabbit control. • Rabbit Herbivory History o Duration and Intensity: Both islands have experienced prolonged rabbit presence (>300 years). However, data on grazing intensity for Vondeling Island is unavailable. Considering its smaller size, rabbit herbivory pressure could be relatively higher compared to Robben Island. o Herbivory Pressure Variability: No evidence of rabbit population fluctuations on Vondeling Island exists. This differs from Robben Island, which experienced periods of low rabbit numbers. The lack of variability might indicate slower recovery for palatable species, as a persistent herbivore pressure could limit their seed bank regeneration.

2. Prediction of Potential Vegetation Response:	• Species Composition: Based on Robben Island findings, we expect early successional palatable species like *T. fruticosa* and *Ehrharta* spp. to recover well on Vondeling Island. However, the lack of information on pre-existing plant communities makes it difficult to predict the presence and recovery potential of late successional palatable species. Early successional species will likely dominate as on Robben Island, with limited recovery of late successional species due to factors like the small island size, potentially limited seed dispersal from the mainland, and competition dynamics. • Diversity: Based on Robben Island, species diversity might initially decline due to the loss of some unpalatable species unable to compete with resurgent palatable species. However, this could be followed by an increase in diversity over the long term as other plant groups recolonise from the mainland. • Grazing Capacity: Grazing capacity is likely to increase due to the recovery of palatable species. We can expect a shift towards more palatable species, particularly early successional ones like *T. fruticosa* and *Ehrharta* spp. similar to Robben Island. However, the smaller size and limited habitat diversity of Vondeling Island might limit the overall increase in grazing capacity compared to Robben Island.
3. Scenario Modelling:	• Passive vs. Active Restoration: Passive restoration might be sufficient on Vondeling Island due to its proximity to the mainland. However, active restoration through planting native species, habitat manipulation, and seed bank restoration could accelerate recovery and potentially increase the diversity and grazing capacity of the post-rabbit vegetation. • Eradication vs. Control Methods: Complete eradication using trapping or poisoning would be preferable to minimize the risk of rabbit recolonisation and ensure the long-term success of vegetation recovery. However, humane, and ethical considerations should be carefully addressed when choosing the control method.

4. Monitoring and Adaptation:	• Monitoring vegetation composition, diversity, and grazing capacity after rabbit control is crucial to assess the accuracy of predictions and adapt management strategies as needed. This could include regular vegetation surveys, grazing exclosure plots, and monitoring of rabbit populations.
5. Limitations:	• The lack of data on soil conditions, pre-existing herbivores, and specific plant functional groups on Vondeling Island limits the prediction accuracy. Conducting thorough ecological surveys is crucial for a more refined analysis. • Recommendations: o Conduct comprehensive ecological surveys to address knowledge gaps about soil conditions, habitat types, plant communities, and pre-existing herbivores. o Design a restoration plan tailored to the island's needs, including passive or active restoration interventions. o Implement a robust monitoring program to track progress and adjust strategies based on data.
6. Overall Prediction:	The predictions of vegetation response to rabbit control on Vondeling Island are based on limited information and may not fully capture the complexities of the island's ecosystem. Conducting thorough ecological surveys and comprehensive research is crucial for refining the predictions and developing effective management plans. The success of rabbit control and vegetation restoration will depend on various factors, including the chosen control method, implemented restoration interventions, and ongoing monitoring and adaptation efforts. By addressing the knowledge gaps and implementing well-informed management plans, land managers can increase the chances of successful rabbit control and vegetation recovery on Vondeling Island.

VII. Implications for Conservation and Restoration

A. Potential Benefits of Rabbit Control

The study's findings offer a promising outlook for conservation and restoration on South African offshore islands. They confirm that rabbit removal, through eradication or control measures, presents a powerful tool for restoring native vegetation and enhancing biodiversity. Across the islands considered in this study, the findings predict:

- Recovery of palatable plant species: Early successional species like *T. fruticosa* and *Ehrharta* spp. are likely to thrive, followed by a potential increase in late successional species, particularly on islands closer to the mainland.
- Increased diversity: While initial declines in diversity might occur due to changing competition dynamics, long-term diversity could increase with the reintroduction of lost species and the creation of more complex vegetation structures.
- Enhanced ecosystem resilience: Recovering vegetation can improve soil stability, reduce erosion, and provide habitat for native fauna, creating a more resilient ecosystem overall.

B. Challenges of Rabbit Control and Restoration

However, implementing rabbit control and subsequent restoration initiatives also presents challenges:

- Island-specific considerations: Each island has unique characteristics like size, habitat diversity, and soil conditions, requiring tailored control and restoration strategies.
- Monitoring and adaptation: Long-term monitoring and adaptive management are crucial to track progress, adjust interventions, and ensure the success of restoration efforts.
- Resource limitations: Effective control and restoration require significant resources, including funding, expertise, and technology.

C. Recommendations for Future Research

To refine our understanding and optimise future efforts, further research is essential in key areas:

- Data collection: Filling knowledge gaps on specific islands, including detailed habitat surveys, soil analyses, and comprehensive plant species inventories, is crucial for accurate predictions and effective management.
- Long-term monitoring: Implementing robust monitoring programs to track changes in vegetation composition, diversity, and ecosystem function over time allows for assessment of the effectiveness of interventions and adapt strategies as needed.
- Herbivore interactions: Understanding the role of other herbivores, including seabirds and rodents, in island ecosystems is crucial for predicting their potential impact on post-rabbit control vegetation dynamics.
- Prioritisation of islands: While comprehensive research is ideal, prioritising islands based on ecological significance, threat level, feasibility of restoration, and potential for resource mobilisation can ensure efficient allocation of research efforts.

D. Recommended Management Strategies

Based on the study's findings and identified challenges, here are some specific management strategies that can be implemented:

- Passive vs. active restoration: Choosing the appropriate approach depends on the island's characteristics and desired outcomes. Passive restoration might be sufficient on islands close to the mainland with less habitat diversity, while active restoration, including planting and seed bank restoration, could be necessary on smaller or more isolated islands.
- Eradication vs. control methods: Complete eradication offers long-term benefits but requires careful consideration of ethical implications and potential recolonisation risks. Control methods might be suitable in some cases but continued monitoring and potential follow-up interventions are crucial.
- Stakeholder engagement: Stakeholder engagement fosters ownership, success, and knowledge exchange, building capacity for sustainable restoration beyond projects.
- Adaptive management: Implementing flexible management plans that incorporate monitoring data and allow for adjustments based on real-world observations is essential for ensuring the long-term success of restoration efforts.
- Funding and resource mobilisation: Exploring potential funding sources such as government grants, private donations, and international conservation organisations can help bridge the resource gap. Additionally, seeking partnerships with universities, research institutions, NGOs,

and local communities can leverage expertise and resources for efficient and sustainable restoration efforts.

By embracing a research-informed and adaptable approach, land managers can harness the potential of rabbit control to restore native vegetation, enhance biodiversity, and create more resilient ecosystems on South Africa's offshore islands. The findings of this study offer a valuable roadmap for guiding future conservation and restoration efforts on these degraded but important island ecosystems.

VIII. Conclusion

The invasive European rabbit (*Oryctolagus cuniculatus*) poses a significant ecological threat to South African offshore islands, jeopardising native vegetation and ecosystem stability. This chapter investigates the potential for rabbit control to reverse these impacts, employing a general theoretical framework adapted to the specific characteristics of Robben, Dassen, Jutten, Schaapen, Seal, and Vondeling islands. Findings from the chapter reveal a promising outlook for vegetation recovery following rabbit control. Across the islands, an initial resurgence of early successional, palatable species such as *Tetragonia fruticosa* and *Ehrharta* spp. is anticipated. In the long term, recolonisation by late successional species and increased vegetation diversity are expected, particularly on islands closer to the mainland where dispersal is facilitated. This shift towards a more complex and resilient vegetation structure signifies a potential return to a functional island ecosystem. However, successful restoration presents challenges. Island-specific factors such as size, habitat heterogeneity, and pre-existing herbivore interactions necessitate tailored rabbit control and restoration strategies. Long-term monitoring and adaptive management are crucial to track progress, adjust interventions, and ensure sustainability. The implications of this study extend beyond these specific islands. It highlights the potential of rabbit control as a powerful tool for restoring invaded island ecosystems globally. By providing a framework for predicting vegetation response and identifying key challenges and opportunities, this research offers valuable guidance for conservation practitioners and land managers.

IX. References

Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

Asian Development Bank. 2023. Invasive alien species: A dual threat to biodiversity and economies. Available at https://blogs.adb.org/blog/invasive-alien-species-dual-threat-biodiversity-and-economies [accessed 6 December 2023].

Bello-Rodríguez V, Mateo RG, Pellissier L, Cubas J, Cooke B, González-Mancebo JM. 2021. Forecast increase in invasive rabbit spread into ecosystems of an oceanic island (Tenerife) under climate change. *Ecological Applications* 31: e02206.

Berruti A. 1986. The predatory impact of feral cats *Felis catus* and their control on Dassen Island *South African Journal of Antarctic Research* 16: 123-127.

Brooke RK, Prins AJ. 1986. Review of alien species on South African offshore islands. *South African Journal of Antarctic Research* 16: 102-109.

Bruton M. 2021. Biological invasions in South Africa. *Transactions of the Royal Society of South Africa* 76: 301-305.

Cooper J, Brooke RK. 1982. Past and present distribution of the feral European rabbit *Oryctolagus cuniculus* on southern African offshore islands. *South African Journal of Wildlife Research* 12: 5-71.

Cooper J, Brooke RK. 1986. Alien plants and animals on South African continental and oceanic islands: species richness, ecological impacts and management. In: Macdonald IAW, Kruger FJ, Ferrar AA editors. *The ecology and management of biological invasions in southern Africa*. Cape Town: Oxford University Press. p. 133-142.

Cubas J, Severin DH, Villafuerte R, Bello-Rodríguez V, Rodríguez-Luengo JL, del Arco M, Martín-Esquivel JL, González-Mancebo JM. 2019. Endemic plant species are more palatable to introduced herbivores than non-endemics. *Proceedings of the Royal Society B: Biological Sciences* 286: 20190136.

Davies S, Jordaan M, Karsten M, Terblanche J, Turner A, van Wilgen N, Veldtman R, Zengeya T, Measey J. 2020. Experience and lessons from alien and invasive animal control projects in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology*. Cham: SpringerOpen. p. 1302-1381.

de Vos A, Manville RH, Van Gelder RG. 1956. Introduced mammals and their influence on native biota. *Zoologica (New York)* 41: 163-194.

Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles J-M, Bradshaw CJ, Courchamp F. 2021. High and rising economic costs of biological invasions worldwide. *Nature* 592: 571-576.

Fontanesi L, Utzeri VJ, Ribani A. 2021. 1 The evolution, domestication and world distribution of the European rabbit (*Oryctolagus cuniculus*). In: Fontanesi L editor. *The Genetics and Genomics of the Rabbit*. Wallingford, Oxfordshire: CAB International.

Gillham ME. 1963. Some interactions of plants, rabbits and sea-birds on South African islands. *Journal of Ecology* 51: 275-294.

IPBES (ed). 2023. *Thematic Assessment Report on Invasive Alien Species and their Control*. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Bonn.

Kumschick S, Foxcroft LC, Wilson JR. 2020. Analysing the risks posed by biological invasions to South Africa. *Biological Invasions in South Africa*: 573-596.

Mazza G, Tricarico E, Genovesi P, Gherardi F. 2014. Biological invaders are threats to human health: an overview. *Ethology Ecology & Evolution* 26: 112-129.

Measey J, Hui C, Somers MJ. 2020. Terrestrial vertebrate invasions in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology* No. 14. Cham, Swtzerland: Springer Open. p. 115-151.

Nankivell JW. 1934. Robben Island. *The South African Geographical Journal* 17: 29-34.

Schweizer D, Jones HP, Holmes ND. 2016. Literature review and meta-analysis of vegetation responses to goat and European rabbit eradications on islands. *Pacific Science* 70: 55-71.

Skead CJ. 2011. Historical incidence of the larger land mammals in the broader Western and Northern Cape In: Boshoff AF, Kerley GIH, Lloyd PH editors. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.

Williams AJ, Klages NTW, Crawford RJM. 2000. Functional ecosystems: Coastal islands. In: Durham BD, Pauw JC editors. *Summary Marine Biodiversity Status Report for South Africa*. Pretoria: National Research Foundation.

World Economic Forum. 2023. Invasive species cost the global economy $423 billion every year. Available at https://www.weforum.org/agenda/2023/09/invasive-species-cost-global-economy-billions/ [accessed 6 December 2023].

ANNEXURE I: TIMELINE OF IMPORTANT HISTORICAL AND ECOLOGICAL EVENTS ON ROBBEN ISLAND, SOUTH AFRICA

Year/Period	Notable events
18000 -12000 YA	Robben Island is part of the mainland in a glacial period when sea level is 130 m vertically lower and the coast tens of kilometres further west than present[13, 27, 17] The island is a low hill connected to Blaauwberg mountain by a ridge now about 15 m below sea level[17]
12000 YA	Robben Island is cut off from the mainland by ca. 10 km of south Atlantic Ocean when sea levels rise at the end of the glacial period[17]
1591	Three English vessels commanded by Captain George Raymond visit the island[18] Fauna dominated by Cape Fur Seals (*Arctocephalus pusillus* Schreber, 1775), African Penguins (*Spheniscus demersus* Linnaeus, 1758), White Pelicans (*Pelecanus onocrotalus* Linnaeus, 1758) and Mole Snakes (*Pseudaspis cana* Linnaeus, 1758) [21]
1601	Dutch navigator Admiral Joris van Spilbergen names island "Cornelia" [18] Dassies (*Procavia capensis* (Pallas, 1766)) translocated from Dassen Island by Admiral van Spilbergen[16] Sheep placed on island by English ship for benefit of fellow sea-travellers[16]
1608	Cattle (*Bos taurus* Linnaeus, 1758) introduced to island[16]
1614	10 English convicts marooned on island by Sir Thomas Herbert[24] [18] Convicts are tasked to look after small flock of sheep (*Ovi aries* Linnaeus, 1758) that was to serve as a meat supply on subsequent visits[24]
1632	Goringhaicona - sedentary, non-pastoral hunter-gatherers[29] - move to island with help of an English Captain[24] Leave island well before 1652[24]
1638	Penguin (*Spheniscus demersus* Linnaeus, 1758) and seal (*Arctocephalus pusillus* Schreber, 1775) numbers have declined to very low levels[16]
1652	Dutch settle at the Cape[24] Dutch prisoners sent to island[24] Abundant seals, penguins and bird life[24] Garden planted[24] Primitive lighthouse constructed and a fire burnt nightly[18]
1653	More dassies moved to island from Dassen Island[7]
1654	European rabbits (*Oryctolagus cuniculus* Linnaeus, 1758) introduced to island by Dutch Colonial Governor Jan van Riebeeck[23, 8, 16, 21]

Year/Period	Notable events
1655	Pigs removed from island because of damage caused to penguins and environment[16]
1656	Supplementary rabbits introduced to island by van Riebeeck[23, 8]
1657	First group of Dutch slaves[24] Forced to crush seashells for use as lime, cut stone for buildings and light signalling fires [24] Supplementary rabbits introduced to island by van Riebeeck[23, 8]
1658	First deliberate translocation of an indigenous mainland species - steenbok (*Raphicerus campestris* Thunberg 1811) ewe and her young[16] Supplementary rabbits introduced to island by van Riebeeck[23, 8] First rabbit births recorded[25]
1659	Last known mention of Dassies on the island[23]
1661	Signs of overgrazing become apparent[16]
1666	25 (incl. women and children) people living on island[24]
End of 17th century	Island sandy and treeless[24] Rich in penguins and seals[24]
1740	Seals desert island after ±80 years of intensive hunting[16]
1806	British build new prison settlement on southeastern side of island [24] Convicts set to quarry slates on island[18, 24] Business rights given to John Fitzpatrick and John Murray to quarry stone and establish whaling station respectively[24]
1846	British prison closed[24] Hospital (General infirmary) established[24] Hospital buildings erected for "lunatics" and "lepers" (moved from Hemel en Aarde, Caledon) [18] 72 ailing patients, 68 ''lunatics" and 54 "lepers" [24] Small staff[24]
1846 - 1931	About 500 people lived in hospital settlement and cared for hundreds of lepers[18] Convicts acted as labourers[18] Population may have at one time reached as many as 1500[1]
1881	Feral cats (*Felis catus* Linnaeus, 1758) introduced to island by 1881[10]
1889	First afforestation plan Control of rabbits, sheep, cattle recommended[6]
1891 - 1911	Afforestation plantings begin in 1891and carried on for next 20 years[6] Initial species included: *Acacia cultriformis* G.Don, *Acacia saligna* (Labill.) Wendl. and *Lycium horridum* Thunb. (Cape box thorn) [6]

Year/Period	Notable events
1931	Hospital closed[24]
1933	Island deserted except for lighthouse keepers[18, 24] Used for fishing and hunting by a privileged few[24] Vegetation survey of island conducted by Professor RS Adamson for the Cape Geographical Society[1] The island is in a "deserted condition" as a result of being overrun by rabbits[1]
1934	Nankivell[18] mentions an unsuccessful effort having been made "a few years previously" to eradicate rabbits by digging them out
1936	Robben Island declared military property[24]
1939 - 1945	Main battery of Signal Hill transferred to island[24] Three 9.2-inch guns of the 5th Heavy Battery, weighing ten tons and needing seven men to fire them positioned on the island[24] Two-six-inch calibre guns of the Cornelia Battery mounted on island to cover the Blouberg channel[24] Ruined buildings demolished and material used in construction of new harbour in Murray's Bay[24] Roads, underground magazines, gun emplacements and observation towers constructed and completed by 1940[24] Introduction of several species of Australian flora[5] Cape Garrison Artillery, Coastal Artillery School and South African Permanent Garrison Artillery as well as medical and hospital staff, chaplains and civilian labourers stationed on island[24]
1946-1959	Military remains in charge of island, but there is a reduction in the number of garrisons and activities[24] Springbok (*Antidorcas marsupials Z*immermann, 1780), Eland (*Taurotragus oryx* Pallas 1766) and Blue Wildebeest (*Connochaetes taurinus* Burchell, 1824) introduced to island after World War II but prior to 1955[10] Blue wildebeest soon shot out[10] Families of military personnel main occupants of island[24]
1959	Island handed over to Police Department and converted into a maximum security institution[24]
1961	Prison opened[24]
1963	Three Fallow Deer (*Dama dama* Linnaeus, 1758) individuals from Groote Schuur Estate, Cape Town, introduced to island[25, 10]
1967	Two ostriches (*Struthio camelus* Linnaeus, 1758) one male one female introduced to island[14]
1973	Steenbok re-introduced to island[5]
1975	Springbok population on island augmented with new introductions[10]
1985	Bontebok (*Damaliscus pygargus pygargus* Pallas, 1767) introduced on island to form a breeding subgroup for farmers and reserves in the Western Cape[26, 11] Hunting of Fallow deer[9]

Year/Period	Notable events
	Cape Golden Moles (*Chrysochloris asiatica* Linnaeus, 1758) fairly common in gardens in the settlement[11]
1988	Cape Golden Moles well distributed in grassland[11]
1994	Floral and faunal surveys find 200 taxa on island of which 50 are alien[16] Of the ± 150 indigenous taxa, only 2 represent mammals - the Cape golden mole and the occasional Cape fur seal[16] The remaining eight or more mammalian taxa found on the island represented either wild alien taxa, domestic alien taxa, or indigenous South African species introduced to the island[16] The surveys did not include invertebrates, except the housefly (*Musca domestica* Linnaeus, 1758) and honeybee (*Apis mellifera* Linnaeus, 1758) [16]
1995	Declared National Monument and handed over to Department of Arts, Culture and Science[19] Hunting and trapping stopped and for all practical purposes, any control of large mammal populations ceases[10]
1996	Declared a National Museum[21]
1997	Robben Island Museum (RIM) assumes responsibility for managing island from the Department of Correctional Services[19] Robben Island Museum opened to the public[24]
1998	Unsuccessful attempt to remove cats (summer 1998/1999) [10] 107 individuals culled[10] Stomach contents show European rabbits most frequent item in diet[2, 22] Around 10 cats remain, and these increased in number during ensuing years resulting in a steady decrease in breeding productivity of African Black Oystercatchers (*Haematopus moquini* Bonaparte, 1856) on island[22]
1999	Declared an Institution under Cultural Institutions Act of 1999 Declared a World Heritage Site (by World Heritage Committee) [21]
2005	Sixty-one (61) cats removed (shot or trapped), about equal number estimated to be left on island[12] No pregnant or lactating females found and cats in good condition[12] Unsuccessful attempt to remove Fallow Deer[22]
2006	Declared a National Heritage Site under National Heritage Resources Act of 1999 Integrated Conservation Management Plan produced[21] Ninety-five cats culled, estimated 12-15 cats remain on island[12]
2007	More cats removed from island[22] Adult Fallow Deer males observed breaking branches with their antlers to gain access to vegetation outside their reach[22] Adults of both sexes observed eating a variety of other materials including stranded kelp (*Ecklonia maxima* (Osbeck) Papenfuss), newspaper and cardboard littered on the island, garbage rummaged from rubbish bins and even a rabbit carcase[22]

Year/Period	Notable events
2008	Cats finally eradicated from island with at least 290 cats estimated to have been removed since 2005[22] Culling of Fallow Deer individuals[30] Proliferation of rabbits thought to be in response to removal of feral cats[28] Grazing substantially reduces cover of pipe grass (*Ehrharta villosa* Schult.f.*)* on the island[22] Carrying capacity of the island for grazers appears to have been exceeded and the availability of browse substantially reduced: ground cover eradicated over much of the island and a distinct browse-line evident on vegetation at height of at least 1.2 m[30, 22] Bontebok, springbok, fallow deer and rabbits starving to death because of a lack of vegetation[28, 30] Rabbits seen feeding off kelp and climbing acacia thorn trees to feed high up among the thorns[30] Problem believed to have been caused by explosion of feral rabbit population which is 'eating everything in sight' and delay in reducing the number of fallow deer[28, 30] Bontebok population declines from 21 individuals to only two probably because rabbit grazing has substantially reduced the coverage of pipe grass *E villosa* on the island. [1, 15, 22] Last two Bontebok die out in May despite RIM managers belatedly bringing in fodder[30, 22] Conditions on the island generate extremely bad press for RIM[3, 4, 28, 30]
2009	Rabbit population decreases to ¼ of what it had been in 2008 as result of food limitation (carcasses observed) [12, 22] Control activities conducted and rabbit numbers further substantially reduced (4786 rabbits culled between November 2008 and May 2008) [12, 22] Fallow Deer population allowed to increase unchecked[22]
2010	Three rabbits observed in *Eucalyptus* plantation by author during vegetation sampling in March and none in November. Fallow deer shot. Numbers reduced from 220 to 30[20]
2011	No rabbits observed on the island by author during vegetation sampling in March and November
2012	No rabbits observed on the island by author during vegetation sampling in March and November
2013	No rabbits observed on the island by researcher during vegetation sampling in March and November

REFERENCES

1 Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

2 Aitken AP. 1999. Analysis of diet and genetic variability of feral cats (*Felis catus*) on Robben Island. BSc (Hons) Thesis, University of Cape Town, Cape Town.

3 Anon. 2008. Rabbits a threat to Robben Island. 'Available at' https://www.iol.co.za/news/south-africa/rabbits-a-threat-torobben-island-420389 [accessed 8 February 2017]

4 Anon. 2008. Robben Island's rabbits to be culled. 'Available at' https://www.iol.co.za/news/south-africa/robben-islands-rabbits-to-be-culled-420363 [accessed 8 February 2017]

5 Brooke RK, Prins AJ. 1986. Review of alien species on South African offshore islands. *South African Journal of Antarctic Research* 16: 102-109.

6 Chapman R, Le Maitre DC, Holmes PM (eds). 2000. *Robben Island: a baseline terrestrial ecology study and recommendations for vegetation rehabilitation*. Environmentek CSIR Report No. ENV-Sc 99115. Stellenbosch.

7 Cooper J. 1985. Biology of the Bank Cormorant, part 3: foraging behaviour *Ostrich: Journal of African Ornithology* 56 86- 95.

8 Cooper J, Brooke RK. 1982. Past and present distribution of the feral European rabbit *Oryctolagus cuniculus* on southern African offshore islands. *South African Journal of Wildlife Research* 12: 5-71.

9 Cooper J, Brooke RK. 1986. Alien plants and animals on South African continental and oceanic islands: species richness, ecological impacts and management. In: Macdonald IAW, Kruger FJ, Ferrar AA editors. *The ecology and management of biological invasions in southern Africa*. Cape Town: Oxford University Press. p. 133-142.

10 Crawford R, Dyer B. 2000. Wildlife of Robben Island. In: Underhill L editor. *Bright Continent Guide*. Cape Town: Avian Demography Unit.

11 Crawford RJM, David JHM, Dyer BM, Jarvis JUM, Shannon LJ, Spinks A, Upfold L, Crawford DAE, Crawford PJM, Knoll C*, et al.* (eds). 1998. *Terrestrial vertebrates of Robben Island*. Sea Fisheries Research Institute. South Africa.

12 de Villiers MS, Mecenero S, Sherley RB, Heinze E, Kieser J, Leshoro TM, Merbold L, Nordt A, Parsons NJ, Peter HU. 2010. Introduced European rabbits (*Oryctolagus cuniculus*) and domestic cats (*Felis catus*) on Robben Island: Population trends and management recommendations. *South African Journal of Wildlife Research* 40: 139-148.

13 Dingle RV, Rogers J. 1972. Pleistocene palaeogeography of the Agulhas Bank. *Transactions of the Royal Society of South Africa* 40: 155–165.

14 Heyl CW (ed). 1986. *Die voellewe van Robbeneiland en implikasies vir bewaring*. Kaapse Provinsialie Administrasie.

15 Lloyd JW, Linger MT. 1986. Report on the vegetation of Robben Island. *'n Natuurbewaringsondersoek van Robbeneiland*. Cape Town: Cape Nature

16 Lloyd PH (ed). 1994. *A review of non-human mammals on Robben Island*. Unpublished report.

17 Miller D. 1991. A geological description of Robben Island. *South African Lapidary Magazine* 23: 5-8.

18 Nankivell JW. 1934. Robben Island. *The South African Geographical Journal* 17: 29-34.

19 Parsons & Associates (ed). 1998. *Assessment of the groundwater resources of Robben Island*. Somerset West, South Africa.

20 Philander R. 2017. Robben Island to cull deer. 'Available at' https://www.iol.co.za/capeargus/news/robben-island-to-cull-deer-9940208 [accessed 26 October 2017]

21 Robben Island Museum. 2006. *Integrated Conservation Management Plan (ICMP) for the Robben Island World Heritage Site*. Cape Town: Robben Island Museum

22 Sherley RB. 2016. Unusual foraging behaviour in two introduced mammals following degradation of their island habitat. *Biodiversity Observations* 7: 1-10.

23 Skead CJ. 1980. *Historical mammal incidence in the Cape Province Vol. 1. The Western and Northern Cape*. Cape Town: Department of Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope.

24 Smallberg M. n.d. *Robben Island: history summary*. Robben Island Education Department.

25 Smithers RHN (ed). 1983. *The mammals of the southern African sub-region*. University of Pretoria. Pretoria.

26 Smithers RHN (ed). 1986. *South African red data book - terrestrial mammals*. National Scientific Programmes: CSIR Report No. SANSP 125.

27 Tankard AJ. 1976. Cenozoic sea-level changes: a discussion. *Annals of the South African Museum* 71: 1–17.

28 Vosloo E. 2008. Eco-xenophobia' for island's deer 'Available at' https://www.iol.co.za/news/south-africa/eco-xenophobia-for-islands-deer--403624 [accessed 8 February 2017]

29 Wells JC. 1998 Eva's men: gender and power in the establishment of the Cape of Good Hope, 1652-74. *Journal of African History*: 417–437.

30 Yeld J. 2008. Robben Island conservation 'in a shambles'. 'Available at' http://www.iol.co.za/news/south-africa/robben-island-conservation-in-a-shambles-1.398514#.Utf_RYWRa1s [accessed 8 February 2017]

ANNEXURE II: CONSOLIDATED PLANT LIST FOR ROBBEN ISLAND INCORPORATING SURVEYS BY ADAMSON (1934), BEZENG (2011) AND THIS STUDY (2013). STATUS: 'A'=ALIEN 'N'=NATIVE 'O'=UNKNOWN AND 'G'=GARDEN PLANTS.

Family	**Accepted name**	**Survey year**			**Status**
		1934	**2011**	**2013**	
Aizoaceae	*Aizoon canariense* L.		*		A[2]
	Carpobrotus acinaciformis (L.) L.Bolus		*		N[2]
	Conicosia pugioniformis (L.) N. E. Br.	*	*	*	N[2]
	Delosperma sp.		*		O[2]
	Disphyma crassifolium (L.) L.Bolus		*		O[2]
	Dorotheanthus apetalus (L.f.) N.E.Br.		*		N[2]
	Drosanthemum floribundum (Haw.) Schwantes	*	*		N[2]
	Erepsia dunensis (Sond.) Klak	*	*		N[2]
	Galenia secunda (L.) Sond.		*		N[2]
	Malephora purpureocrocea Schwantes (unresolved)		*		O[2]
	Mesembrianthemum sp.	*			N[2]
	Mesembryanthemum crystallinum L.	*	*	*	N[2]
	Mesembryanthemum nodiflorum L.		*		N[2]
	Mesembryanthemum sp.1		*		N[2]
	Mesembryanthemum sp.2		*		N[2]
	Phyllobolus canaliculatus (Haw.) Bittrich (unresolved)		*	*	N[2]
	Tetragonia decumbens Mill.	*	*		N[2]
	Tetragonia fruticosa L.	*	*	*	N[2]
Alliaceae	*Allium* sp.		*		A[2]
Amaranthaceae	*Amaranthus deflexus* L.		*		O[2]
	Atriplex canescens (Pursh) Nutt.		*		A[2]
	Atriplex cinerea Poir.			*	O
	Atriplex prostrata Boucher ex DC.		*		A[2]
	Atriplex rosea L.		*		A[2]
	Atriplex sp.	*			A[2]
	Chenolea diffusa Thunb.	*	*		A[2]
	Chenopodium album L.	*	*	*	A[2]
	Chenopodium murale L.		*	*	A[2]
	Chenopodium rubrum L.	*			O
	Dysphania botrys (L.) Mosyakin & Clemants		*		A[2]
	Exomis microphylla var. *axyrioides* (Fenzl ex Moq.) Aellen	*	*		O[2]
	Guilleminea densa (Willd. ex Schult.) Moq.		*		A[2]
	Salicornia meyeriana Moss		*		N[2]
	Salsola kali L.		*		A[2]
	Sarcocornia perennis (Mill.) A.J.Scott		*		N[2]
	Sarcocornia sp.1		*		N[2]
	Allium oleraceum L.	*	*		A[2]
	Allium sp.		*		A[2]

Family	**Accepted name**	**Survey year**			**Status**
		1934	**2011**	**2013**	
	Amaryllis belladonna L.		*		N^{2}
	Brunsvigia orientalis (L.) Aiton ex Eckl.	*	*		N^{2}
	Haemanthus coccineus L.	*	*		N^{2}
	Leucojum aestivum L.		*		O^{2}
	Narcissus elegans (Haw.) Spach		*		A^{2}
	Narcissus sp.	*			G^{1}
Anacardiaceae	*Harpephyllum caffrum* Bernh.		*		O^{2}
	Schinus molle L.	*	*		A^{2}
	Schinus terebinthifolia Raddi		*		A^{2}
Apiaceae	*Capnophyllum africanum* (L.) Gaertn.	*	*	*	N^{2}
	Dasispermum capense (Lam.) Magee & B.-E.van Wyk	*			O
	Foeniculum vulgare Mill.		*		A^{2}
	Torilis arvensis (Huds.) Link		*	*	N^{2}
Apocynaceae	*Acokanthera oblongifolia* (Hochst.) Benth. & Hook.f. ex B.D.Jacks.	*			G^{1}
	Acokanthera oppositifolia (Lam.) Codd		*		N^{2}
	Asclepias sp		*		N^{2}
	Carissa macrocarpa (Eckl.) A.DC.		*		N^{2}
	Catharanthus roseus (L.) G.Don		*		A^{2}
	Cynanchum zeyheri Schltr.	*	*		N^{2}
	Gomphocarpus fruticosus (L.) W.T. Aiton	*	*		N^{2}
	Nerium oleander L.	*	*		A^{2}
	Orbea variegata (L.) Haw.	*	*		N^{2}
	Vinca major L.	*			G^{1}
Araceae	*Lemna gibba* L.	*	*		N^{2}
	Zantedeschia aethiopica (L.) Spreng.	*	*	*	N^{2}
Araliaceae	*Hedera helix* L.		*		A^{2}
Araucariaceae	*Araucaria columnaris* (G.Forst.) Hook.	*			G^{1}
	Araucaria heterophylla (Salisb.) Franco		*		A^{2}
Arecaceae	*Phoenix canariensis* Chabaud	*	*		A^{2}
	Phoenix reclinata Jacq.		*		A^{2}
	Washingtonia robusta H.Wendl.		*		A^{2}
Asparagaceae	*Agave americana* L.	*	*		A^{2}
	Agave sp.		*		A^{2}
	Albuca fragrans Jacq.	*	*		G^{2}
	Asparagus asparagoides (L.) Druce	*	*		N^{2}
	Asparagus capensis L.	*	*	*	N^{2}
	Asparagus sp.		*		N^{2}

Family	Accepted name	Survey year			Status
		1934	2011	2013	
	Dracaena draco (L.) L.		*		A^2
	Yucca filamentosa L.		*		A^2
	Yucca gloriosa L.	*	*		A^2
Asteraceae	*Asteraceae* sp. 1		*		O^2
	Asteraceae sp. 2		*		O^2
	Asteraceae sp. 3		*		O^2
	Asteraceae sp. 4		*		O^2
	Asteraceae sp. 5		*		O^2
	Matricaria sp.	*	*		A^2
Basellaceae	*Anredera cordifolia* (Ten.) Steenis		*		N^2
Boraginaceae	*Amsinckia menziesii* (Lehm.) A.Nelson & J.F.Macbr.		*		O^2
	Echium strictum L.f.	*			G^1
	Echium vulgare L.		*		A^2
Brassicaceae	*Brassica* sp.	*	*		O^2
	Lepidium didymum L.	*	*		A^2
	Rapistrum rugosum (L.) All.		*		A^2
Cactaceae	*Epiphyllum phyllanthus* (L.) Haw.	*	*		A^2
	Opuntia stricta (Haw.) Haw.		*		A^2
Campanulaceae	*Wahlenbergia androsacea* A.DC.	*	*	*	G^2
Caryophyllaceae	*Dianthus caryophyllus* L.		*		A^2
	Polycarpon tetraphyllum (L.) L.	*	*		N^2
	Sagina saginoides (L.) H.Karst		*		O^2
	Silene cretica L.	*	*	*	A^2
	Spergula rubra J. Presl & C. Presl	*			O
	Spergula arvensis L.			*	O
	Spergularia media (L.) C.Presl	*	*		N^2
Casuarinaceae	*Casuarina cunninghamiana* Miq.	*	*		A^2
Celastraceae	*Catha edulis* (Vahl) Endl.		*		A^2
Colchicaceae	*Ornithoglossum dinteri* K.Krause		*		N^2
	Ornithoglossum sp.1		*		N^2
	Ornithoglossum viride (L.f.) Dryland. Ex W.T.Aiton	*	*	*	N^2
Combretaceae	*Combretum kraussii* Hochst.		*		O^2
Compositae	*Arctotheca calendula* (L.) Levyns	*	*		N^2
	Arctotheca sp.		*		N^2

Family	Accepted name	Survey year			Status
		1934	2011	2013	
	Arctotis hirsuta (Harv.) Beauverd	*	*		N^2
	Argyranthemum frutescens (L.) Sch.Bip.	*	*		A^2
	Artemisia absinthium L.	*			G^1
	Artemisia afra Jacq. ex Willd.		*		A^2
	Berkheya rigida (Thunb.) "Bolus & Wolley-Dod ex Ewart, Jean White & B.Rees"		*		N^2
	Brachylaena discolor DC.		*		O^2
	Chrysanthemoides monilifera (L.) Norl.		*		O^2
	Conyza bonariensis (L.) Cronquist	*	*		A^2
	Cotula coronopifolia L.	*	*		N^2
	Cotula filifolia Thunb.	*	*		N^2
	Cotula pusilla Thunb.	*			O
	Cotula turbinata L.	*			O
	Dimorphotheca pluvialis (L.) Moench	*	*		N^2
	Dittrichia graveolens (L.) Greuter		*	*	O^2
	Gazania hybrid cultivars		*		N^2
	Helichrysum crassifolium D.Don	*			O
	Helichrysum luteoalbum (L.) Rchb.	*			O
	Helichrysum patulum (L.) D.Don		*	*	N^2
	Hypochaeris glabra L.	*		*	O
	Laphangium luteoalbum (L.) Tzvelev		*		N^2
	Metalasia densa (Lam.) P.O.Karis		*		N^2
	Metalasia sp.1		*		N^2
	Oncosiphon grandiflorum (Thunb.) Källersjö		*		N^2
	Oncosiphon sabulosum (Wolley-Dod) Källersjö		*		N^2
	Oncosiphon suffruticosum (L.) Källersjö	*	*	*	N^2
	Senecio angulatus L.	*	*		N^2
	Senecio elegans L.		*		N^2
	Senecio littoreus Thunb.	*			O
	Senecio maritimus L.f.	*	*		N^2
	Sonchus oleraceus (L.) L.	*	*	*	N^2
	Tagetes minuta L.			*	O
Convolvulaceae	*Ipomaea paniculatus* R. Br. (unresolved sp name)	*			G^1
	Ipomoea mauritiana Jacq.		*		N^2
Crassulaceae	*Aeonium spathulatum* (Hornem.) Praeger	*	*		N^2
	Cotyledon orbiculata L.	*	*		N^2
	Crassula decumbens Thunb.	*	*		G^2
	Crassula glomerata P.J. Bergius	*			
	Crassula multicava Lem.		*		O^2
	Crassula natans Thunb.		*	*	N^2
	Crassula ovata (Mill.) Druce		*		N^2
	Crassula thunbergiana Schult.	*	*		N^2
	Crassula umbellata Thunb.	*	*		N^2
	Crassula vaillantii (Willd.) Roth	*	*		N^2

Family	Accepted name	Survey year			Status
		1934	2011	2013	
	Crassula sp.			*	N[2]
	Kalanchoe beharensis Drake		*		G[2]
Cucurbitaceae	*Citrullus lanatus* (Thunb.) Matsum. & Nakai	*	*		N[2]
	Cucumis africanus L.f.	*	*		G[2]
	Cucumis anguria L.		*		O[2]
	Cucumis myriocarpus Naudin		*		N[2]
Cupressaceae	*Cupressus macrocarpa* Hartw.	*	*		A[2]
	Cupressus sempervirens L.		*		A[2]
Cyperaceae	*Cyperus textilis* Thunb.		*		N[2]
	Isolepis antarctica (L.) Roem. Schult.	*	*		N[2]
	Isolepis incomtula Nees	*	*		N[2]
	Isolepis sp.			*	N[2]
Didiereaceae	*Portulacaria afra* Jacq.	*	*		N[2]
Ebenaceae	*Euclea racemosa* L.		*		N[2]
Euphorbiaceae	*Euphorbia drummondii* Boiss.		*		A[2]
	Euphorbia peplus L.	*	*	*	A[2]
	Euphorbia polygonifolia L.	*	*		N[2]
	Ricinus communis L.	*	*		A[2]
Frankeniaceae	*Frankenia pulverulenta* L.	*	*		A[2]
Geraniaceae	*Erodium moschatum* (L.) L'Her.	*	*	*	A[2]
	Geranium incanum Burm.f.		*		O[2]
	Geranium molle L.		*		A[2]
	Pelargonium capitatum (L.) L'Hér.		*		N[2]
	Pelargonium cucullatum (L.) L'Hér.		*		N[2]
	Pelargonium peltatum (L.) L'Her.	*			G[1]
	Pelargonium sidoides DC.			*	O
	Pelargonium zonale (L.) L'Her. Ex Aiton	*			G[1]
Gesneriaceae	*Paliavana racemosa* (Vell.) Fritsch		*		A[2]
Iridaceae	*Chasmanthe floribunda* (Salisb.) N.E.Br.	*			
	Ferraria crispa Burm.	*	*		N[2]
	Moraea collina Thunb.	*	*	*	N[2]
	Moraea setifolia (L.f.) Druce	*	*		N[2]
	Romulea obscura Klatt	*	*		N[2]
	Romulea rosea (L.) Eckl.	*	*		N[2]
Lamiaceae	*Ballota africana* (L.) Benth.	*	*		N[2]

Family	**Accepted name**	**Survey year**			**Status**
		1934	**2011**	**2013**	
	Leonotis leonurus (L.) R.Br.		*		N^2
	Salvia lanceolata Lam.		*		N^2
Leguminosae	*Acacia cyclopis* Cunn. ex Loudon	*	*	*	A^2
	Acacia saligna (Labill.) Wendl.	*			A
	Ceratonia siliqua L.		*		A^2
	Crotalaria capensis Jacq.	*	*		N^2
	Erythrina caffra Thunb.		*		N^2
	Medicago arabica (L.) Huds.	*	*		A^2
	Medicago polymorpha L.	*	*		G^2
	Psoralea repens P.J.Bergius	*	*		N^2
	Trifolium tomentosum L.	*	*		A^2
Malvaceae	*Grewia occidentalis* L.		*		N^2
	Hibiscus rosa-sinensis L.	*	*		A^2
	Lagunaria patersonia (Andrews) G. Don		*		A^2
	Malva arborea (L.) Webb & Berthel.	*	*		G^2
	Malva neglecta Wallr.		*		A^2
	Malva parviflora L.	*	*		A^2
	Malva sp.1		*		A^2
Menispermaceae	*Cissampelos capensis* L.f.	*	*	*	N^2
Molluginaceae	*Pharnaceum subtile* E. Mey.	*	*		N^2
Moraceae	*Ficus carica* L.	*	*		A^2
	Ficus microcarpa L.f.		*		A^2
	Morus alba L.		*		A^2
Myrtaceae	*Callistemon viminalis* (Sol. ex Gaertn.) G.Don		*		A^2
	Corymbia gummifera (Gaertn.) K.D.Hill & L.A.S Johnson	*	*		A^2
	Eucalptus lehmannii (Shauer) Benth.	*	*	*	A^2
	Eucalyptus cladocalyx F.Muell.	*	*	*	A^2
	Eucalyptus globulus Labill.	*	*		A^2
	Eucalyptus sp.1		*		A^2
	Eucalyptus sp.2		*		A^2
	Eucalyptus sp.3		*		A^2
	Eucalyptus sp.4		*		A^2
	Leptospermum laevigatum (Gaertn.) F.Muell.	*	*		A^2
	Melaleuca bracteata F.Muell.		*		A^2
	Metrosideros excelsa Sol. ex Gaertn.		*		A^2
	Syzygium cordatum Hochst. ex Krauss		*		N^2
Nyctaginaceae	*Bougainvillea glabra* Choisy	*	*		A^2
	Mirabilis jalapa L.	*	*		A^2

Family	Accepted name	Survey year			Status
		1934	2011	2013	
Oleaceae	*Ligustrum lucidum* W.T.Aiton		*		A[2]
	Olea europaea subsp. *cuspidata* (Wall. & G.Don) Cif.		*		N[2]
	Oleaceae sp.1		*		A[2]
Orchidaceae	*Satyrium odurum* Sond.	*	*		A[2]
Orobanchaceae	*Orobanche ramosa* L.	*			O
Oxalidaceae	*Oxalis corniculata* L.	*	*		N[2]
	Oxalis pes-caprae L.	*	*	*	A[2]
Papaveraceae	*Corydalis decumbens* (Thunb.) Pers.	*			O
	Cysticapnos vesicaria (L.) Fedde		*		N[2]
Phytolaccaceae	*Phytolacca dioica* L.	*	*		A[2]
	Phytolacca dodecandra L'Her.	*			G[1]
Pinaceae	*Pinus halepensis* Mill.	*	*	*	A[2]
	Pinus radiata D.Don		*		A[2]
Pittosporaceae	*Pittosporum* sp.1		*		A[2]
Plantaginaceae	*Plantago coronopus* L.	*	*		A[2]
Plumbaginaceae	*Plumbago auriculata* Lam.	*	*		G[2]
Poaceae	*Agrostis* sp.		*		N[2]
	Ammophila arenaria (L.) Link	*	*		A[2]
	Arundo donax L.	*	*		A[2]
	Avena barbata Pott ex Link		*		A[2]
	Avena fatua L.			*	A
	Avena sativa L.	*	*		A[2]
	Bromus catharticus Vahl.	*	*		A[2]
	Bromus diandrus Roth		*	*	A[2]
	Bromus japonicus Thunb.		*		A[2]
	Bromus pectinatus Thunb	*			O
	Bromus rigidus Roth	*			O
	Cynodon dactylon (L.) Pers.	*	*	*	N[2]
	Ehrharta brevifolia Schrad.	*	*		N[2]
	Ehrharta longiflora Sm.	*	*	*	N[2]
	Ehrharta villosa Schult.f.	*	*	*	N[2]
	Elymus distichus (Thunb.) Melderis	*	*		N[2]
	Fingerhuthia africana Lehm.		*		A[2]
	Hordeum murinum L.	*	*		A[2]
	Lagurus ovatus L.		*		A[2]
	Lolium temulentum L.	*	*		A[2]

Family	Accepted name	Survey year			Status
		1934	2011	2013	
	Pennisetum clandestinum Hochst. ex Chiov.		*		A^2
	Pennisetum villosum Fresen.	*	*		A^2
	Phalaris minor Retz.	*	*		A^2
	Poa annua L.	*	*		A^2
	Poaceae sp.1		*		O^2
	Poaceae sp.2		*		O^2
	Sporobolus virginicus (L.) Kunth		*	*	N^2
	Vulpia myuros (L.) C.C.Gmel			*	O
Polygalaceae	*Muraltia satureioides* Burch. ex DC.		*		A^2
	Muraltia spinosa (L.) F.Forest & J.C.Manning (unresolved)		*		A^2
	Polygala myrtifolia L.		*		G^2
	Emex australis Steinh.	*	*	*	A^2
	Polygonaceae sp.1		*		G^2
	Rumex pulcher L.	*			O
Portulacaceae	*Portulaca oleracea* L.		*		A^2
Primulaceae	*Anagallis arvensis* L.	*	*	*	A^2
	Anagallis sp.		*		A^2
Restionaceae	*Elegia tectorum* (L.f.) Moline & H.P.Linder		*		O^2
	Thamnochortus spicigerus (Thunb.) Spreng.		*		A^2
Rosaceae	*Prunus armeniaca* L.		*		A^2
Salicaceae	*Dovyalis caffra* (Hook.f. & Harv.) Sim	*	*		N^2
Sapotaceae	*Sideroxylon inerme* L.		*		N^2
Saxifragaceae	Saxifragaceae sp.		*		O^2
Scrophulariaceae	*Hemimeris montana* L.f.	*			
	Hemimeris racemosa (Houtt.) Merr.		*		N^2
	Myoporum laetum G. Forst.	*	*		A^2
	Phyllopodium capillare (L.f.) Hilliard		*		N^2
	Polycarena capillaris (L.f.) Benth.	*			O
	Zaluzianskya villosa F.W. Schmidt	*	*	*	N^2
Solanaceae	*Datura stramonium* L.		*		A^2
	Lycium afrum L.	*	*		N^2
	Lycium ferocissimum Miers	*	*		N^2
	Lycopersicon esculentum Mill.		*		A^2
	Nicotiana glauca Graham	*	*		A^2
	Physalis peruviana L.	*	*		A^2
	Solanum africanum Mill.		*		N^2

Family	Accepted name	Survey year			Status
		1934	2011	2013	
	Solanum americanum Mill.	*	*		A[2]
	Solanum anguivi Lam.		*		N[2]
	Solanum guineense L.		*		O[2]
	Solanum linnaeanum Hepper & P.-M.L.Jaeger		*		N[2]
	Solanum sodomaeum L. (unresolved)	*			O
Strelitziaceae	*Strelitzia reginae* Banks		*		G[2]
Tamaricaceae	*Tamarix chinensis* Lour.	*	*		A[2]
Tecophilaeaceae	*Cyanella lutea* L.f.	*			O
	Cyanella hyacinthoides Royen ex L.	*			O
	Cyanella orchidiformis Jacq.		*		N[2]
Tropaeolaceae	*Tropaeolum majus* L.	*	*		A[2]
Urticaceae	*Didymodoxa capensis* (L.f.) Friis & Wilmot-Dear	*	*		N[2]
	Urtica urens L.	*	*	*	A[2]
Vitaceae	*Vitis vinifera* L.	*	*		G[2]
Xanthorrhoeaceae	*Aloe arborescens* Mill.	*	*		N[2]
	Aloe barberae Dyer		*		G[2]
	Aloe camperi Schweinf.		*		G[2]
	Aloe ferox Mill.	*	*		G[2]
	Aloe maculata All.	*	*		N[2]
	Aloe thraskii Baker		*		G[2]
	Gasteria sp.1		*		G[2]
	Phormium tenax J.R.Forst. & G.Forst.		*		A[2]
	Trachyandra ciliata (L.f.) Kunth	*	*		N[2]
	Trachyandra divaricata (Jacq.) Kunth	*	*		N[2]
	Trachyandra sp.			*	N[2]
Zygophyllaceae	*Zygophyllaceae* sp.1		*		O[2]

References

1 Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

2 Bezeng BS. 2012. Invasion of alien species on Robben Island: causes and impacts on phylogenetic diversity of native plant communities. Magister Scientiae, University of Johannesburg, Johannesburg.

ANNEXURE III: POPULATION DYNAMICS OF INTRODUCED ANIMALS ON ROBBEN ISLAND, SOUTH AFRICA

Year/Period	Population dynamics of introduced animals													
	Sheep	Dassies	Cattle	Rabbits	Pigs	Steenbok	Goats	Cats	Springbok	Eland	Blue Wildebeest	Fallow Deer	Ostriches	Bontebok
1601	Introduced: 8[11]	Introduced: 2[11]												
1608			Introduced[11]											
1614	Present: Small flock[19]													
1652	Present: Tiny flock[19]													
1653		Supplementation[4]												
1654				Introduced[11]										
1655					First pigs removed from island[11]									
1656				Supplementation[17, 5, 11]										
1657				Supplementation [17, 5, 11]										
1658				Supplementation[17, 5, 11] and first births[20]		Introduced: 2 (Ewe & young) [11] Soon died[8]								
1659	200[11]	Increasing[11]		50[11]										
1661				Hundreds[11]	Excess of 100[11]									
1666	850[19]		10[19]		30[19]		40[19]							
1846 - 1931	Periodically 300 sheep were landed, and in winter rapidly fattened[12]		More than 100 fine milch cows, bred at Elsenberg, were kept near well-built dairy[12]		Pigs were also kept[12]		Present[1]							
1881								Introduced[7]						
1933	1[12]			Very abundant[1] Over-run island[12]			7[12]							
1946-1959									Introduced after World War II but prior to 1955[7]	Introduced after World War II but prior to 1955[7]	Introduced after the World War II[7] Soon shot out[7]			
1963												Introduced: 3[20, 7]		
1967													Introduced: 2 (Female and male) [10]	
1973						Re-introduced[2]								
1975									Population augmented[7]					
1977												40[20]		
1978													50 adult[3]	
1985				Fewer than 10[14]		38[8] 50[13]			38[13]	11[13]		Around 12[13, 14] Numbers reduced by hunting[6]		Introduced[8]
1995						150 - 200[8]			80[8]	4 (1 male and 3 females) [8]		20 – 40[8]		25[8]
1996										3 females (male euthanised after falling and breaking a leg) [8]				
1998				31[8]		253[8]		Attempt to remove cats [7]	55 - 58[8]	3 females[8]		31[8]	26 (13 male and 13 female) [8]	44[8]

Year/Period	Population dynamics of introduced animals													
	Sheep	Dassies	Cattle	Rabbits	Pigs	Steenbok	Goats	Cats	Springbok	Eland	Blue Wildebeest	Fallow Deer	Ostriches	Bontebok
								107 individuals killed[7] Around 10 cats remain[16]						
1999				Around 100[7]						5 (2 bulls, one old one young, introduced from West Coast National Park) [7]		44[7]		
2002										4[18]				
2003				Around 2100[9]										
2004				Around 2400[9]					42[22]					
2005				Around 3100[9]				61 cats removed from island[9] At least 61 cats estimated to be left on island[9]				Unsuccessful attempt to remove fallow deer[16] 119 (median count) [16] 145 (maximum count) [16]		
2006				Around 4100[9]				95 cats killed[9] 12-15 cats remain on island[9]						
2007								Cat removal activities conducted[16]	25[22]			146 (median count) [16] 223 (maximum count) [16]		80 in April[22] 50 removed in July[22] 21 recorded in September[16]
2008				Around 24100[9]				Cats though to have been eradicated from island [16]	20[21] 12[22]			150[21] 138 (median count) [16] 307 (maximum count) [16] 90 after culling in April[22]		2[21, 16] Died out by May[16]
2009				Around 1200 (~18000 rabbits killed by food shortage and 4786 rabbits culled)								161 (median count) [16] 225 (maximum count) [16]		
2010				Control activities conducted and rabbit numbers further reduced Three rabbits observed by author in March No rabbits observed in November					5 – 10[18]	1[18]		30[15]		
2011				No rabbits observed by authors										
2012				No rabbits observed by author										
2013				No rabbits observed by author										

REFERENCES

1 Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

2 Brooke RK, Prins AJ. 1986. Review of alien species on South African offshore islands. *South African Journal of Antarctic Research* 16: 102-109.

3 Chapman R, Le Maitre DC, Holmes PM (eds). 2000. *Robben Island: a baseline terrestrial ecology study and recommendations for vegetation rehabilitation*. Environmentek CSIR Report No. ENV-Sc 99115. Stellenbosch.

4 Cooper J. 1985. Biology of the Bank Cormorant, part 3: foraging behaviour *Ostrich: Journal of African Ornithology* 56 86- 95.

5 Cooper J, Brooke RK. 1982. Past and present distribution of the feral European rabbit *Oryctolagus cuniculus* on southern African offshore islands. *South African Journal of Wildlife Research* 12: 5-71.

6 Cooper J, Brooke RK. 1986. Alien plants and animals on South African continental and oceanic islands: species richness, ecological impacts and management. In: Macdonald IAW, Kruger FJ, Ferrar AA editors. *The ecology and management of biological invasions in southern Africa*. Cape Town: Oxford University Press. p. 133-142.

7 Crawford R, Dyer B. 2000. Wildlife of Robben Island. In: Underhill L editor. *Bright Continent Guide*. Cape Town: Avian Demography Unit.

8 Crawford RJM, David JHM, Dyer BM, Jarvis JUM, Shannon LJ, Spinks A, Upfold L, Crawford DAE, Crawford PJM, Knoll C*, et al.* (eds). 1998. *Terrestrial vertebrates of Robben Island*. Sea Fisheries Research Institute. South Africa.

9 de Villiers MS, Mecenero S, Sherley RB, Heinze E, Kieser J, Leshoro TM, Merbold L, Nordt A, Parsons NJ, Peter HU. 2010. Introduced European rabbits (*Oryctolagus cuniculus*) and domestic cats (*Felis catus*) on Robben Island: Population trends and management recommendations. *South African Journal of Wildlife Research* 40: 139-148.

10 Heyl CW (ed). 1986. *Die voellewe van Robbeneiland en implikasies vir bewaring*. Kaapse Provinsialie Administrasie.

11 Lloyd PH (ed). 1994. *A review of non-human mammals on Robben Island*. Unpublished report.

12 Nankivell JW. 1934. Robben Island. *The South African Geographical Journal* 17: 29-34.

13 Norton PM (ed). 1986. *Report on the large mammals of Robben Island*. Kaapse Provinsialie Administrasie.

14 Palmer NG. 1986. Small mammals of Robben Island. *'n Natuurbewaringsondersoek van Robbeneiland*. Cape Town: Cape Nature.

15 Philander R. 2017. Robben Island to cull deer. 'Available at' https://www.iol.co.za/capeargus/news/robben-island-to-cull-deer-9940208 [accessed 26 October 2017]

16 Sherley RB. 2016. Unusual foraging behaviour in two introduced mammals following degradation of their island habitat. *Biodiversity Observations* 7: 1-10.

17 Skead CJ. 1980. *Historical mammal incidence in the Cape Province Vol. 1. The Western and Northern Cape*. Cape Town: Department of Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope.

18 Skead CJ. 2011. Historical incidence of the larger land mammals in the broader Western and Northern Cape In: Boshoff AF, Kerley GIH, Lloyd PH editors. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.

19 Smallberg M. n.d. *Robben Island: history summary*. Robben Island Education Department.

20 Smithers RHN (ed). 1983. *The mammals of the southern African sub-region*. University of Pretoria. Pretoria.

21 Vosloo E. 2008. Eco-xenophobia' for island's deer 'Available at' https://www.iol.co.za/news/south-africa/eco-xenophobia-for-islands-deer--403624 [accessed 8 February 2017]

22 Yeld J. 2008. Robben Island conservation 'in a shambles'. 'Available at' http://www.iol.co.za/news/south-africa/robben-island-conservation-in-a-shambles-1.398514#.Utf_RYWRa1s [accessed 8 February 2017]

ANNEXURE IV: CHAPTER 3 — SUPPLEMENTARY MATERIAL 1

Table S1 Durbin-Watson tests for serial autocorrelation in relationships between inter-annual rainfall variation and plant species composition change (mean NMDS axis 1 score) following the control of invasive alien European rabbits on Robben Island. Durbin-Watson (DW) statistics close to 0 represent positive autocorrelation, 2- no autocorrelation and 4- negative autocorrelation. Only results for significant (*P* ≤ 0.05) regressions (see Table 3.3 in the main text) shown.

Sites	Rainfall					
	TSUR		TAUR		TWR	
	DW	*P*	DW	*P*	DW	*P*
Strand	0.93	0.002	1.03	0.004	0.83	<0.001
Eucalyptus	1.39	0.062	0.91	0.002	1.02	0.005
Inland dune	-	-	2.75	0.971	-	-

Table S2 Change in percent contributions to Bray-Curtis compositional dissimilarity and mean plant species cover (% ± SE) of plant species that underlay vegetation compositional change following the control of invasive alien European rabbits on Robben Island. Only species accounting for the top 95% of contrasted compositional dissimilarities shown. Significant differences determined using repeated measures ANOVA/ Wilcoxon two-sample paired tests. FDR-adjusted *P* values (classical one-stage method) provided for reference.

Sites	Species	% contribution to dissimilarity	Year				Test statistic F/W	*P-value*	FDR adjusted *P*
			2010	2011	2012	2013			
Strand	**Annual herbs**								
	Silene cretica	3.94	0.00	0.00	3.70 ± 2.28	3.00 ± 1.44	0.50	0.750	0.938
	Oncosiphon suffruticosum	7.03	0.30 ± 0.33	0.00	4.30 ± 2.33	7.00 ± 3.75	3.22	0.050	0.176
	Perennial herbs								
	Conicosia pugioniformis	8.38	9.00 ± 1.91	2.00 ± 1.03	2.30 ± 1.31	3.00 ± 1.91	5.97	0.007	0.069
	Zantedeschia aethiopica	1.24	0.70 ± 0.42	0.00	0.70 ± 0.42	0.70 ± 0.67	< 0.01	1.000	1.000
	Annual grasses								
	Ehrharta longiflora	27.04	0.00	0.00	20.70 ± 4.46	31.00 ± 3.89	-1.50	0.250	0.448
	Bromus diandrus	1.23	0.00	0.00	0.70 ± 0.42	1.30 ± 1.33	-0.60	1.000	1.000
	Perennial grasses								
	Ehrharta villosa .	5.64	0.00	0.30 ± 0.33	4.30 ± 2.85	5.00 ± 3.64	1.50	0.269	0.448
	Cynodon dactylon	1.91	0.30 ± 0.33	0.00	1.30 ± 0.99	1.70 ± 0.61	1.00	0.402	0.574
	Woody shrubs								
	Tetragonia fruticose	28.60	22.70 ± 2.51	40.00 ± 5.89	42.00 ± 7.38	38.70 ± 7.64	4.89	0.015	0.072
	Asparagus capensis	9.50	3.70 ± 2.09	0.30 ± 0.33	6.00 ± 3.10	4.00 ± 2.00	1.52	0.251	0.448

Eucalyptus	**Annual herbs**								
	Oncosiphon suffruticosum	5.25	0.00	0.00	0.67 ± 0.42	1.33 ± 0.67	3.00	0.500	0.591
	Euphorbia peplus	2.79	0.00	0.00	0.00	1.67 ± 1.67	-	-	-
	Chenopodium murale	2.57	0.00	0.00	0.33 ± 0.33	0.33 ± 0.33	1.50	1.000	0.840
	Perennial herbs								
	Phyllobolus canaliculatus	41.49	0.67 ± 0.42	0.67 ± 0.67	8.67 ± 3.29	8.33 ± 6.01	8.29	0.002	0.008
	Oxalis pes-caprae	12.78	0.33 ± 0.33	0.00	0.33 ± 0.33	3.00 ± 1.13	2.34	0.147	0.309
	Woody shrubs								
	Tetragonia fruticosa	29.82	0.00	0.00	6.00 ± 2.68	13.33 ± 7.28	14.00	0.563	0.591
Inland dune	**Perennial herbs**								
	Conicosia pugioniformis	8.02	11.70 ± 1.74	2.70 ± 1.61	2.70 ± 2.29	3.30 ± 1.43	7.25	0.003	0.011
	Annual grasses								
	Ehrharta longiflora	2.10	1.00 ± 1.00	0.00	0.33 ± 0.33	3.00 ± 1.34	2.65	0.119	0.167
	Bromus diandrus	9.42	0.00	0.00	10.70 ± 4.43	13.00 ± 5.26	-0.02	1.000	1.000
	Perennial grasses								
	Ehrharta villosa	23.25	1.00 ± 1.00	6.00 ± 2.83	20.30 ± 9.00	36.30 ± 14.20	3.42	0.045	0.105
	Woody shrubs								
	Tetragonia fruticosa	30.62	16.30 ± 6.54	37.70 ± 9.49	48.30 ± 8.82	42.00 ± 6.91	12.51	< 0.001	0.002
	Cissampelos capensis	16.96	25.00 ± 6.57	21.70 ± 4.88	26.70 ± 6.01	19.30 ± 4.02	0.51	0.682	0.796

Table S3 Multivariate multiple regressions showing relationships between inter-annual rainfall variation and plant species cover changes that underlay vegetation compositional change following the control of European rabbits on Robben Island. Rao's *F* statistic was used to test for overall multivariate significance while *t* tests determined the significance of separate combinations of independent and dependent variables. Only regressions for species accounting for the top 95% of compositional change shown.

		Rainfall														
Sites	Life form/species	Overall			TSUR				TAUR				TWR			
		R^2	*F*	*P*	R^2	*Coeff*	*t*	*P*	R^2	*Coeff*	*t*	*P*	R^2	*Coeff*	*t*	*P*
Strand	**Annual herbs**															
	Silene cretica	0.32	3.07	0.050	0.26	-0.479	-0.28	0.781	0.30	1.579	1.25	0.226	0.21	2.683	0.54	0.592
	Oncosiphon suffruticosum	0.22	1.88	0.166	-	-	-	-	-	-	-	-	-	-	-	-
	Perennial herbs															
	Conicosia pugioniformis	0.33	3.31	0.041	0.01	3.380	1.77	0.092	0.13	-4.190	-2.95	0.008	< 0.01	-4.039	-0.73	0.474
	Zantedeschia aethiopica	0.09	0.70	0.565	-	-	-	-	-	-	-	-	-	-	-	-
	Annual grasses															
	Ehrharta longiflora	0.98	343.10	< 0.001	0.80	-2.089	-4.47	< 0.001	0.90	4.782	13.77	< 0.001	0.67	10.353	7.64	< 0.001
	Bromus diandrus	0.13	1.01	0.409	-	-	-	-	-	-	-	-	-	-	-	-
	Perennial grasses															
	Ehrharta villosa	0.15	1.22	0.330	-	-	-	-	-	-	-	-	-	-	-	-
	Cynodon dactylon	0.27	2.46	0.093	-	-	-	-	-	-	-	-	-	-	-	-
	Woody shrubs															
	Tetragonia fruticosa	0.29	2.74	0.070	-	-	-	-	-	-	-	-	-	-	-	-
	Asparagus capensis	0.01	0.04	0.990	-	-	-	-	-	-	-	-	-	-	-	-
Eucalyptus	**Annual herbs**															

	Oncosiphon suffruticosum	0.29	2.73	0.071	-	-	-	-	-	-	-	-	-	-	-	-
	Euphorbia peplus	0.13	1.00	0.413	-	-	-	-	-	-	-	-	-	-	-	-
	Chenopodium murale	0.09	0.67	0.582	-	-	-	-	-	-	-	-	-	-	-	-
	Perennial herbs															
	Phyllobolus canaliculatus	0.43	5.00	0.009	0.37	0.588	0.55	0.586	0.42	0.733	0.79	0.441	0.20	-0.525	-0.42	0.682
	Oxalis pes-caprae	0.42	4.90	0.010	0.14	-1.130	-1.86	0.078	0.08	0.715	1.34	0.195	0.31	2.179	3.06	0.006
	Woody shrubs															
	Tetragonia fruticosa	0.52	7.30	0.002	0.41	-1.315	-1.26	0.224	0.41	1.836	1.98	0.061	0.40	2.337	1.98	0.062
Inland dune	**Perennial herbs**															
	Conicosia pugioniformis	0.45	5.53	0.006	0.02	1.916	1.59	0.127	0.18	-3.243	-3.25	0.004	< 0.01	-0.065	-0.03	0.973
	Annual grasses															
	Ehrharta longiflora	0.31	3.05	0.050	0.10	-1.136	-1.24	0.229	0.04	0.491	0.65	0.525	0.24	3.419	2.33	0.031
	Bromus diandrus	0.54	7.67	0.001	0.46	-0.425	-0.31	0.761	0.52	1.963	1.72	0.101	0.34	1.543	0.70	0.493
	Perennial grasses															
	Ehrharta villosa	0.31	3.04	0.050	0.14	-3.437	-1.67	0.111	0.21	3.839	2.24	0.036	0.13	5.394	1.63	0.119
	Woody shrubs															
	Tetragonia fruticosa	0.39	4.32	0.017	0.06	-1.953	-1.78	0.090	0.23	2.782	3.06	0.006	0.02	1.429	0.81	0.426

Table S4 Durbin-Watson tests for serial autocorrelation in relationships between inter-annual rainfall variation and plant species cover changes that underlay vegetation compositional change following the control of invasive alien European rabbits on Robben Island. Durbin-Watson (DW) statistics close to 0 represent positive autocorrelation, 2- no autocorrelation and 4- negative autocorrelation. Only results for significant (*P* ≤ 0.05) regressions shown (see Table S3 above).

Sites	Life form/species	Rainfall					
		TSUR		TAUR		TWR	
		DW	*P*	DW	*P*	DW	*P*
Strand	**Palatable**						
	Ehrharta longiflora	0.70	< 0.001	0.73	< 0.001	0.69	<0.001
	Less palatable						
	Conicosia pugioniformis	-	-	2.12	0.610	-	-
Inland dune	**Highly palatable**						
	Tetragonia fruticosa	-	-	2.41	0.846	-	-
	Palatable						
	Ehrharta longiflora	-	-	-	-	1.98	0.477
	Less palatable						
	Ehrharta villosa	-	-	1.85	0.338	-	-
	Conicosia pugioniformis	-	-	1.96	0.445	-	-

Table S5 Plant species presence-absence and mean species cover (%) following the control of invasive alien European rabbits on Robben Island. Data organised for optimal interpretation using constrained seriation[1].

Sites	Species	Year			
		2010	2011	2012	2013
Strand	*Sporobolus virginicus* (L.) Kunth	1.00 ± 0.68			
	Sonchus oleraceus (L.) L.	0.33 ± 0.33		0.33 ± 0.33	
	Conicosia pugioniformis (L.) N. E. Br.	9.00 ± 1.91	2.00 ± 1.03	2.33 ± 1.31	3.00 ± 1.91
	Asparagus capensis L.	3.67 ± 2.09	5.67 ± 2.80	6.00 ± 3.10	4.00 ± 2.00
	Tetragonia fruticosa L.	22.70 ± 2.51	40.00 ± 5.89	42.00 ± 7.38	38.70 ± 7.64
	Oncosiphon suffruticosum (L.) Kallersjo	0.33 ± 0.33	0.33 ± 0.33	4.33 ± 2.33	7.00 ± 3.75
	Zantedeschia aethiopica (L.)	0.67 ± 0.42		0.67 ± 0.42	0.67 ± 0.67
	Cynodon dactylon (L.) Pers.	0.33 ± 0.33		1.33 ± 0.99	1.67 ± 0.61
	Vulpia myuros (L.) C.C.Gmel			0.67 ± 0.67	
	Isolepis sp.			1.00 ± 0.68	
	Crassula sp.			0.33 ± 0.33	
	Ehrharta villosa Schult.f.		0.33 ± 0.33	4.33 ± 2.85	5.00 ± 3.64
	Moraea collina Thunb.			1.33 ± 0.99	
	Spergula arvensis L.			0.33 ± 0.33	
	Ehrharta longiflora Sm.			20.70 ± 4.46	31.00 ± 3.89
	Bromus diandrus Roth.			0.67 ± 0.42	1.33 ± 1.33
	Silene cretica L.			3.67 ± 2.28	3.00 ± 1.44
	Euphorbia peplus L.				0.67 ± 0.67
	Anagallis arvensis L.				0.33 ± 0.33
	Phyllobolus canaliculatus (Haw.) Bittrich				0.33 ± 0.33
	Hypochaeris glabra L.				0.33 ± 0.33
Eucalyptus	*Phyllobolus canaliculatus* (Haw.) Bittrich	1.33 ± 0.67	0.67 ± 0.67	8.67 ± 3.29	8.33 ± 6.01
	Oxalis pes-caprae L.	0.67 ± 0.67		0.33 ± 0.33	3.00 ± 1.13
	Ehrharta longiflora Sm.			0.33 ± 0.33	0.67 ± 0.67
	Crassula natans Thunb.			0.33 ± 0.33	0.33 ± 0.33
	Tetragonia fruticosa L.			6.00 ± 2.68	13.30 ± 7.28
	Oncosiphon suffruticosum (L.) Kallersjo			0.67 ± 0.42	1.33 ± 0.67
	Chenopodium murale L.			0.33 ± 0.33	0.33 ± 0.33
	Torilis arvensis (Huds.) Link				0.33 ± 0.33
	Euphorbia peplus L.				1.67 ± 1.67
	Conicosia pugioniformis (L.) N. E. Br.				0.33 ± 0.33
Inland Dune	*Ornithoglossum viride* (L.f.) Dryland. Ex W.T.Aiton	0.33 ± 0.33			
	Wahlenbergia androsacea A.DC	0.33 ± 0.33			
	Emex australis Steinh.	0.33 ± 0.33			
	Sporobolus virginicus (L.) Kunth	0.33 ± 0.33			
	Trachyandra sp.	0.67 ± 0.42			

---

[1] Brower JC, Kile KM. 1988. Seriation of an original data matrix as applied to palaeoecology. *Lethaia* 21: 79-93.

Zantedeschia aethiopica (L.)	0.33 ± 0.33			
Phyllobolus canaliculatus (Haw.) Bittrich		0.33 ± 0.33		
Asparagus capensis L.		0.33 ± 0.33		
Ehrharta villosa Schult.f.	1.00 ± 1.00	6.00 ± 2.83	20.30 ± 9.00	36.30 ± 14.20
Cissampelos capensis L.f.	25.00 ± 6.57	21.70 ± 4.88	26.70 ± 6.01	19.30 ± 4.02
Oncosiphon suffruticosum (L.) Kallersjo	1.33 ± 1.33	0.33 ± 0.33	5.67 ± 2.28	1.33 ± 0.99
Conicosia pugioniformis (L.) N. E. Br.	11.70 ± 1.74	2.67 ± 1.61	2.67 ± 2.29	3.33 ± 1.43
Tetragonia fruticosa L.	16.30 ± 6.54	37.70 ± 9.49	48.30 ± 8.82	42.00 ± 6.91
Isolepis sp.			0.33 ± 0.33	
Torilis arvensis (Huds.) Link			3.33 ± 1.69	
Ehrharta longiflora Sm.	1.00 ± 1.00		0.33 nh ± 0.33	3.00 ± 1.34
Vulpia myuros (L.) C.C.Gmel			1.33 ± 0.42	
Anagallis arvensis L.			0.33 ± 0.33	
Bromus diandrus Roth.			10.70 ± 4.43	13.00 ± 5.26
Avena fatua L.				2.00 ± 1.26
Capnophyllum africanum (L.) Gaertn.				1.33 ± 0.84

ANNEXURE V: CHAPTER 3 — SUPPLEMENTARY MATERIAL 2

Overview

In this supplementary document, we present details about how we identified and eliminated the confounding effects of inter-annual rainfall variation on the results of our study by using a pseudo-before-after control-impact experimental design (BACI) and correlational rainfall-vegetation relationships. Our study was based on an experimentally unplanned attempt to remove invasive European rabbits from Robben Island, as detailed in the Materials and Methods section. The unplanned nature of our study resulted in our monitoring vegetation a full year after rabbit control efforts had begun. Due to this, we could not apply the BACI design, which is commonly used to assess impact in longitudinal observational studies, without a before-impact control. In addition, since we were unable to design and implement planned treatments and randomization, we could only evaluate rainfall variation's influence on vegetation response using correlative statistical control and therefore could not demonstrate direct causation. To overcome the challenges, we used an earlier vegetation survey of the island by Adamson (1934) as a BACI-like control and strengthened our interpretation of correlative rainfall-vegetation relationships by providing plausible mechanisms, showing links between putative causes and outcomes, and sourcing independent evidence to support the conclusions. (Adamson 1934) surveyed vegetation on Robben Island in 1933-1934 when the island was overrun with rabbits. The results of this survey were used as a BACI-like control by assuming that conditions on the island in 1933-1934 were similar to those prior to rabbit control in 2009 and 2010.

Below, we provide detailed descriptions of how we applied the above-mentioned approaches to each of our three study sites (strand, eucalyptus, and inland dune) to: i) evaluate and cancel out the effects of interannual rainfall variation on vegetation response; and ii) determine how grazing capacity and underlying species cover would have changed when if interannual rainfall had been constant and average across our study period. We have attempted to ensure that each section of this document is comprehensive and self-contained, so a significant amount of information has been repeated in the separate sections.

Strand sites

Statistical correlation indicates that interannual rainfall variation influenced much (~83%) of the change in species composition following rabbit control at strand sites. Interannual variation in TAUR had the greatest influence (~67%) on species composition change, followed by TSUR (negative correlation; ~42%) and TWR (~29%). Species composition changed moderately between the first- and second years following rabbit control, slightly more markedly between the second- and third, and slightly between the third- and fourth across the sites.

Based on our interpretation of the underlying vegetation dynamics and the correlation between rainfall and vegetation, we determined that the vegetation composition would have moderately changed across the strand sites following rabbit control, given constant and average inter-annual rainfall. Mean annual NMDS axis one scores would have changed moderately (by ~0.19 NMDS axis scores) across the sites between the first- and second years following rabbit control and remained constant thereafter. The increase in the cover of *Tetragonia fruticosa* and *Ehrharta longiflora* would have been of major importance, the emergence of *Ehrharta villosa* of intermediate importance, and the emergence of *Cynodon dactylon* and decline in the cover of *Oncosiphon suffruticosum* and *Conicosia pugioniformis* of minor importance in driving the change in vegetation composition. Specifically, the cover of *T. fruticosa* and *E. longiflora* would have increased moderately and markedly between the first and second years, whereas the cover of *E. villosa* and *C. dactylon* would have slightly increased from zero. The covers of all four species would have remained constant in subsequent years. In contrast, the cover of *O. suffruticosum* and *C. pugioniformis* would have sharply decreased between the first- and second years following rabbit control and remained constantly low thereafter.

Below, we present details of our determination of how each of the species that contributed to species composition change at strand sites would have responded to rabbit control, given constant and average inter-annual rainfall.

Tetragonia fruticosa

Inter-annual rainfall variation had no apparent effect on the cover of the woody shrub *T. fruticosa* after rabbit control. The shrub's cover increased moderately (by 17.30%) between the first and second years following the control, slightly (by 2.00%) between the second and third years, and then decreased slightly (by 3.30%) between the third and fourth years (Annex IV Table S2). *Tetragonia fruticosa* is a woody shrub with succulent leaves and a well-developed root system, which may consist of shallow long-spreading roots or deep roots that penetrate the soil to reasonable depths depending on soil conditions (van Breda, et al. 1991, Todd 2000). These succulent plants can tolerate drought by utilising water stored in their tissues and can switch between CAM and C3 photosynthesis to grow during periods of low water availability (Hoffman, et al. 2009). The leaf succulence and well-developed root systems of *T. fruticosa* may explain why the plant's cover increased despite worsening drought conditions between the first and second years after rabbit control.

It is possible that interannual variation in rainfall may have affected the change in the cover of *T. fruticosa* following rabbit control by promoting or suppressing germination of new plants. The seeds *T. fruticosa* germinate sporadically during the autumn after rainwater leaches salt from the soil (van Breda and Barnard 1991). The increase in *T. fruticosa* cover observed between the first- and second years following rabbit control was likely due to regrowth from previously browsed-down shoots. Although European rabbits can consume *T. fruticosa* plants, they usually struggle to eat the woody shoots, allowing the plants to recover from heavy herbivory (Adamson 1934). Hence, although they can be heavily browsed, *T. fruticosa* plants are rarely entirely consumed by rabbits. The increase in TAUR from considerably below the long-term average in the first- and second years following rabbit control to moderately above average in the third year would have increased leaching episodes and promoted more germination events. The subsequent decrease in TAUR to slightly below average in the fourth year following rabbit control would have restricted germination and seedling recruitment, contributing to the slight reduction in *T. fruticosa* cover. The lack of statistical significance in the regression between inter-annual rainfall variation and change in *T. fruticosa* cover can be attributed to the fact that the growth of established *T. fruticosa* plants is not directly dependent on rainfall, owing to the plant's ability to tolerate low moisture conditions. As a result, a regression analysis between rainfall and species cover may not reveal a significant relationship since other factors besides rainfall may be responsible for determining the variability in the species cover.

Given constant and average inter-annual rainfall, the increase in *T. fruticosa* cover would have remained one of the dominant drivers of vegetation composition change following rabbit control. However, the cover of *T. fruticosa* would have increased moderately between the first and second years after rabbit control due to both the regrowth of adult plants from browsed-down shoots and recruitment from the seedbank and remained constant in subsequent years.

Ehrharta longiflora

Inter-annual rainfall variation appears to have had a significant impact on almost all (~98%) of the changes in cover observed in the annual grass *E. longiflora* following rabbit control. The cover of the grass showed a marked increase (by 20.70%) from zero between the second- and third years after rabbit control, remaining relatively stable between the third and fourth (Annex IV Table S2). The emergence and increase

(~90% and ~67%) in grass cover between the second- and third years following rabbit control appear to have been driven by increases in TAUR and TWR from considerably and moderately below to moderately and slightly above the long-term average. However, the increase in TSUR from considerably below to moderately above the long-term average considerably suppressed (~80%) the increase in grass cover.

Ehrharta longiflora is a cool-season annual that survives summer stress as dormant seed (Moore, et al. 2007a, Fisher, et al. 2009, Winston, et al. 2014). Dormant seeds become non-dormant at the end of summer to take advantage of favourable growing conditions in winter (Moore and Moore 2007a). Germination of *E. longiflora* is influenced by soil moisture and takes place following autumn and winter rainfall (Western Australian Herbarium 1998, Bossard, et al. 2000, Moore and Moore 2007a). The below-average total autumn and winter rainfall during the first two years following rabbit control most likely suppressed *E. longiflora* germination. *Ehrharta longiflora* reproduces entirely from seed (Winston, et al. 2014) and failure to germinate would have resulted in its complete absence. The emergence and rapid increase in *E. longiflora* cover between the second- and third years following rabbit control probably resulted from the increase in total autumn and winter rainfall, which raised soil moisture to suitable levels for germination, and total winter rainfall, which facilitated rapid growth. The increase in total summer rainfall may have limited the increase in *E. longiflora* cover between the second- and third years following rabbit control by supporting more plant growth during the dry summer period and reducing the extent of open ground available for germination in autumn and winter. *Ehrharta longiflora* requires open ground for germination (Winston, et al. 2014). The cover of *E. longiflora* increased markedly after its emergence between the second and third years, reaching its upper equilibrium in the third year. Although the favourable wet conditions experienced in the third year stretched into the fourth year following rabbit control, the cover of *E. longiflora* remained constant. This was probably because the annual grass had covered all the available open ground.

Ehrharta longiflora is a palatable plant species (van Oudtshoorn 2012) and was a preferred food for rabbits on Robben Island (Gillham 1963). Despite this, annual plants like *E. longiflora* that grow for a limited period may endure heavy rabbit herbivory, even if they are frequently targeted. Since their short annual vegetation period exposes them to attacks for a shorter duration compared to most other plants, some can survive rabbit herbivory and flower (Farrow 1917). *Ehrharta longiflora* was observed on inland dune sites during the first year after rabbit control. Adamson (1934) noted *E. longiflora* on rock outcrops on strand sites in 1933 and 1934 when the island was overrun with rabbits and the vegetation severely degraded. It is plausible that *E. longiflora* may have existed at the strand sites before rabbit control, albeit with a very low cover.

Given constant and average inter-annual rainfall, an increase in *E. longiflora* cover would have remained one of the dominant drivers of vegetation composition change following rabbit control. However, *E. longiflora* cover would have increased markedly between the first- and second years following rabbit control and remained constant in subsequent years.

Ehrharta villosa

The impact of inter-annual rainfall variation on the change in cover of the perennial grass *E. villosa* following rabbit control appears to have been negligible. The cover of this grass increased slightly (by 0.30%) between the first- and second years following rabbit control and did not significantly change in the subsequent years (Annex IV Table S2). It is evident that inter-annual rainfall variation did not influence the emergence and increase in cover of the perennial grass *E. villosa* between the first- and second years following rabbit control. This is because the increase happened during worsening drought conditions, with TSUR and TWR dropping from moderately and slightly below the long-term average to considerably and moderately below the long-term average, respectively. Total autumn rainfall remained considerably below average during this period.

According to Harrington, et al. (1998), *E. villosa* can withstand drought conditions by utilising its deep root system to access water from beneath the soil surface. Additionally, E. villosa does not depend on seeds for reproduction, survival, spread, and regeneration (Hodder 1997). Seed production is minimal, and the primary mode of reproduction and dispersal is through rhizomes and rhizome fragments (Hodder 1997). Plants that regenerate from rhizomes are more tolerant of dry conditions than those that rely on seed germination. The ability of *E. villosa* to tolerate low soil moisture is the probable reason why the plant's coverage was not negatively impacted during the worsening drought conditions between the first- and second years after rabbit control. Coetzee (2008) notes that *E. villosa* requires fairly deep soil, and Adamson (1934) found that soil depth was generally shallow (3-5 cm) at strand sites. Therefore, it is likely that areas with deep enough soil to support *E. villosa* were limited at these sites, explaining why the perennial grass reached its upper equilibrium in the second year following rabbit control. *Ehrharta villosa* is a competitive plant that can grow over and overshadow competing vegetation due to its long stems (which can reach a height of 2 m or more) (Harrington, et al. 1998).

Although we lack precise information on rabbit preference for *E. villosa* on Robben Island, it appears that herbivory has a significant impact on the abundance of this perennial grass (Lloyd, et al. 1986, Sherley 2016). Lenient grazing is known to promote the growth of *E. villosa* in grasslands (Tainton, et al. 1990). Adamson (1934) did not find *E. villosa* at strand sites in 1933 and 1934 when the island was under heavy rabbit herbivory. Therefore, it is likely that *E. villosa* was absent from strand sites before the implementation of rabbit control measures and only appeared after the cessation of rabbit herbivory.

Given average and constant inter-annual rainfall, the emergence of *E. villosa* would have remained of intermediate importance in driving vegetation composition change following rabbit control. The cover of the perennial grass would still have increased slightly from zero between the first- and second years following rabbit control and remained constant in subsequent years.

Oncosiphon suffruticosum

The impact of inter-annual rainfall variation on the cover of the annual herb *O. suffruticosum*, following rabbit control, appears to have been indirect. The herb's cover remained stable between the first- and second years after rabbit control but increased slightly (by 4.00%) in the second- to third years and even more slightly (by 2.70%) in the third- to fourth years (Annex IV Table S2). *Oncosiphon suffruticosum* is a winter annual or biennial herb that reproduces exclusively from seed (Moore, et al. 2007b, Anon 2014). The herb produces thousands of small seeds in late spring (Anon 2014), which germinate with the onset of winter rains (Anon 2014). Some plants remain vegetative and survive the summer to flower in the following season (Adamson 1934, Moore and Moore 2007b). *Oncosiphon suffruticosum* is a poor competitor that requires bare ground to establish and does not compete well with other species (Moore and Moore 2007b, Anon 2014). The herb can only dominate where competition from grasses or perennial vegetation is absent, particularly due to heavy grazing (Anon 2014). The herb's increase in cover in the fourth year following rabbit control was likely due to the slight decrease in *T. fruticosa* cover, resulting from the decline of TAUR to below the long-term average. The decrease in *T. fruticosa* cover would have created space for *O. suffruticosum* to germinate and increase in cover in response to increased winter rainfall.

Oncosiphon suffruticosum plants are unpalatable to livestock (Le Roux 2005) and also appear to be avoided by rabbits. Adamson (1934) observed *O. suffruticosum* on strand sites in 1933 and 1934 when the island was overrun with rabbits and the vegetation heavily degraded. The annual herb occurred in abundance in areas where rabbits congregated (Adamson 1934). It is therefore most likely that *O. suffruticosum* would have had a higher cover in the years preceding rabbit control when inter-specific competition with more competitive palatable species was much lower.

Given average and constant inter-annual rainfall, the change in emergence of *O. suffruticosum* cover would have remained of intermediate importance in driving vegetation composition change following rabbit control. However, the cover of the annual herb would most likely have sharply decreased between the first- and second years following rabbit control and remained constantly low in subsequent years.

Conicosia pugioniformis

Inter-annual rainfall variation appears to have influenced around one-third (~33%) of the change in cover of the perennial herb *C. pugioniformis* after rabbit control. The cover of the herb decreased slightly (by 7.00%) between the first- and second years after rabbit control but increased much slightly (by 0.30% and 0.70%) between the second, third and fourth years (Annex IV Table S2). Similar to the woody shrub *T. fruticosa*, *C. pugioniformis* is a perennial leaf-succulent that can endure low soil moisture conditions (Schmalzer, et al. 1987). The decline in *C. pugioniformis* cover between the first and second years after rabbit control was therefore likely due to competition with more drought-resistant and competitive plants such as *T. fruticosa*, and not driven by worsening drought conditions.

The reduction in *C. pugioniformis* cover during the first and second years after rabbit control was partially due to limited recruitment of new plants from seeds, which were unable to replace the short-lived adult plants that died from senescence. *Conicosia pugioniformis* is a short-lived plant that reproduces solely through seeds (Schmalzer and Hinkle 1987), and germination occurs during late autumn and early winter. In both the first and second years after rabbit control, TAUR and TWR were below the long-term average, which could have inhibited seed germination. The slight increase in *C. pugioniformis* cover observed between the second, third-, and fourth years following rabbit control was likely due to an increase in TAUR and TWR. This increase raised soil moisture levels, facilitating germination and recruitment of new plants from seed. During the first- and second years following rabbit control, TAUR was considerably below the long-term average, while TWR was slightly and moderately below average. However, in the third and fourth years, TAUR was moderately above average, and TWR was slightly below average. The recruitment of new *C. pugioniformis* plants from seed appeared to be limited by inter-specific competition with other co-occurring species, including the woody shrub *T. fruticosa* and annual grass *E. longiflora*. Both *T. fruticosa* and *C. pugioniformis* have root systems with deep taproots that can penetrate the soil to reasonable depths (Schmalzer and Hinkle 1987, van Breda and Barnard 1991). However, *T. fruticosa* has a comparatively more developed and morphologically versatile root system, developing long spreading roots in shallow soil and deeper roots in deep or harder soil (van Breda and Barnard 1991). In addition, *C. pugioniformis* likely faced intense competition from the taller *E. longiflora* for light and germination space.

Conicosia pugioniformis is poorly grazed by livestock due to the astringent and often salty quality of its succulent tissue (Louw, et al. 1988, de Villiers, et al. 2001). European rabbits seem to avoid the perennial herb. Adamson (1934) observed abundant *C. pugioniformis* plants at strand sites in 1933 and 1934, when the island was overrun with rabbits and the vegetation was heavily degraded. The plants were most abundant in areas where rabbits were observed to congregate (Adamson 1934). Therefore, it is likely that *C. pugioniformis* had a higher cover in the years preceding rabbit control, when more open spaces for germination would have been available.

Given average and constant inter-annual rainfall, the decline in cover of *C. pugioniformis* would have remained of intermediate importance in driving vegetation composition change following rabbit control. However, the cover of the perennial herb would have decreased sharply between the first- and second years following rabbit control and remained constantly low in subsequent years.

Cynodon dactylon

There appears to have been no influence of inter-annual rainfall variation on the change in cover of the perennial grass *C. dactylon* following rabbit control. The cover of the grass decreased slightly (by 0.33%) to zero between the first- and second years after rabbit control, increased slightly (by 1.30%) from zero between the second- and third year, and remained unchanged between the third and fourth years (Annex IV Table S2). However, although there was no statistically significant relationship between inter-annual rainfall variation and the change in cover of *C. dactylon*, the temporary disappearance of the grass in the second year following rabbit control was most likely an artefact of inter-annual rainfall variation. The brief disappearance was clearly in response to a decline in TWR to moderately below the long-term average in the second year following rabbit control.

Cynodon *dactylon* is a geophytic perennial grass that responds to drought conditions by dying down to its underground rhizomes (Brown, et al. 2002, Halvorson, et al. 2003). The extremely low TWR during the second year following rabbit control most likely caused the grass to die down to its subterranean rhizomes due to the resulting dry conditions. The rise in TWR to slightly above the average level most likely caused the re-emergence of the perennial grass between the second- and third years following rabbit control. Cynodon *dactylon* is a strong interspecific competitor, capable of competing for water, nutrients, space, and soil oxygen, owing to its rhizomes and stolons' spreading ability (Kumar, et al. 1982). However, *C. dactylon* has deep roots that require support from deep soil (Corr 1993) and can only occur at low cover at shallow-soiled strand sites where such habitats are limited. *Cynodon dactylon* was absent from Robben Island in 1933 and 1934 when the island was overrun with rabbits (Adamson 1934). The perennial grass is of limited palatability to herbivores (van Breda, et al. 1990, Simmonds, et al. 2000) and probably disappeared from strand sites in 1933 and 1934 because it occurred on a limited area - relatively deep-soiled sites - and was therefore especially susceptible to herbivory. Therefore, the grass would have emerged at strand sites to low cover in response to reduced herbivory pressure following rabbit control.

Given average and constant inter-annual rainfall, *C. dactylon* would have remained of minor importance in driving vegetation composition change following rabbit control. The cover of the perennial grass would have increased slightly from zero between the first- and second years following rabbit control and remained constant in subsequent years.

Zantedeschia aethiopica

The change in cover of the perennial herb *Z. aethiopica* following rabbit control appears to have been unaffected by inter-annual rainfall variation. The cover of the herb decreased slightly (by 0.70%) to zero between the first- and second years after rabbit control, increased slightly (by 0.70%) from zero between the second- and third years, and remained unchanged between the third- and fourth years (Annex IV Table S2). Although there was no statistically significant relationship between inter-annual rainfall variation and change in cover of *Z. aethiopica*, the herb's temporary disappearance in the second year after rabbit control was most likely an artifact of inter-annual rainfall variation. This disappearance was clearly due to the decline in TWR and TSUR to considerably below the long-term average in the second year after rabbit control.

Zantedeschia aethiopica is an evergreen geophytic perennial herb that can survive throughout the year with adequate soil moisture (Singh, et al. 1996). During dry periods, the plant dies down to its underground rhizomes (Perry 1989, Corr 1993). The extremely low TWR during the second year following rabbit control most likely caused *Z. aethiopica* to die down to its subterranean rhizomes. However, the rise in TAUR, TSUR, and TAUR probably led to the re-emergence of the herb between the second- and third years following rabbit control, as the TWR increased slightly above average. Although *Z. aethiopica*, a plant highly toxic to herbivores (Jackson 1986, Scott, et al. 1996, El Mokni, et al. 2012), was present on Robben Island in 1933 and 1934, it was not observed at strand sites by Adamson (1934). The limited sites with soil deep enough to support its rhizomatous roots may have caused the plant's low cover to be overlooked. *Zantedeschia aethiopica* is shade-tolerant and a strong interspecific competitor for space and soil nutrients (Adamson 1927, Meek, et al. 2013), which would have helped it maintain its low cover following rabbit control.

Given average and constant inter-annual rainfall, *Z. aethiopica* would have been of no importance in driving vegetation composition change following rabbit control. The cover of the perennial herb at strand sites would have remained extremely low before and after rabbit control.

Bromus diandrus

There appears to have been no influence of inter-annual rainfall variation on the change in cover of the alien annual grass *B. diandrus* following rabbit control. The cover of the alien annual grass increased slightly (by 0.70%) from zero between the second- and third years after rabbit control, and it did not change between the third- and fourth years (Annex IV Table S2). Nevertheless, while there was no statistically significant relationship between inter-annual rainfall variation and the change in cover of *B. diandrus*, the emergence of the grass in the third year following rabbit control was evidently in response to an increase in TWR, TSUR, and TAUR, all of which rose to equal, moderately, and substantially above the long-term average after the drought conditions of the first two years.

Bromus diandrus is a winter annual that survives seasonal summer stress as dormant seed (Gill, et al. 1985). At the end of summer, the species' seeds lose their dormancy to take advantage of favourable growing conditions in winter. The germination of non-dormant *B. diandrus* seeds is primarily controlled by soil moisture, and staggered germination occurs during late summer and early autumn following heavy rainfall events (Cheam 1986). The absence of *B. diandrus* from strand sites during the first two years following rabbit control was likely due to inadequate soil moisture caused by below-average winter, summer, and autumn rainfall, which inhibited their germination.

Adamson (1934) observed *B. diandrus* on Robben Island in 1933 and 1934, when the island was overrun with rabbits and the vegetation was heavily degraded. Although *B. diandrus* seeds are consumed by rabbits (Martin, et al. 2007), the plant is generally unpalatable to herbivores (Muhl 2008) due to its high fibre content (Myers, et al. 1963). Rabbits prefer to consume soft, green, lush plants (Myers and Poole 1963), which may explain why *B. diandrus* was widespread and abundant at inland and coastal dune sites on the island in 1933 and 1934 (Adamson 1934). However, Adamson (1934) did not mention the presence of *B. diandrus* at strand sites, possibly because the short ephemeral grass had extremely low cover and was overlooked. *Bromus diandrus* has extensive root systems, allowing it to compete with other species for water stored in the soil. However, the soil at strand sites was generally shallow (Adamson 1934), limiting areas where *Bromus diandrus* could grow. Despite being a strong interspecific competitor for light, space, and soil moisture (Menke 1992, Jackson, et al. 2006), the alien grass maintained low cover before and after rabbit control across the sites due to limited soil depth.

Given average and constant inter-annual rainfall, *B. diandrus* would have been of no importance in driving vegetation composition change following rabbit control. The cover of the alien annual grass at strand sites would have remained extremely low before and after rabbit control.

Silene cretica

Variation in inter-annual rainfall appears to have influenced ~32% of the change in cover of the alien annual herb *S. cretica* after rabbit control. The cover of the alien annual herb increased slightly (by 3.70%) from zero between the second- and third years following rabbit control and did not change between the third and fourth years (Annex IV Table S2). The emergence and some of the increase in cover of the alien annual herb between the second- and third years following rabbit control was a clear response to increases in TSUR, TAUR, and TWR, which rose above the long-term average after the drought conditions of the first two years following rabbit control.

Silene cretica is a weedy ephemeral species found in the Mediterranean region (Vural, et al. 2002, Blasi, et al. 2014). Ephemerals typically germinate soon after significant rainfall events and complete their life cycle in less than a month. The low availability of TSUR, TAUR, and TWR during the first two years following rabbit control likely suppressed *S. cretica* germination. Adamson (1934) observed that *S. cretica* plants were widespread and fairly abundant across inland and coastal dune sites in 1933 and 1934 when the island was heavily affected by rabbit herbivory. However, no mention was made of their occurrence at strand sites, probably because Adamson (1934) overlooked these short-lived ephemerals due to their extremely low cover at these locations. *Silene cretica* plants are short and hairy and are not preferred by rabbits (van Leeuwen, et al. 1971, Williams, et al. 1974). Furthermore, plants with shoots that grow close to the ground surface are less susceptible to rabbit attacks than those with tall vertical shoots (Farrow 1917, Crawley 1990). This explains the widespread and abundant occurrence of *S. cretica* plants at inland and coastal dune sites on the island in 1933 and 1934. *Silene cretica* has large, fibrous, and fast-growing root systems (Arnone II, et al. 1997). The soil at strand sites is generally shallow (3 to 5 cm; Adamson 1934), which limits the areas with soil deep enough or underlying rocks with water-bearing fractures to support *S. cretica* plants. As a result, the alien annual herb reached its upper equilibrium in the second year following rabbit control. It is likely that the alien annual herb persisted at strand sites during the years preceding rabbit control, but its cover would have been extremely low due to the low availability of suitably deep soil.

Given average and constant inter-annual rainfall, *S. cretica* would have been of no importance in driving vegetation composition change following rabbit control. The cover of the alien annual herb at strand sites would have remained extremely low before and after rabbit control.

Eucalyptus sites

At eucalyptus sites, rabbit control did not result in any change in the composition of vegetation species, likely due to the inhibiting effect of the alien plantation trees on the dynamics of the understory vegetation. *Eucalyptus* trees, with their high water consumption rate and dense near-surface roots (del Moral, et al. 1969), rapidly deplete soil moisture (Le Maitre, et al. 2002, Dye, et al. 2004, Dye, et al. 2007) and soil nutrients (Bernhard-Reversat 1996, Guo, et al. 2001, Marchante, et al. 2008) from the upper soil layers. This most likely led to less fertile and drier conditions for plant growth at eucalyptus sites, limiting the response of plants to inter-annual rainfall variation and rabbit control. The fluctuations and slight increase in the presence and cover of *T. fruticosa*, *Phyllobolus canaliculatus*, *Oxalis pes-caprae*, *O. suffruticosum*, *Chenopodium murale* and *Euphorbia peplus* following rabbit control may have been dampened responses to inter-annual rainfall variation. Inter-annual rainfall variation accounted for ~58% of vegetation composition change, with no statistically significant effects at the seasonal level.

Based on our interpretation of underlying vegetation dynamics and correlative rainfall–vegetation relationships, we determined that vegetation species composition would still have not changed at eucalyptus sites following rabbit control in the absence of inter-annual rainfall variation. The lack of change in vegetation composition would have been caused by subdued responses of unpalatable and palatable species such as *P. canaliculatus*, *O. pes-caprae* and *T. fruticosa* to rabbit herbivory and control due to the inhibitory effects of eucalyptus plantations on their germination and growth.

Below, we present details of our determination of how each of the species that underlay vegetation species composition change at eucalyptus sites would have responded to rabbit control given constant and average inter-annual rainfall.

Tetragonia fruticosa

Inter-annual rainfall variation had a considerable influence (~52%) on the change in cover of the woody shrub *T. fruticosa* following rabbit control. The cover of the woody shrub increased slightly (by 6.00%) from zero between the second- and third years following rabbit control and remained stable between the third and fourth (Annex IV Table S2). The emergence of *T. fruticosa* and some (~52%) of the increase in cover by the species between the second- and third years following rabbit control was evidently in response to the increase in TAUR, which rose moderately above the long-term average after the drought conditions of the first two years. As previously mentioned in the strand sites section, *T. fruticosa* seeds germinate intermittently in autumn following episodic leaching of salt from soil by rainwater (van Breda and Barnard 1991). The increased TAUR may have provided sufficient water for germination.

In contrast to strand and inland dune sites where some adult *T. fruticosa* plants survived during the drought conditions of the first two years after rabbit control, no plants were found at eucalyptus sites. This could be attributed to greater herbivory pressure on the highly palatable woody shrub at the sites, in addition to the drier conditions caused by *Eucalyptus* trees. The combination of heavy browsing and drought causes *T. fruticosa* individuals to die (Adamson 1934). Browsing pressure under *Eucalyptus* trees might have worsened due to low vegetation cover and fewer *T. fruticosa* individuals. *Tetragonia fruticosa* produces relatively few large seeds, making it highly vulnerable to the negative impacts of heavy summer grazing (Todd 2000). Heavy grazing can lead to reduced recruitment of palatable species due to the inability to set seed, ultimately causing the loss of such species from the rangeland.

Given constant and average inter-annual rainfall, an increase in the cover of *T. fruticosa* would have been of no importance in driving vegetation composition change following rabbit control. The cover of the woody shrub at eucalyptus sites would have remained consistently low because of poor germination due to the depletion of soil moisture by *Eucalyptus* trees.

Phyllobolus canaliculatus

Inter-annual rainfall variation appeared to have influenced ~43% of the change in cover of the perennial herb *P. canaliculatus* following rabbit control. The cover of the herb remained constant (at 0.67%) between the first- and second years following rabbit control, increased slightly (by 8.00%) between the second- and third years, and decreased minutely (by 0.34%) between the third- and fourth years (Annex IV Table S2). The cover of *P. canaliculatus* evidently increased in response to moderately above-average TAUR in the third year, following two years of drought conditions. This deciduous caudiciform plant sheds its leaves and stems during the summer season and can be propagated through cuttings, rooted runners, and seeds (Freeman, et al. 2021, UWC Cape Flats Indigenous Nursery 2021). The increase in TAUR would have led to more germination events, whereas a decline in TAUR below the average in the fourth year, following rabbit control, could have caused a decrease in *P. canaliculatus* cover by affecting germination success and recruitment of new plants. *Phyllobolus canaliculatus* is known for its drought tolerance (Freeman, et al. 2021) and thrives in open, well-drained soil with sufficient sunlight for optimal growth (UWC Cape Flats Indigenous Nursery 2021). Therefore, shading by *Eucalyptus* trees likely played a role in maintaining low *P. canaliculatus* cover before and after rabbit control. Although Adamson (1934) did not mention the presence of the herb in 1933 and 1934 during heavy rabbit herbivory, it most likely persisted due to its low palatability (UWC Cape Flats Indigenous Nursery 2020)). The herb may have been overlooked during Adamson (1934)'s survey due to its low cover.

Given constant and average inter-annual rainfall, an increase in the cover of *P. canaliculatus* would have been of no importance in driving vegetation composition change following rabbit control. The cover of the perennial herb would have remained low before and after rabbit control due to shading by *Eucalyptus* trees.

Oxalis pes-caprae

Inter-annual rainfall variation appears to have influenced ~42% of the change in cover of the geophytic annual herb *O. pes-caprae* following rabbit control. The cover of the herb decreased slightly (by 0.33%) to zero between the first- and second years following rabbit control, increased slightly (by 0.33%) from zero between the second- and third years, and did not change significantly between the third- and fourth years (Annex IV Table S2). The temporary disappearance of the herb in the second year was clearly in response to a decline in TWR to moderately below the long-term average. *Oxalis pes-caprae* reproduces both sexually by seeds and asexually through bulbils (Papini, et al. 2017). *Oxalis* bulbs remain dormant in the summer and sprout in the autumn (Vilà, et al. 2006, Verdaguer, et al. 2010). As a result, peak vegetative growth occurs during autumn and winter, after which flowering starts (Verdaguer, et al. 2010). The slight increases in *O. pes-caprae* cover between the second- and third years following rabbit control would have been in response to increase in TWR to above-average levels. Additionally, the increase in cover between the third* and fourth years following rabbit control would have also been driven by reduced competition from the perennial herb *Phyllobolus canaliculatus* (see discussion on the dynamics of *P. canaliculatus* cover following rabbit control above). The herb is less palatable as it accumulates oxalic acid in its leaves, which is toxic to herbivores if eaten in large quantities (Sala, et al. 2007. As a result, the herb would have persisted during the years prior to rabbit control. Adamson (1934) observed abundant *O. pes-caprae* in 1933 and 1934 when the island was under heavy rabbit herbivory. However, the cover of *O. pes-caprae* at eucalyptus sites would have been kept low before and after rabbit control by intense competition for soil nutrients and sunlight by *Eucalyptus* trees. *Oxalis pes-caprae* performs poorly under conditions of low soil fertility and shade (Verdaguer, et al. 2010).

Given the constant and average inter-annual rainfall, an increase in the cover of *O. pes-caprae* would have been of insignificant importance in driving vegetation composition change following rabbit control. The cover of the annual herb would have remained low before and after rabbit control because of intense competition for soil nutrients and sunlight by *Eucalyptus* trees.

Oncosiphon suffruticosum

Inter-annual rainfall variation appears to have had a limited effect on the change in cover of the annual herb *O. suffruticosum* following rabbit control. The cover of the annual herb increased slightly (by 0.67%) from zero between the second- and third years following rabbit control and remained the same between the third and fourth years (Annex IV Table S2). The emergence of the annual herb in the third year following rabbit control was a clear response to an increase in TAUR and TWR to above the long-term average. *Oncosiphon suffruticosum* is a winter annual that reproduces entirely from seed following autumn and winter rainfall (Moore and Moore 2007b, Anon 2014). Germination failure during the first two years following rabbit control, due to below-average autumn and winter rainfall, would have led to the complete absence of the plant species across eucalyptus sites. *Eucalyptus* trees most likely led to considerably drier than normal germination conditions at eucalyptus sites. The increase to above-average TAUR or TWR in the third- and fourth years following rabbit control would have raised soil moisture to levels suitable for seed germination, even under the dry conditions across the sites. The lack of a significant regression between inter-annual rainfall variation and change in cover of *O. suffruticosum* may be attributed to various factors, such as shading, nutrient-poor soils, and allelopathy, which could have limited the species' growth and distribution after germination, even under suitable moisture conditions.

Given constant and average inter-annual rainfall, an increase in the cover of *O. suffruticosum* would have been of no importance in driving vegetation composition change following rabbit control. The annual herb would not have occurred at eucalyptus sites before and after rabbit control, as the moisture conditions under Eucalyptus plantations would have been too dry for the germination of the plant.

Chenopodium murale

Inter-annual rainfall variation appears to have had a limited effect on the change in cover of the annual herb C. *murale* following rabbit control. The cover of the alien herb increased slightly (by 0.33%) from zero between the second- and third years following rabbit control and remained the same between the third and fourth years (Annex IV Table S2). *Chenopodium murale* is a weedy annual herb that germinates from seed in late winter and early spring (Bajwa, et al. 2019). This plant flourishes in warm temperatures, relying on sufficient soil moisture for its germination. Rainfall serves as a direct source of moisture, causing the seeds to swell, break their seed coat, and initiate sprouting (Bajwa, et al. 2019). The emergence of the annual herb in the third year following rabbit control was a clear response to an increase in TWR to above the long-term average. During the initial two years following rabbit control, germination failure would have occurred due to below-average winter rainfall. This shortfall would have led to the complete absence of the plant species across eucalyptus sites. *Eucalyptus* trees likely created significantly drier germination conditions at these sites. The subsequent increase in TWR above the long-term average in the third and fourth years after rabbit control elevated soil moisture to levels conducive for seed germination, even amidst the dry conditions across the site. *Chenopodium murale*, which is native to parts of Europe, Asia, and North Africa, is alien to Robben Island.

Given constant and average inter-annual rainfall, an increase in the cover of *C. murale* would have been of no importance in driving vegetation composition change following rabbit control. The annual herb would not have occurred at eucalyptus sites before and after rabbit control, as the moisture conditions under Eucalyptus plantations would have been too dry for the germination of the plant.

Euphorbia peplus

The impact of inter-annual rainfall variation on the cover of the alien annual herb *E. peplus* following rabbit control appears to have been limited. The cover of the herb increased slightly (by 1.67%) from zero in the fourth year after rabbit control (Annex IV Table S2). *Euphorbia peplus* emerged clearly in the fourth year following rabbit control due to the increase in TWR to substantially above the long-term average. While the plant species has the ability to reproduce from seed that can germinate and grow throughout the year with adequate soil moisture (Latzel, et al. 2011), the absence of adequate winter rainfall in the preceding three years following rabbit control would have resulted in germination failure, causing the plant species to be completely absent across the sites. The increase to substantially above average TWR in the fourth year following rabbit control would have raised soil moisture to levels suitable for seed germination, even under the dry conditions at eucalyptus sites. The non-significant regression between inter-annual rainfall variation and the change in *E. peplus* cover may be attributed to other factors, such as shading, nutrient-poor soils, and allelopathy. These factors may have limited the growth and distribution of the species after germination, despite suitable moisture conditions, resulting in a lack of a significant effect of rainfall increase on species cover.

Given constant and average inter-annual rainfall, an increase in the cover of *E. peplus* would have been of no importance in driving vegetation composition change following rabbit control. The annual herb would not have occurred at eucalyptus sites before and after rabbit control, as the moisture conditions under *Eucalyptus* plantations would have been too dry for the germination of the plant.

Inland dune sites

Compared to strand sites, inter-annual rainfall variation influenced much less (~37%) of the change in species composition following rabbit control at inland dune sites. Species composition changed moderately between the first- and second years following rabbit control and slightly during the second, third and fourth year. Inter-annual variation in TAUR appears to have influenced ~25% of the change in species composition caused by interannual rainfall variation. Inter-annual variation in TAUR appears to have influenced ~36% of the ~39% change in grazing capacity caused by inter-annual rainfall variation.

Based on our interpretation of the underlying vegetation dynamics and the correlation between rainfall and vegetation, we determined that vegetation composition would have moderately changed across the inland dune sites following rabbit control, given constant and average inter-annual rainfall. Mean annual NMDS axis one scores would have changed moderately (by ~0.17 NMDS axis scores) across the sites between the first- and second years following rabbit control, and slightly (by ~0.01 NMDS axis scores) thereafter. The increase in the cover of *T. fruticosa* and *E. villosa* would have been of major importance, the decline of *B. diandrus* and *C. pugioniformis* of intermediate importance, and the emergence of *E. longiflora* of minor importance in driving the change in vegetation composition. Specifically, the cover of *T. fruticosa* would have increased markedly between the first and second years and remained constant thereafter, whereas the cover of *E. villosa* would have increased moderately across the years following rabbit control. In contrast, the cover of *B. diandrus* and *C. pugioniformis* would have decreased moderately and sharply between the first- and second years following rabbit control and remained constant at reduced and low cover thereafter. The cover of *E. longiflora* would have slightly increased from zero between the first- and second years following rabbit control and remained constant in subsequent years.

Below, we present details of our determination of how each of the species that underlay vegetation species composition change at inland dune sites would have responded to rabbit control given constant and average inter-annual rainfall.

Tetragonia fruticosa

Inter-annual rainfall variation appears to have influenced ~39% of the change in cover of the woody shrub *T. fruticosa* following rabbit control. The cover of the shrub increased significantly (by 21.40%) between the first- and second years after rabbit control, moderately (by 10.60%) between the second- and third and decreased slightly (by 6.30%) between the third- and fourth (Annex IV Table S2). As with the strand sites, it appears that the increase in TAUR from considerably below to moderately above the long-term average contributed to ~23% of the increase in *T. fruticosa* cover between the second- and third years following rabbit control. This is likely due to the higher frequency and intensity of autumn leaching episodes, which increased the shrub's germination success (see the discussion on *T. fruticosa* dynamics at strand sites above).

Similarly, the increase in *T. fruticosa* cover between the first- and second years following rabbit control was likely due to the recovery of browsed-down shoots, in response to reduced rabbit herbivory pressure. *Tetragonia fruticosa* plants are highly adapted to conditions of low soil moisture due to their succulent leaves and well-developed root systems (van Breda and Barnard 1991, Hoffman, et al. 2009). The adaptability of *T. fruticosa* could account for why below average and decreasing TSUR and TWR did not hinder the woody shrub's positive response to the release from herbivory pressure between the first and second years after rabbit control (see the discussion on *T. fruticosa* cover dynamics at strand sites). The subsequent decline in TAUR to below average in the fourth year after rabbit control would have again resulted in reduced germination and seedling recruitment, leading to a slight decrease in *T. fruticosa* (see the discussion on *T. fruticosa* cover dynamics at strand sites). In comparison to strand sites, there was a significant increase in *T. fruticosa* cover at inland dune sites, likely due to the greater availability of soil moisture in the deeper soils found at inland dune sites.

Given constant and average inter-annual rainfall, an increase in the cover of *T. fruticosa* would have remained one of the dominant drivers of vegetation composition change following rabbit control. However, the cover of *T. fruticosa* would have increased markedly between the first- and second years following rabbit control, due to both the regrowth of adult plants from browsed-down shoots and recruitment from the seed bank and remained constant in subsequent years.

Ehrharta villosa

Inter-annual rainfall variation appears to have influenced ~31% of the change in cover of the perennial grass *E. villosa* following rabbit control. The cover of *E. villosa* increased slightly (by 5.00%) between the first- and second years following rabbit control and moderately (by 14.30% and 16.00%, respectively) between the second-, third- and fourth years (Annex IV Table S2). However, the increase in *E. villosa* cover between the first- and second years following rabbit control could not have been influenced by inter-annual rainfall variation as it occurred during worsening drought conditions. *Ehrharta villosa* can withstand drought conditions due to their deep roots (Harrington, et al. 1998) and ability to regenerate from rhizomes and rhizome fragments (Hodder 1997), and therefore were not completely affected by the drought conditions (see the discussion on *E. villosa* cover dynamics at strand sites for more details). The slight increase during the drought conditions could have been driven by regeneration from rhizomes.

Contrary to the situation at strand sites, the greater soil depth at inland dune sites facilitated the growth of deep-rooted *E. villosa* plants, resulting in a continued increase in the grass's coverage during the second-, third-, and fourth years following rabbit control. The increase in cover of the perennial grass between the second-, third-, and fourth years following rabbit control was likely partly driven by an increase in TAUR, which appears to have contributed to ~21% of the increase. During the first- and second years following rabbit control, TAUR was considerably below the long-term average, but rose to moderately above and slightly below average in the third and fourth years. Although *E. villosa* primarily reproduces and disperses through rhizomes and rhizome fragments, it also produces limited seeds, which germinate between spring and early summer (Hodder 1997, Cowell 2013).. While increased TAUR likely contributed to the greater increase in cover of *E. villosa* in subsequent years following rabbit control by raising soil moisture to suitable levels for seed germination and recruitment, much of the increase in cover is likely due to rhizome growth. The perennial grass can spread by rhizome growth at rates between 34 and 75 cm per month (Hodder 1997).

Ehrharta villosa. is negatively affected by herbivory and is known to become more abundant when grassland is moderately grazed (Tainton, et al. 1990), It is an aggressive inter-specific competitor on deep sandy habitats (Hertling 1997, Harrington, et al. 1998, Verboom, et al. 2003). Release from herbivory pressure following rabbit control would have allowed *E. villosa* to recover its competitive ability and increase in cover, displacing other less competitive species. Adamson (1934) observed *E. villosa* at inland dune sites in 1933 and 1934 when the island was under heavy rabbit herbivory. The grass seemed to be negatively affected by rabbit herbivory as it only occurred among bushes of the hard, spiny and unpalatable woody shrubs such as *Lycium afrum* L. and *Lycium ferocissimum* Miers (Adamson 1934).

Given average and constant inter-annual rainfall, increase in cover of *E. villosa* would have remained one of the dominant drivers of vegetation composition change following rabbit control. *Ehrharta villosa* cover would have increased moderately across the years following rabbit control.

Bromus diandrus

Inter-annual rainfall variation appears to have influenced approximately half (~54%) of the change in cover of the invasive annual grass *B. diandrus* following rabbit control. The cover of the alien grass increased moderately (by 10.70%) from zero between the second- and third years following rabbit control and remained stable between the third- and fourth years (Annex IV Table S2). The emergence of *B. diandrus* after the third year following rabbit control was clearly in response to an increase in TAUR to moderately above and TWR slightly above the long-term average after the drought conditions of the first two years.

Bromus diandrus is a winter annual grass that reproduces solely through seeds (Cheam 1986, Jackson, et al. 2006). Its seeds have high summer temperature-induced dormancy and usually germinate in winter

(Gill and Blacklow 1985). However, occasional drops in temperature after heavy thunderstorms in late summer and early autumn can also trigger germination (Cheam 1986). The absence of *B. diandrus* from inland dune sites during the first two years following rabbit control was due to inadequate autumn and winter rainfall, which prevented non-dormant *B. diandrus* seeds from germinating. Soil moisture is the primary factor that regulates the germination of non-dormant *B. diandrus* seeds (Cheam 1986). Adamson (1934) did not observe *B. diandrus* on Robben Island in 1933 and 1934, likely because the alien grass, which is native to the Mediterranean region (Kon, et al. 1988), had not yet been introduced to the island. *Bromus diandrus* is unpalatable to herbivores (van Breda, et al. 1990) and would have dominated strand vegetation before rabbit control. Moreover, it is tall and has deep roots, enabling it to shade out and outcompete other species for deeper soil sites (Menke 1992, Jackson, et al. 2006). Additionally, the grass outcompetes native species for soil moisture by early germination and sheer volume of numbers (Menke 1992, Jackson, et al. 2006). *Bromus diandrus* has high seed production, with a single plant capable of producing up to a thousand seeds (Jackson, et al. 2006).

Given average and constant inter-annual rainfall, *B. diandrus* would have remained of intermediate importance in driving vegetation composition change following rabbit control. The cover of the alien annual grass at strand sites would have moderately decreased between the first- and second years following rabbit control and remained constant in subsequent years.

Conicosia pugioniformis

Inter-annual rainfall variation appears to have influenced about 45% of the change in cover of the perennial herb *C. pugioniformis* following rabbit control. The cover of the herb decreased slightly (by 9.00%) between the first- and second years following rabbit control, remained unchanged (at 2.70%) between the second- and third years, and increased slightly (by 0.60%) between the third- and fourth years (Annex IV Table S2). Similar to strand sites, the decline in *C. pugioniformis* cover between the first- and second years was likely not driven by worsening drought conditions but rather by competition with more competitive and drought-resistant plants, such as *T. fruticosa*. Additionally, limited recruitment of new plants from seed to replace short-lived adult plants that died from senescence may have contributed to the decline in cover (see discussion on *C. pugioniformis* dynamics at strand sites above). However, unlike at strand sites, increased TAUR and TWR between the second- and third years did not lead to an increase in *C. pugioniformis* cover. Instead, increased TAUR may have indirectly suppressed *C. pugioniformis* cover by driving the increase in cover of the more competitive *T. fruticosa*. The slight increase in *C. pugioniformis* cover between the third and fourth years may have been a response to the decline in *T. fruticosa* cover caused by the decrease in TAUR to slightly below the long-term average.

Given average and constant inter-annual rainfall, the decline in the cover of *C. pugioniformis* would have remained of intermediate importance in driving vegetation composition change following rabbit control. The cover of the perennial herb would most likely have decreased sharply between the first- and second years following rabbit control and remained constantly low in the subsequent years.

Ehrharta longiflora

Inter-annual rainfall variation seems to have played a role in influencing a portion (~33%) of the change in cover of the annual grass *E. longiflora* following rabbit control. The cover of the grass decreased slightly (by 1.00%) to zero in the first- and second years after rabbit control, followed by a slight increase (0.33%) from zero in the second and third years, and no change between the third- and fourth years (Annex IV Table S2). *Ehrharta longiflora* is a shallow-rooted winter annual (Moore and Moore 2007a, Winston, et al. 2014). The germination of *E. longiflora* is regulated by soil moisture, with seeds germinating after autumn and winter rainfall (Western Australian Herbarium 1998, Bossard, et al. 2000, Moore and Moore 2007a). The decline in TWR to below the average most likely contributed to the disappearance of the grass between the first- and second years.

Ehrharta longiflora re-emerged in the third year following rabbit control, likely due to above-average TWR. Between the third- and fourth years, there was a noticeable increase in the species' cover, ~25% of which can be attributed to the subsequent above-average increase in TWR in the fourth year. This grass is known to be palatable and is a favoured food for rabbits on Robben Island (Gillham 1963, van Oudtshoorn 2012) and was not observed at inland dune sites during heavy rabbit herbivory in 1933 and 1934 (Adamson 1934). The grass most likely re-emerged in inland dune sites during the first year following rabbit control, but its positive response to release from herbivory pressure may have been limited by the availability of suitable habitat. *Ehrharta longiflora* requires disturbed open sites for successful establishment (Winston, et al. 2014), which were not readily available at the densely vegetated inland dune sites.

Given average and constant inter-annual rainfall, emergence of *E. longiflora* would have remained of minor importance in driving grazing capacity change following rabbit control. However, *E. longiflora* cover would have increased slightly from zero between the first- and second years following rabbit control and remained constant in the proceeding years.

REFERENCES

Adamson RS. 1927. The plant communities of Table Mountain: preliminary account. *Journal of Ecology* 15: 278-309.

Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

Anon 2014. Declared Plant Policy under the Natural Resources Management Act 2004. Calomba daisy (*Oncosiphon suffruticosum*). Government of South Australia.

Arnone II JA, Kestenholz C. 1997. Root competition and elevated CO_2: effects on seedling growth in *Linum usitatissimum* populations and *Linum–Silene cretica* mixtures. *Functional Ecology* 11: 209-214.

Bajwa AA, Zulfiqar U, Sadia S, Bhowmik P, Chauhan BS. 2019. A global perspective on the biology, impact and management of *Chenopodium album* and *Chenopodium murale*: two troublesome agricultural and environmental weeds. *Environmental Science and Pollution Research* 26: 5357-5371.

Bernhard-Reversat F. 1996. Nitrogen cycling in tree plantations grown on a poor sandy savanna soil in Congo. *Applied Soil Ecology* 4: 161–172.

Blasi C, Capotorti G, Copiz R, Guida D, Mollo B, Smiraglia D, Zavattero L. 2014. Classification and mapping of the ecoregions of Italy. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* 148: 1255-1345.

Bossard CC, J.M. R, Hoshovsky MC. 2000. *Invasive plants of California's wildlands*. Berkeley: University of California Press.

Brown K, Brooks K. 2002. *Bushland weeds. A practical guide to their management. With case studies from the Swan Coastal Plain and beyond*. Perth: Environmental Weeds Action Network (Inc).

Cheam AH. 1986. Patterns of change in seed dormancy and persistence of *Bromus diandrus* Roth. (Great brome) in the field. *Australian Journal of Agricultural Research* 37 471-481.

Coetzee K. 2008. Blaauwberg Conservation Area: management guidelines for larger wildlife and their habitats. *Report prepared for the Biodiversity Management Branch, City of Cape Town*.

Corr BE. 1993. *Zantedeschia* research in the United States: past, present and future. *Acta Horticulturae* 337: 177-188.

Cowell CR. 2013. Investigating the most favourable seed establishment methods for restoring Sand Plain Fynbos on old fields. MTH, Cape Peninsula University of Technology, Cape Town.

Crawley MJ. 1990. Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology* 27: 803-820.

de Villiers AJ, van Rooyen MW, Theron GK. 2001. Seedbank phytosociology of the Strandveld Succulent Karoo, South Africa: a pre-mining benchmark survey for rehabilitation. *Land Degradation and Development* 12: 119-130.

del Moral R, Muller CH. 1969. The allelopathic effect of *Eucalyptus camaldulensis American Midland Naturalist* 83: 254–282.

Dye P, Jacobs S, Drew D. 2004. Verification of 3-PG growth and water-use predictions in twelve *Eucalyptus* plantation stands in Zululand, South Africa *Forest Ecology and Management* 193: 197-218.

Dye P, Versfeld D. 2007. Managing the hydrological impacts of South African plantation forests: An overview. *Forest Ecology and Management* 251: 121-128.

El Mokni R, Hédi El Aouni M. 2012. *Zantedeschia aethiopica* (Araceae) a new species naturalized in the Northwest of Tunisia. *Flora Mediterranea* 22: 191-196.

Farrow EP. 1917. On the ecology of the vegetation of Breckland. III. General effects of rabbits on the vegetation. *Journal of Ecology* 5: 1-18.

Fisher JL, Loneragan WA, Dixon K, Veneklaas EJ. 2009. Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. *Biological Conservation* 142: 256-269.

Freeman D, Balcom J, Chmielewski J. 2021. Genus: *Phyllobolus*. Available at https://www.succulentguide.com/cactus/?genus=Phyllobolus [accessed 22 March 2021]

Gill GS, Blacklow WM. 1985. Variations in seed dormancy and rates of development of Great Brome, *Bromus diandrus* Roth., as adaptations to the climates of southern Australia and implications for weed control. *Australian Journal of Agricultural Research* 36: 295-304.

Gillham ME. 1963. Some interactions of plants, rabbits and sea-birds on South African islands. *Journal of Ecology* 51: 275-294.

Guo LB, Sims REH. 2001. Effects of light, temperature, water and meat works effluent irrigation on eucalypt leaf litter decomposition under controlled environmental conditions. *Applied Soil Ecology* 17: 229–237.

Halvorson WL, Guertin P (eds). 2003. *Factsheet for: Cynodon dactylon (L.) Pers.* U.S. Geological Survey / Southwest Biological Center. Tucson.

Harrington KC, Hodder LM, Outred HA. Biology and control of pypgrass*, 1 August 1998*: New Zealand Plant Protection Society. pp. 259-259.

Hertling UM. 1997. *Ammophila arenaria* (l.) Link (Marram grass) in South Africa and its potential invasiveness. DPhil, Rhodes University, Grahamstown.

Hodder LM. 1997. The biology and control of *Ehrharta villosa*, South African pypgrass. MSc, Massey University.

Hoffman MT, Carrick PJ, Gillson L, West AG. 2009. Drought, climate change and vegetation response in the succulent karoo, South Africa. *South African Journal of Science* 105: 54-61.

Jackson N, Cudney D, DiTomaso J, C. B, Lee V, Drewitz J, Bossard S, Randall L, Hansen-Winter B, Faber P, *et al.* 2006. *Invasive plants of California's wildland*. California Invasive Plant Council.

Jackson WPU. 1986. The Cape white arum lily, *Zantedeschia aethiopica*. *Veld & Flora* 72: 44-45.

Kon KF, Blacklow WM. 1988. Identification, distribution and population variability of Great brome (*Bromus diandrus* Roth) and Rigid brome (*Bromus rigidus* Roth). *Australian Journal of Agricultural Research* 39 1039-1050.

Kumar A, Abrol IP. 1982. Relative tolerance of grasses to sodic soils *Indian Farming* 32: 41-43.

Latzel V, Malíková L, Klimešová J. 2011. Compensatory growth of *Euphorbia peplus* regenerating from a bud bank. *Botany* 89: 313-321.

Le Maitre DC, van Wilgen BW, Gelderblom C, Bailey C, Chapman R, Nel J. 2002. Invasive alien trees and water resources in South Africa: case studies of the costs and benefits of management *Forest Ecology Management* 160: 143-159.

Le Roux A. 2005. *Namaqualand – South African Wild Flower Guide 1*. Cape Town: Botanical Society of South Africa.

Lloyd JW, Linger MT. 1986. Report on the vegetation of Robben Island. *'n Natuurbewaringsondersoek van Robbeneiland*. Cape Town: Cape Nature

Louw G, Beukes T. 1988. Ken ons veldplante. *Die Noordwester*: 6-12.

Marchante E, Kjoller A, Struwe S, Freitas H. 2008 Short- and long- term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. *Applied Soil Ecology* 40: 210–217.

Martin GR, Twigg LE, Lena Z. 2007. Seasonal changes in the diet of the European rabbit (*Oryctolagus cuniculus*) from three different Mediterranean habitats in south-western Australia. *Wildlife Research* 34: 25-42.

Meek CS, Richardson DM, Mucina L. 2013. Plant communities along the Eerste River, Western Cape, South Africa: Community descriptions and implications for restoration. *Koedoe* 55: 1-14.

Menke JW. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia* 20: 22-25.

Moore CB, Moore JH. 2007a. Annual veldgrass: *Ehrarta longiflora* Smith. HerbiGuide - The Pesticide Expert on a Disk Available at http://www.herbiguide.com.au/Descriptions/hg_Annual_Veldtgrass.htm. [accessed 25 September 2017]

Moore CB, Moore JH. 2007b. Colombia Daisy: *Oncosiphon suffruticosum* (L.) Kallersjo. HerbiGuide - The Pesticide Expert on a Disk. Available at http://www.herbiguide.com.au/Descriptions/hg_Colomba_Daisy.htm. [accessed 25 September 2017]

Muhl SA. 2008. Alien grass invasion of Renosterveld: Influence of soil variable gradients. MSc, Stellenbosch University, Stellenbosch.

Myers K, Poole WE. 1963. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations IV. The effects of rabbit grazing on sown pastures. *Journal of Ecology* 51: 435-451.

Papini A, Signorini MA, Foggi B, Della Giovampaola E, Ongaro L, Vivona L, Santosuosso U, Tani C, Bruschi P. 2017. History vs. legend: Retracing invasion and spread of *Oxalis pes-caprae* L. in Europe and the Mediterranean area. *PLOS ONE* 12: e0190237.

Perry PL. 1989. A new species of *Zantedeschia* (Araceae) from the western Cape. *South African Journal of Botany* 55: 447-451.

Schmalzer PA, Hinkle CR (eds). 1987. *Species biology and potential for controlling four exotic plants (Ammophila Arenaria, Carpobrotus Edulis, Cortaderia Jubata, And Gasoul Crystallinum) on Vandenberg Air Force Base, California*. National Aeronautics and Space Administration, John F. Kennedy Space Center. Florida.

Scott JK, Neser S. 1996. Prospects for the biological control of the environmental weed, *Zantedeschia aethiopica* (arum lily). Paper presented at the Proceedings of the 11th Australian Weeds Conference, Melbourne, Australia, 30 September-3 October.

Sherley RB. 2016. Unusual foraging behaviour in two introduced mammals following degradation of their island habitat. *Biodiversity Observations* 7: 1-10.

Simmonds H, Holst P, Bourke C. 2000. *The palatability, and potential toxicity of Australian weeds to goats*. Kingston: Rural Industries Research and Development Corporation.

Singh Y, van Wyk AE, Baijnath H. 1996. Taxonomic notes on the genus *Zantedeschia* Spreng.(Araceae) in southern Africa. *South African Journal of Botany* 62: 321-324.

Tainton NM, Bransby DI, Booysen Pd. 1990. *Common veld and pasture grasses of Natal* (2nd edn). Pietermaritzburg: Shuter and Shooter.

Todd SW. 2000. Patterns of seed production and shrub association in two palatable Karoo shrub species under contrasting land use intensities. *African Journal of Range and Forage Science* 17: 22-26.

UWC Cape Flats Indigenous Nursery. 2020. UWC Nature Reserve: *Phyllobolus canaliculatus*. Available at https://uwccfnursery.blogspot.com/2020/05/phyllobolus-canaliculatus [accessed 13 January 2022]

UWC Cape Flats Indigenous Nursery. 2021. Propagating *Phyllobolus canaliculatus* (Vingerkanna). Available at https://www.pinterest.co.uk/pin/593490057135262691/ [accessed 22 March 2021]

van Breda PAB, Barnard SA. 1991. *100 veld plants of the winter rainfall region: A guide to the use of veld plants for grazing*. Pretoria: Department of Agricultural Development.

van Breda PAB, Nel EJ, Bayer MB (eds). 1990. *Palatability of plant species – winter rainfall region: Little Karoo and Ceres Karoo* Elsenburg Agricultural Development Institute

van Leeuwen CG, van der Maarel E. 1971. Pattern and process in coastal dune vegetations. *Acta Bot. Neerl.* 20 191-197.

van Oudtshoorn F. 2012. *Guide to grasses of southern Africa*. Pretoria: Briza Publications.

Verboom GA, Linder HP, Stock WD. 2003. Pylogenetics of the grass genus *Ehrharta*: evidence for radiation in the summer-arid zone of the South African Cape. *Evolution* 57: 1008-1021.

Verdaguer D, Sala A, Vilà M. 2010. Effect of environmental factors and bulb mass on the invasive geophyte *Oxalis pes-caprae* development *Acta Oecologica* 36: 92–99.

Vilà M, Bartomeus I, Gimeno I, Traveset A, Moragues E. 2006. Demography of the invasive geophyte *Oxalis pes-caprae* across a Mediterranean island. *Annals of Botany* 97: 1055–1062.

Vural M, Dönmez AA. 2002. Two new taxa of *Silene* (Caryophyllaceae) from Turkey. *Annales Botanici Fennici* 39: 153-158.

Western Australian Herbarium. 1998. FloraBase - the Western Australian Flora. Department of Parks and Wildlife. Available at https://florabase.dpaw.wa.gov.au. [accessed 22 March 2021]

Williams B, Wells TCE, Wells DA. 1974. Grazing management of Woodwalton Fen: seasonal changes in the diet of cattle and rabbits. *Journal of Applied Ecology* 11: 499-516.

Winston R, DesCamp W, Andreas J, Randall CB, Milan J, Schwarzländer M. 2014. *New invaders of the Southwest*. Washington, DC: Forest Health Technology Enterprise Team, United States Department of Agriculture.

ANNEXURE VI: CHAPTER 4 — SUPPLEMENTARY MATERIAL 1

Table S1 Plant species presence-absence and mean species cover (% ± SE) following the control of invasive alien European rabbits on Robben Island. Data organised for optimal interpretation using constrained seriation[2]. Significant ($P \leq 0.05$) differences determined using Friedman/Wilcoxon two-sample paired tests[3]. FDR-adjusted *P* values (classical one-stage method) provided for reference.

Sites	Species	Year				Test statistic	*P-value*	FDR adjusted *P*
		2010	2011	2012	2013			
Strand	*Sporobolus virginicus* (L.) Kunth	1.00 ± 0.68				-	-	-
	Sonchus oleraceus (L.) L.	0.33 ± 0.33		0.33 ± 0.33		1.50	1.000	1.000
	Conicosia pugioniformis (L.) N. E. Br.	9.00 ± 1.91	2.00 ± 1.03	2.33 ± 1.31	3.00 ± 1.91	12.13	0.002	0.022
	Asparagus capensis L.	3.67 ± 2.09	5.67 ± 2.80	6.00 ± 3.10	4.00 ± 2.00	4.64	0.216	0.396
	Tetragonia fruticosa L.	22.70 ± 2.51	40.00 ± 5.89	42.00 ± 7.38	38.70 ± 7.64	8.09	0.035	0.172
	Oncosiphon suffruticosum (L.) Kallersjo	0.33 ± 0.33	0.33 ± 0.33	4.33 ± 2.33	7.00 ± 3.75	7.55	0.047	0.172
	Zantedeschia aethiopica (L.)	0.67 ± 0.42		0.67 ± 0.42	0.67 ± 0.67	2.43	0.538	0.740
	Cynodon dactylon (L.) Pers.	0.33 ± 0.33		1.33 ± 0.99	1.67 ± 0.61	6.10	0.110	0.303
	Vulpia myuros (L.) C.C.Gmel			0.67 ± 0.67		-	-	-
	Isolepis sp.			1.00 ± 0.68		-	-	-
	Crassula sp.			0.33 ± 0.33		-	-	-
	Ehrharta villosa Schult.f.		0.33 ± 0.33	4.33 ± 2.85	5.00 ± 3.64	5.21	0.162	0.356
	Moraea collina Thunb.			1.33 ± 0.99		-	-	-
	Spergula arvensis L.			0.33 ± 0.33		-	-	-
	Ehrharta longiflora Sm.			20.70 ± 4.46	31.00 ± 3.89	16.00	0.313	0.492
	Bromus diandrus Roth.			0.67 ± 0.42	1.33 ± 1.33	2.00	1.000	1.000
	Silene cretica L.			3.67 ± 2.28	3.00 ± 1.44	3.00	1.000	1.000
	Euphorbia peplus L.				0.67 ± 0.67	-	-	-
	Anagallis arvensis L.				0.33 ± 0.33	-	-	-
	Phyllobolus canaliculatus (Haw.) Bittrich				0.33 ± 0.33	-	-	-

---

[2] Brower JC, Kile KM. 1988. Seriation of an original data matrix as applied to palaeoecology. *Lethaia* 21: 79-93.

[3] The Exact Wilcoxon two-sample paired test was used in cases were species had only two years of mean cover values above zero.

	Hypochaeris glabra L.				0.33 ± 0.33	-	-	-
Eucalyptus	*Phyllobolus canaliculatus* (Haw.) Bittrich	1.33 ± 0.67	0.67 ± 0.67	8.67 ± 3.29	8.33 ± 6.01	11.69	0.003	0.021
	Oxalis pes-caprae L.	0.67 ± 0.67		0.33 ± 0.33	3.00 ± 1.13	7.73	0.042	0.147
	Ehrharta longiflora Sm.			0.33 ± 0.33	0.67 ± 0.67	2.00	1.000	1.000
	Crassula natans Thunb.			0.33 ± 0.33	0.33 ± 0.33	1.50	1.000	1.000
	Tetragonia fruticosa L.			6.00 ± 2.68	13.30 ± 7.28	14.00	0.563	0.985
	Oncosiphon suffruticosum (L.) Kallersjo			0.67 ± 0.42	1.33 ± 0.67	3.00	0.500	0.985
	Chenopodium murale L.			0.33 ± 0.33	0.33 ± 0.33	1.50	1.000	1.000
	Torilis arvensis (Huds.) Link				0.33 ± 0.33	-	-	-
	Euphorbia peplus L.				1.67 ± 1.67	-	-	-
	Conicosia pugioniformis (L.) N. E. Br.				0.33 ± 0.33	-	-	-
Inland Dune	*Ornithoglossum viride* (L.f.) Dryland. Ex W.T.Aiton	0.33 ± 0.33				-	-	-
	Wahlenbergia androsacea A.DC	0.33 ± 0.33				-	-	-
	Emex australis Steinh.	0.33 ± 0.33				-	-	-
	Sporobolus virginicus (L.) Kunth	0.33 ± 0.33				-	-	-
	Trachyandra sp.	0.67 ± 0.42				-	-	-
	Zantedeschia aethiopica (L.)	0.33 ± 0.33				-	-	-
	Phyllobolus canaliculatus (Haw.) Bittrich		0.33 ± 0.33			-	-	-
	Asparagus capensis L.		0.33 ± 0.33			-	-	-
	Ehrharta villosa Schult.f.	1.00 ± 1.00	6.00 ± 2.83	20.30 ± 9.00	36.30 ± 14.20	8.18	0.033	0.059
	Cissampelos capensis L.f.	25.00 ± 6.57	21.70 ± 4.88	26.70 ± 6.01	19.30 ± 4.02	3.76	0.324	0.378
	Oncosiphon suffruticosum (L.) Kallersjo	1.33 ± 1.33	0.33 ± 0.33	5.67 ± 2.28	1.33 ± 0.99	7.92	0.038	0.059
	Conicosia pugioniformis (L.) N. E. Br.	11.70 ± 1.74	2.67 ± 1.61	2.67 ± 2.29	3.33 ± 1.43	8.51	0.029	0.059
	Tetragonia fruticosa L.	16.30 ± 6.54	37.70 ± 9.49	48.30 ± 8.82	42.00 ± 6.91	14.19	<0.001	0.001
	Isolepis sp.			0.33 ± 0.33		-	-	-
	Torilis arvensis (Huds.) Link			3.33 ± 1.69		-	-	-
	Ehrharta longiflora Sm.	1.00 ± 1.00		0.33 ± 0.33	3.00 ± 1.34	7.73	0.042	0.059
	Vulpia myuros (L.) C.C.Gmel			1.33 ± 0.42		-	-	-
	Anagallis arvensis L.			0.33 ± 0.33		-	-	-

Bromus diandrus Roth.	10.70 ± 4.43	13.00 ± 5.26	12.00	0.44	0.440
Avena fatua L.		2.00 ± 1.26	-	-	-
Capnophyllum africanum (L.) Gaertn.		1.33 ± 0.84	-	-	-

ANNEXURE VII: CHAPTER 4 — SUPPLEMENTARY MATERIAL 2

Overview

In this supplementary document, we discuss how we implemented a pseudo-before-after control-impact (BACI) experimental design and used correlative statistical rainfall-vegetation relationships to identify and remove the confounding effects of inter-annual rainfall variation on the results. As detailed in the Materials and Methods section of the main text, our study was based on an attempt to restore vegetation on Robben Island by removing alien invasive European rabbits. We initiated vegetation monitoring a year after the commencement of rabbit control activities. As a result, without a before-impact control, we could not implement the BACI design, which is commonly used to assess impact in longitudinal observational studies. Furthermore, we evaluated the influence of rainfall variation on vegetation response using correlative statistical control and thus could not directly demonstrate causality. To overcome the challenges, we used an earlier vegetation survey of the island by Adamson (1934) as a BACI-like control. Additionally, we bolstered the correlative interpretations of rainfall–vegetation relationships in our results whenever possible by providing plausible mechanisms, demonstrating links between putative causes and outcomes, and sourcing supporting independent evidence from the published literature. Adamson (1934) conducted a vegetation survey on Robben Island in 1933 and 1934, when it was overrun with rabbits. We used the results of this survey as a BACI-like control, assuming that conditions on the island then were similar to those in the period preceding rabbit control in 2009 and 2010.

Below, we present detailed accounts of how we used the approaches mentioned above to i) evaluate and remove the influence of inter-annual rainfall variation on vegetation response; and ii) determine how species diversity, richness, and evenness, as well as underlying species cover, would have changed given constant and average inter-annual rainfall. We provide separate accounts for our three study sites (strand, eucalyptus, and inland dune). As we intended to ensure that each of the sections of this document was as comprehensive and self–contained as possible, there is considerable repetitive use of information presented in the main text and separate parts of this document.

Strand sites

The statistical correlation suggests that interannual rainfall variation influenced a considerable proportion of the change in species diversity (~39%) and richness (~41%) at strand sites following rabbit control. Inter-annual rainfall variation appears to have had no influence on species evenness. Species diversity and richness increased, while evenness remained constant across the sites.

Based on our interpretation of underlying vegetation dynamics and correlative rainfall-vegetation relationships, we determined that species diversity across strand sites would have decreased following rabbit control, given constant and average inter-annual rainfall. The decrease in diversity would have been driven by a decline in species richness resulting from the emergence of two species (*Ehrharta villosa* and *Cynodon dactylon*) and the disappearance of three (*Anagallis arvensis.*, *Euphorbia peplus* (alien), and *Hypochaeris glabra* (alien)) in response to rabbit control. Eight species (*Conicosia pugioniformis*, *Oncosiphon suffruticosum, Tetragonia fruticosa*, *Ehrharta longiflora*, *Zantedeschia aethiopica*, *Bromus diandrus*, *Silene cretica* and *Asparagus capensis*) would have maintained their presence before and after rabbit control. *Tetragonia fruticosa* and *E. longiflora* would have increased from medium and low to high cover, while *C. pugioniformis* and *O. suffruticosum* would have declined conversely. *Zantedeschia aethiopica*, *B. diandrus*, *S. cretica,* and *A. capensis* would have maintained low cover. Species evenness would have declined following rabbit control as species cover would have been dominated by four species (*C. pugioniformis*, *O. suffruticosum*, *E. peplus,* and *A. arvensis*) before and only two (*T. fruticosa* and *E. longiflora*) after rabbit control.

Below, we present details of our determination of how each species that underlay vegetation diversity, richness and evenness change at strand sites would have responded to rabbit control given constant and average inter-annual rainfall.

Ehrharta longiflora Bromus diandrus and *Silene cretica*

The emergence of the annual grasses *E. longiflora*, *B. diandrus* and annual herb *S. cretica* in the third year following rabbit control was clearly in response to increases in TSUR and TAUR from considerably below their long-term averages at the end of the drought conditions that prevailed during the first two years following rabbit control. Total summer rainfall was moderately and substantially below the long-term average during the first- and second years following rabbit control and rose moderately above and equal to the average in the third and fourth. Total autumn rainfall was considerably below the long-term average during the first- and second years following rabbit control and rose to moderately above and slightly below average in the third and fourth.

Ehrharta longiflora, B. diandrus and *S. cretica* are winter annuals that survive dry summer as dormant seeds. The seeds lose dormancy at the end of summer to take advantage of favourable growing conditions in winter (Gill, et al. 1985, Cheam 1986, Vural, et al. 2002, Jackson, et al. 2006, Blasi, et al. 2014, Winston, et al. 2014). Soil moisture is the overriding factor in controlling the germination of non-dormant *E. longiflora, B. diandrus* and *S. cretica* seeds, and staggered germination occurs during late summer and early autumn following heavy rainfall events (Cheam 1986, Western Australian Herbarium 1998, Moore, et al. 2007a). The absence of *E. longiflora, B. diandrus* and *S. cretica* from strand sites during the first two years following rabbit control was probably because of their inability to germinate because of inadequate soil moisture caused by below-average summer and autumn rainfall.

Adamson (1934) observed *E. longiflora*, *B. diandrus* and *S. cretica* on Robben Island in 1933 and 1934 when the island was overrun with rabbits and the vegetation heavily degraded. *Bromus diandrus* and *S. cretica* are generally unpalatable to herbivores (van Breda, et al. 1990, Coetzee 2008). Although *B. diandrus* seeds are consumed by rabbits (Martin, et al. 2007), the plant is not favoured because of its high fibre content (Myers, et al. 1963). Rabbits prefer to consume soft, green, lush plants (Myers and Poole 1963). *Silene cretica* plants are short and hairy, and rabbits generally avoid feeding on low-growing (Farrow 1917, Crawley 1990) and hairy (van Leeuwen, et al. 1971, Williams, et al. 1974) species. This probably explained the widespread and abundant occurrence of *B. diandrus* and *S. cretica* plants at inland and coastal dune sites on the island in 1933 and 1934 (Adamson 1934). However, no mention was made by Adamson (1934) about the presence of *B. diandrus* and *S. cretica* at strand sites. This was probably because Adamson (1934) could have overlooked the short ephemeral grasses because of their extremely low cover at strand sites. *Bromus diandrus* and *S. cretica* have extensive root systems (Menke 1992, Arnone II, et al. 1997, Jackson, et al. 2006), which enable them to compete with other species for water stored in the soil. However, the soil at strand sites was generally shallow (3 to 5 cm; Adamson 1934). As a result, areas with soil deep enough to support *B. diandrus* and *S. cretica* plants were most likely limited at the sites. Therefore, it is most likely that *B. diandrus* and *S. cretica* would have been present at strand sites before and after rabbit control, given constant and average inter-annual rainfall. However, because of the low availability of suitably deep soils to support *B. diandrus* and *S. cretica* plants at strand sites, the cover of the species would have been constant and extremely low.

Ehrharta longiflora, in contrast to *B. diandrus* and *S. cretica,* is palatable to herbivores (van Oudtshoorn 2012) and was a favoured feed for rabbits on Robben Island (Gillham 1963). The annual grass cannot withstand heavy grazing as it has creeping branched roots and rhizomes that are easily pulled up by herbivores (Moore and Moore 2007a). However, Adamson (1934) observed *E. longiflora* on rock outcrops on strand sites when the island was overrun with rabbits and the vegetation heavily degraded. Ephemerals like *E. longiflora* that grow for a limited period may survive rabbit herbivory even if they are subjected to heavy attack. Their short annual period of occurrence exposes them to attack for a considerably less period than is the case with most other plants, such that some of them manage to survive rabbit herbivory and can flower and set seed (Farrow 1917). It is therefore most likely that *E. longiflora* was present at strand sites during rabbit herbivory, albeit at very low cover. Given constant and average inter-annual rainfall, the annual grass would have been continuously present – and increased to high cover – following rabbit control.

Anagallis arvensis, *Euphorbia peplus*, *Hypochaeris glabra* and *Phyllobolus canaliculatus*

The emergence of the annual herbs *A. arvensis*, *E. peplus*, *H. glabra* and perennial herb *P. canaliculatus* in the fourth year following rabbit control was, on the other hand, clearly in response to an increase in TWR to moderately above the long-term average. Total winter rainfall was slightly and moderately below and slightly above the long-term average in the first, second- and third years following rabbit control and increased to moderately above average in the fourth. *Anagallis arvensis*, *E. peplus* and *H. glabra* are small, low-growing shallow-rooted winter ephemerals that require bare and moist soil to reproduce from seed or re-sprout from hypocotyls (Esler 1980, Esler 1987, Christodoulakis 1996, Burrows, et al. 1999, Latzel, et al. 2011, Anon 2017a, d). Because of their shallow roots and need for bare soil for germination/re-sprouting, *A. arvensis*, *E. peplus*, and *H. glabra* were most likely restricted to areas with shallow soils where larger and more competitive species could not establish (Esler 1980, Esler 1987, Burrows, et al. 1999, Anon 2017a, c, d). Shallow soil conditions may have led to drier than normal conditions at these sites. As a result, the rise of winter rainfall to slightly above average in the third year following rabbit control could have been insufficient to raise soil moisture to levels suitable for the germination/re-sprouting of the annual herbs. Only an increase in winter rainfall to moderately above the long-term average in the fourth year following rabbit control appears to have been sufficient to raise soil moisture levels above the germination/re-sprouting thresholds of the ephemeral herbs and driven their emergence. Ecological information on the perennial herb *P. canaliculatus* is not readily available. We hypothesise, however, that the geophyte – which favours deeper dune soil (Manning, et al. 2008) – would also not have been able to acquire adequate soil moisture from the shallow soils at strand sites. Like *A. arvensis*, *E. peplus*, and *H. glabra*, the perennial herb most likely could only occur at strand sites in the fourth year because of the increase in winter rainfall to moderately above the long-term average. *Phyllobolus canaliculatus* is a geophyte with tuberous roots and long creeping, softly woody branches that root at the nodes (Manning and Paterson-Jones 2008).

Adamson (1934) observed *A. arvensis*, *E. peplus*, *H. glabra* on Robben Island in 1933 and 1934 when the island was overrun with rabbits and the vegetation heavily degraded. *Anagallis arvensis* and *E. peplus* occurred abundantly across the island, while *H. glabra* was restricted to a rock outcrop at the strand sites (Adamson 1934). The weedy *A. arvensis* and *E. peplus* were considered by Adamson (1934) to have increased in cover and spread into open areas created by rabbit herbivory. *Anagallis arvensis* and *E. peplus* are unpalatable to herbivores (Bullock 1952, Gillham 1963, Rothwell, et al. 1986, Simmonds, et al. 2000, Rivero, et al. 2001, Anon 2017c) while *H. glabra* is, to some extent, palatable (Cowan 1945, van Dyne, et al. 1965, Struik 1967). Release from competition with more competitive rabbit-sensitive species would have enabled the unpalatable *A. arvensis* and *E. peplus* to expand to more moist deeper soils. However, rabbit herbivory would have curtailed the response of the more palatable *H. glabra* to the release from competition pressure. This would explain the expansion of *A. arvensis* and *E. peplus* and the comparatively restricted occurrence of *H. glabra* in 1934. Given constant and average inter-annual rainfall, it is most probable that *A. arvensis*, *E. peplus* and *H. glabra* would have disappeared from strand sites following rabbit control. The low-growing and shallow-rooted ephemerals would have been restricted by competition with the taller and competitively dominant annual grasses *E. longiflora* (Bidwell, et al. 2006, Fisher, et al. 2009), *B. diandrus* (Parker, et al. 1982, Menke 1992, Jackson, et al. 2006) and annual herb *S. cretica* (Arnone II and Kestenholz 1997) to drier bare shallow sites where they could only germinate under conditions of considerably higher than usual winter rainfall. As a result, the ephemeral herbs would not be able to germinate at strand sites in years of average winter rainfall. However, they would occur at the sites in years of considerably higher than average winter rainfall. We hypothesise that the deeper-rooted perennial herb *P. canaliculatus* would have faced more severe restrictions in the shallow soils at strand sites. The perennial herb would have occurred at extremely low cover at strand sites as habitat with suitably deep soil to support would have been limited. Even at these sites, *P. canaliculatus* would most likely have been able to germinate and establish only under conditions of higher-than-normal winter rainfall. Unlike *A. arvensis*, *E. peplus* and *H. glabra*, *P. canaliculatus* was absent from Robben Island in 1933 and 1934 (Adamson 1934). The deeper-rooted, somewhat palatable perennial herb probably disappeared from strand sites because it occurred on a limited area – relatively deep soil sites – and was, therefore, especially susceptible to herbivory. It could have also been because winter rainfall in 1933 and 1934 was inadequate to support germination and establishment of *P. canaliculatus* at strand sites. Therefore, the perennial herb *P. canaliculatus* would likely not have occurred at strand sites before and after rabbit control, given constant and average inter-annual rainfall.

Ehrharta villosa

The emergence of the perennial grass *E. villosa* in the second year following rabbit control clearly could not have been influenced by inter-annual rainfall variation as it occurred despite worsening drought conditions. Total summer rainfall and TWR dropped from moderately and slightly below the long-term average to considerably and moderately below the long-term average between the second-and-third years following rabbit control, while TAUR remained considerably below average. As inter-annual variation in TSUR, TAUR and TWR could not be associated with the emergence of *E. villosa;* it is reasonable to deduce that its emergence was directly linked to the cessation of rabbit herbivory. Although *E. villosa* is not highly palatable to herbivores (Louw, et al. 1988), it is nevertheless negatively affected by grazing and is known to become more abundant when grassland is leniently grazed (Tainton, et al. 1990). Although precise information about rabbit preference for *E. villosa* on Robben Island is unavailable, rabbit herbivory appears to have had a considerable effect on the abundance of the perennial grass on the island (Lloyd, et al. 1986, Sherley 2016). *Ehrharta villosa* was absent from strand sites in 1933 and 1934 and occurred at inland dune sites as refugee plants among bushes of *Lycium afrum* L. and *Lycium ferocissimum* Miers or in tufts of *T. fruticosa* or *Cissampelos capensis* (Adamson 1934). *Ehrharta villosa* requires fairly deep soil (Coetzee 2008). The soil at strand sites was generally shallow (3 to 5 cm; Adamson 1934). As a result, areas with soil deep enough to support *E. villosa* plants were most likely limited at the sites. The deep-rooted (Harrington, et al. 1998) perennial grass probably disappeared from strand sites in 1934 because it occurred on a limited area – relatively deep soil sites – and was therefore especially susceptible to herbivory. The low cover of *E. villosa* at strand sites following rabbit control was likely caused by the limited availability of habitats with suitably deep soils to support the perennial grass.

Sporobolus virginicus

Unlike other species such as the annual herb *S. oleraceus*, perennial herb *Z. aethiopica* and perennial grass *C. dactylon* that disappeared temporarily in the second year following rabbit control and re-emerged afterwards, *S. virginicus* never re-emerged following its disappearance. Like the perennial grass *E. villosa*, *S. virginicus* rarely set seeds and reproduces, survives, and spreads through rhizomes (Marcum, et al. 1992, Knevel 2001, Masters, et al. 2007, Williams 2007). The rhizomes have deep root systems, are adapted to coarse textured soils, possess high salt tolerance and require low moisture for growth (Jones, et al. 2004). *Sporobolus virginicus*, like *E. villosa*, also appears to have withstood the drought conditions of the first two years following rabbit control and responded directly to cessation of rabbit herbivory. However, the perennial grass is palatable to herbivores (Mfitumukiza 2004) and is an important grazing plant during the dry season (Barrett-Lennard 2003, Jones and Hanna 2004). As a result, the grass should have increased in cover and not disappeared following rabbit control. The disappearance of *S. virginicus* was probably caused by being outcompeted for limited deep soil sites on strandveld by other more competitive deep-rooted species like *E. villosa*. *Sporobolus virginicus* – which occurs as a pioneer species on sandy beaches (Naidoo and Mundree 1993) – was most likely absent from strand sites during rabbit herbivory and then briefly re-emerged following rabbit control before being outcompeted for limited deep soil sites by other more competitive re-emerging deep rooted species. Adamson (1934) did not observe *S. virginicus* on Robben Island in 1933 and 1934 when the Island was under heavy rabbit herbivory. The brief emergence of the perennial grass *S. virginicus* following rabbit control was most likely an indirect result of the drought conditions that prevailed during the first two years which precluded the establishment and increase in cover of more competitive species such as *E. villosa*. Given constant and average inter-annual rainfall, *S. virginicus* would have been absent from strand sites as rabbit herbivory and the occurrence of more competitive species would have precluded its establishment.

Zantedeschia aethiopica and *Cynodon dactylon*

The temporary disappearance of the perennial herb *Z. aethiopica* and grass *C. dactylon* in the second year following rabbit control appears to have been an artefact of inter-annual rainfall variation. The brief disappearance of the species in the second year following rabbit control was clearly in response to worsening drought conditions. Total winter rainfall and TSUR declined from slightly and moderately to considerably below the long-term average between the first- and second years following rabbit control while TAUR remained considerably below average. *Zantedeschia aethiopica* is a rhizomatous herbaceous perennial plant that is adapted to periodic drought (Corr 1993). The plant dies down to an underground fleshy rhizome during dry periods (Corr 1993). The rhizomes typically have numerous buds which develop when adequate water becomes available (Corr 1993). Likewise, *C. dactylon* is a geophyte that perennates by subterranean buds (Halvorson, et al. 2003b). The perennial grass also responds to drought conditions by dying down to underground rhizomes (Brown, et al. 2002, Halvorson and Guertin 2003b). The low rainfall during the second year following rabbit control most likely resulted in extremely low soil moistures that caused *Z. aethiopica* and *C. dactylon* to die down to their subterranean rhizomes. Rise in TWR, TSUR and TAUR most likely caused the re-emergence of the perennial herb and grass between the second- and third years following rabbit control. Like the case for *B. diandrus* and *S. cretica* (see above), areas with soil deep enough to support rhizomatous *Z. aethiopica* and *C. dactylon* plants were most likely limited at strand sites. *Zantedeschia aethiopica* which is highly toxic to herbivores (Jackson 1986, Scott, et al. 1996, El Mokni, et al. 2012) was present on Robben Island in 1933 and 1934 while the more palatable *C. dactylon* was reportedly absent (Adamson 1934). Both species were however not observed by Adamson (1934) at strand sites. Adamson (1934) could have overlooked the presence of *Z. aethiopica* on strand sites because of their extremely low cover due to limited sites with suitably deep soil. The more palatable *C. dactylon* – like *E. villosa* above – probably disappeared from strand sites in 1934 because it occurred on a limited area – relatively deep soil sites – and was therefore especially susceptible to herbivory. *Zantedeschia aethiopica* would have been present at low cover at strand sites both before and after rabbit control given constant and average inter-annual rainfall. The more palatable *Cynodon dactylon* was most likely absent from strand sites during rabbit herbivory and re-emerged following rabbit control. However, because of low availability of suitably deep soils to support *Z. aethiopica* and *C. dactylon* plants at strand sites, the cover of the species would have been extremely low.

Vulpia myuros, *Sonchus oleraceus*, *Isolepis* sp., *Moraea collina*, *Spergula arvensis* and *Crassula* sp.

The transient occurrence of the five species - the annual grass *V. myuros* and annual herbs *S. oleraceus*, *Isolepis* sp., *M. collina*, *S. arvensis* and *Crassula* sp. – in the third year following rabbit control appears to have been another artefact of inter-annual rainfall variation. The brief emergence of the species in the third year following rabbit control was clearly in response to increase in TAUR to above the long-term average. Total autumn rainfall was considerably below the long-term average during the first- and second years following rabbit control and briefly rose to moderately above average in the third year before declining to slightly below average in the fourth year. All five species were absent during the first- and second years following rabbit control and only emerged in the third year when TAUR rose to moderately above the long-term average before disappearing again in the fourth year when TAUR declined to slightly below average. All the species are short, aggressive, early maturing winter ephemerals that require bare moist soil to reproduce from seed or re-sprout from rhizomes or corms (Toelken 1981, Anon , e, n.d.-b, c). Their seeds will usually only germinate after a good rain so as to ensure new seed production (Toelken 1981, Anon). The species rarely occur in closed communities because of their low stature. As result they can only occur at the shallowest spots on strand sites that other taller plant species such as the annual and perennial grasses *E. longiflora* and *E. villosa* cannot establish from. Because of the shallowness of the soil, conditions there are drier, and above average TAUR is needed to keep the soil wet for successful germination. The process is probably like the case of the ephemeral annual herbs *E. peplus*, *A. arvensis*, *H. glabra* and perennial herb *P. canaliculatus* which only appear in years of above average TWR (see above). *Euphorbia peplus*, *A. arvensis*, *H. glabra* and *P. canaliculatus* like *V. myuros*, *S. oleraceus*, *Isolepis* sp., *M. collina*, *S. arvensis* and *Crassula* sp. are short semi-prostrate ruderal species that prefer open spaces. Therefore, the annual grass *V. myuros* and annual herbs *S. oleraceus*, *Isolepis* sp., *M. collina*, *S. arvensis* and *Crassula* sp. would most likely not have occurred at strand sites given constant and average inter-annual rainfall. The annual grass *V. myuros* and herbs *S. oleraceus* and *S. arvensis* were not observed by Adamson (1934) on Robben Island in 1933 and 1934. *Isolepis* sp., *M. collina* and *Crassula* sp. occurred on the island but were absent from strand sites (Adamson 1934).

Oncosiphon suffruticosum, *Conicosia pugioniformis*, *Tetragonia fruticosa* and *Asparagus capensis*

The four species that occurred persistently following rabbit control - the annual herb *O. suffruticosum*, perennial herb *C. pugioniformis* and woody shrubs *T. fruticosa* and *A. capensis* - were clearly able to do so because of their ability to withstand the drought conditions of the first two years following rabbit control. *Tetragonia fruticosa* plants are highly adapted to conditions of low soil moisture. The shrub has succulent leaves and is able to use water stored in leaves to endure drought conditions (van Breda, et al. 1991, Hoffman, et al. 2009). In addition, *T. fruticosa* plants have fairly well-developed root systems that can penetrate the soil to considerable depths (van Breda and Barnard 1991). Like the woody shrub *T. fruticosa*, *C. pugioniformis* is a perennial leaf-succulent that can tolerate low soil moisture (Schmalzer, et al. 1987). *Asparagus capensis* is a small spiny-stemmed dense woody shrub (Manning and Paterson-Jones 2008) that is adapted to withstand drought conditions through woody stems and small needle-like leaves (Anon 2014). *Oncosiphon suffruticosum* is a winter annual or biennial herb that is well adapted to semi-arid conditions (Moore, et al. 2007b, Anon 2014). The herb – which reproduces solely from seed – produces thousands of small seeds in late spring that germinate with the onset of the winter rains (Moore and Moore 2007b, Anon 2014). Some plants remain vegetative and survive the summer to flower in the following season (Adamson 1934, Moore and Moore 2007b). As a result, the change in cover of the species following rabbit control most likely reflected direct response to cessation of rabbit herbivory pressure.

Oncosiphon suffruticosum, *C. pugioniformis*, *T. fruticosa* and *A. capensis* occurred on Robben Island in 1934 when the island was overrun with rabbits and the vegetation heavily degraded (Adamson 1934). *Oncosiphon suffruticosum*, *C. pugioniformis T. fruticosa* occurred abundantly while *A. capensis* was restricted to rock outcrops at strand sites (Adamson 1934). While *O. suffruticosum*, *C. pugioniformis* and *A. capensis* are poor interspecific competitors that occur in disturbed open localities where grasses or perennial vegetation has been reduced, especially by heavy grazing (Schmalzer and Hinkle 1987, Moore and Moore 2007b, Anon 2014), *Tetragonia fruticosa* is highly competitive (van Breda and Barnard 1991). It is therefore most likely that, given constant and average inter-annual rainfall, the unpalatable annual herb *O. suffruticosum* that was abundant at strand sites in 1934, decreased to low cover following rabbit control. Likewise, the less palatable (Louw and Beukes 1988) perennial herb *C. pugioniformis* — which occurred in abundance at strand sites in 1934 — most likely decreased to low cover following rabbit control. In contrast, the highly palatable (van Breda, et al. 1990) woody shrub *T. fruticosa* — which occurred in some abundance at strand sites in 1934 — most likely increased to high cover following rabbit control. The cover of the unpalatable (van Breda, et al. 1990) spiny-stemmed dense woody shrub *A. capensis* — which occurred at low cover on rock outcrops at strand sites in 1934 — most likely remained low following rabbit control. This was probably due to the restricted availability of suitable rocky habitat.

Eucalyptus sites

Like at strand sites, interannual rainfall influenced a considerable amount of the change in species diversity (~76%), richness (~91%) and evenness (44%) following rabbit control at eucalyptus sites. Species diversity, richness and evenness increased from zero between the second- and third years following rabbit control and did not change between the third and fourth. Inter-annual variation in TAUR appears to have influenced ~66% of the ~76% change in species diversity caused by inter-annual rainfall variation. Total summer rainfall, TAUR and TWR accounted for ~75%, ~79% and ~66% of the change in richness.

Based on our interpretation of underlying vegetation dynamics and correlative rainfall-vegetation relationships, we determined that given constant and average inter-annual rainfall species diversity, richness and evenness would not have changed at eucalyptus sites following rabbit control. This is because there would been no loss or gain in species. The four species present at the sites (*Crassula natans, T. fruticosa*, *Oxalis pes-caprae* and *P. canaliculatus*) would have maintained their low cover before and after rabbit control. Additionally, species evenness would have remained constant across eucalyptus sites as the relative abundances of species (i.e., equally infrequent) would remained similar before and after rabbit control.

Below, we present details of our determination of how each of the species that underlay vegetation diversity, richness and evenness change at eucalyptus sites would have responded to rabbit control given constant and average inter-annual rainfall.

Ehrharta longiflora and *Oncosiphon suffruticosum*,

The emergence of the annual grass and herb *E. longiflora*, and *O. suffruticosum* in the third year following rabbit control was obviously in response to increase in TAUR and TWR to above the long-term average. Both plants are winter annuals that reproduce entirely from seed following autumn and winter rainfall (Western Australian Herbarium 1998, Bossard, et al. 2000, Moore and Moore 2007b, Anon 2014). Total winter rainfall increased from slightly and moderately below the long-term average during the first- and second years following rabbit control to slightly and moderately above the long-term average in the third and fourth. Total autumn rainfall was considerably below the long-term average during the first- and second years following rabbit control and rose to moderately above and slightly below average in the third and fourth. Germination failure during the first two years following rabbit control because of below-average autumn and winter rainfall would have led to the complete absence of the plant species across eucalyptus sites. Eucalyptus trees most likely led to considerably drier than normal germination conditions at eucalyptus sites. The increase to above average TAUR or TWR in the third- and fourth years following rabbit control would have raised soil moisture to levels suitable for seed germination even under the dry conditions across the sites. Therefore, given constant and average inter-annual rainfall, *E. longiflora* and *O. suffruticosum* would not have occurred at eucalyptus sites before and after rabbit control as the moisture conditions under *Eucalyptus* plantations would have been too dry for the germination of the plants.

Crassula natans

The emergence of the annual herb *C. natans* in the third year following rabbit control was obviously in response to increase in TSR, TAR and TWR to above and equal the long-term average after the first two years when it was below average. *Crassula natans* is an ephemeral herb whose seeds germinate only after a good rain (Toelken 1981). The plant, which often completes its life cycle in less than one month, occurs as long as water is available, and specimens have been recorded in each month of the year (Toelken 1981). Adamson (1934) did not report the presence of *C. natans,* in 1933 and 1934 when Robben Island was under heavy rabbit herbivory. However, this could have been a misidentification as he reported the presence of several other *Crassula* species. Given constant and average inter-annual rainfall *C. natans,* would have occurred at eucalyptus sites before and after rabbit control albeit at low cover. This would have been due to the drier than normal conditions at the sites caused by the effects of *Eucalyptus* trees on soil moisture.

Tetragonia fruticosa

The emergence of the woody shrub *T. fruticosa* in the third year following rabbit control was obviously in response to the increase in TAUR to moderately above the long-term average following the drought conditions of the first two years. Total autumn rainfall was moderately above and slightly below average in the third- and fourth but considerably below average in the first- and second- years after rabbit control. *Tetragonia fruticosa* seeds germinate intermittently in autumn following episodic leaching of salt from soil by rainwater (van Breda and Barnard 1991). The increased TAUR will have provided sufficient water for germination in the dry conditions under *Eucalyptus* trees. Adamson (1934) reported the occurrence of *T. fruticosa* on Robben Island in 1933 and 1934 when Robben Island was under heavy rabbit herbivory. Given constant and average inter-annual rainfall, *T. fruticosa* would have maintained constant and low cover before and after rabbit control because of poor germination due to depletion of soil moisture by *Eucalyptus* trees.

Torilis arvensis, *Euphorbia peplus* and *Conicosia pugioniformis*

The annual herbs *T. arvensis*, *E. peplus* and perennial herb *C. pugioniformis* clearly emerged in the fourth year following rabbit control in response to the increase in TWR to substantially above the long-term average. Total winter rainfall was slightly and moderately below and slightly above average in the preceding years. The plant species reproduce solely from seed (Schmalzer and Hinkle 1987, Latzel, et al. 2011, DiTomaso, et al. 2013). Although *C. pugioniformis* is perennial, adult plants die out under very dry conditions and can only be reproduced by seed (Adamson 1934). While the seeds of the annual herbs *T. arvensis* and *E. peplus c*an germinate and grow during any period of the year given adequate soil moisture (Latzel, et al. 2011, Hyde, et al. 2014), *C. pugioniformis* seeds germinate in late autumn and early winter. The increase to substantially above average TWR in the fourth year following rabbit control would have raised soil moisture to levels suitable for seed germination even under the dry conditions at eucalyptus sites. Germination failure during the preceding three years following rabbit control because of inadequate winter rainfall would have led to the complete absence of the plant species across the sites. Therefore, given constant and average inter-annual rainfall, *T. arvensis*, *E. peplus* and *C. pugioniformis* would not have occurred at eucalyptus sites before and after rabbit control as the moisture conditions under *Eucalyptus* plantations would have been too dry for the germination of the plants.

Oxalis pes-caprae

The temporary disappearance of the annual herb *O. pes-caprae* in the second year following rabbit control was clearly in response to a decline in TWR to moderately below the long-term average. The herb reproduces both sexually by seeds and asexually through bulbils (Papini, et al. 2017). *Oxalis* bulbs remain dormant in the summer and sprout in the autumn (Vilà, et al. 2006, Verdaguer, et al. 2010). As a result, peak vegetative growth occurs during autumn and winter, after which flowering starts (Verdaguer, et al. 2010). The slight increases in cover by *O. pes-caprae* between the second-, third- and fourth years following rabbit control would have been in response to the subsequent increase in TWR to above average levels. Adamson (1934) observed abundant *O. pes-caprae* in 1933 and 1934 when the island was under heavy rabbit herbivory. As a result, the herb would have persisted at eucalyptus sites before and after rabbit control given constant and average inter-annual rainfall. However, the cover of *O. pes-caprae* at the sites would have been kept low by intense competition for soil nutrients and sunlight by *Eucalyptus* trees. *Oxalis pes-caprae* performs poorly under conditions of low soil fertility and shade (Verdaguer, et al. 2010).

Phyllobolus canaliculatus

The persistent occurrence of the perennial herb *P. canaliculatus* was due to its ability to tolerate the drought conditions of the first two years following rabbit control. *Phyllobolus canaliculatus* is drought tolerant (Freeman, et al. 2021) and grows well in open well-drained soil (UWC Cape Flats Indigenous Nursery 2021). Although Adamson (1934) does not mention the presence of the herb in 1933 and 1934 when the island was under heavy rabbit herbivory, it would have most likely persisted prior to rabbit control as it is also less palatable. The herb may have been overlooked during the survey by Adamson (1934) because of its low cover. Therefore, given constant and average inter-annual rainfall, *P. canaliculatus* would have persisted at eucalyptus sites before and after rabbit control. However, the cover of the perennial herb would have been consistently low because of shading by *Eucalyptus* trees. The species requires sunny conditions for germination and optimal growth (UWC Cape Flats Indigenous Nursery 2021).

Inland dune sites

Unlike at strand and eucalyptus sites, inter-annual rainfall variation appears to have had no influence on change in species diversity, richness and evenness following rabbit control at inland dune sites. All three diversity measures did not change following rabbit control at the sites. However, the lack of change in the measures appears to have been an artifact caused by the transient emergence of several species (*P. canaliculatus A. capensis*, *V. myuros*, *Isolepis* sp., *T. arvensis,* and *A. arvensis*) in response to higher-than-normal autumn and winter rainfall in the second- and third years following rabbit control. The emergence of the transient species masked underlying species diversity changes and rainfall-vegetation relationships at the sites.

Based on our interpretation of vegetation dynamics and individual rainfall-species relationships, we determined that given constant and average inter-annual rainfall, species diversity across inland dune sites would have decreased following rabbit control. The decrease in diversity would have been driven by a decline in species richness resulting from the emergence of one species (*E. longiflora*) and the disappearance of five (*Wahlenbergia androsacea*, *Emex australis*, *Ornithoglossum viride*, *Trachyandra* sp. and *Z. aethiopica*) in response to rabbit herbivory control. Seven species (*E. villosa*, *T. fruticosa*, *O. suffruticosum*, *C. pugioniformis*, *B. diandrus*, *Cissampelos capensis* and *Isolepis* sp.) would have maintained their presence before and after rabbit control. *Ehrharta villosa* and *T. fruticosa* would have increased from low to high cover, while *O. suffruticosum* and *C. pugioniformis* would have declined conversely. The cover of *B. diandrus* would have declined from high to medium while *C. capensis* and *Isolepis* sp. maintained low cover. Species evenness would have declined following rabbit control as species cover would have been dominated by six species (*O. viride*, *E. australis*, *Trachyandra* sp., *O. suffruticosum*, *C. pugioniformis,* and *B. diandrus*) before and only two (*T. fruticosa* and *E. villosa*) after rabbit control.

Below, we present details of our determination of how each of the species that underlay vegetation diversity, richness and evenness change at eucalyptus sites would have responded to rabbit control given constant and average inter-annual rainfall.

Bromus diandrus

The emergence of the annual grass *B. diandrus* after the third year following rabbit control was clearly in response to increase in TAUR to moderately above and TWR slightly above the long-term average after the drought conditions of the first two years. Total autumn rainfall was considerably below the long-term average during the first- and second years following rabbit control and rose to moderately above average in the third year before declining to slightly below average in the fourth year. *Bromus diandrus* is an winter annual grass that reproduces entirely from seed (Cheam 1986, Jackson, et al. 2006). Its seeds, whose dormancy is induced by high summer temperatures, mostly germinate in winter (Gill and Blacklow 1985).

However, occasional drops in temperature following heavy thunderstorms during late summer and early autumn may bring about germination (Cheam 1986). The absence *B. diandrus* from inland dune sites during the first two years following rabbit control was clearly a result of their inability to germinate because of inadequate autumn and winter rainfall. Soil moisture is the overriding factor in controlling germination of non-dormant *B. diandrus* seeds (Cheam 1986). Total winter rainfall was slightly and moderately below and slightly above the long-term average in the first, second- and third years following rabbit control and increased to moderately above average in the fourth.

Adamson (1934) did not observe *B. diandrus* on Robben Island in 1933 and 1934. This was most likely because the alien grass, which is native to the Mediterranean region (Kon, et al. 1988), had not yet been introduced to the island. *Bromus diandrus* is unpalatable to herbivores (van Breda, et al. 1990) and would have dominated vegetation on inland dune sites before rabbit control. In addition, *B. diandrus*, is tall and has deep roots which enable it to shade out and outcompete other species for deeper soil sites (Menke 1992, Jackson, et al. 2006). Furthermore, the grass outcompetes native species for soil moisture by means of early germination and sheer volume of numbers (Menke 1992, Jackson, et al. 2006). Seed production by *B. diandrus* is high, with a single plant capable of producing up to a thousand seeds (Jackson, et al. 2006). Therefore, given constant and average inter-annual rainfall, *B. diandrus* would have dominated vegetation at inland dune sites before rabbit control and persisted in reduced but considerable quantities after control.

Avena fatua and *Capnophyllum africanum*

The emergence of the annual grass *A. fatua* and herb *C. africanum* in the fourth year following rabbit control was clearly in response to increase in TWR to moderately above the long-term average. Total winter rainfall was slightly and moderately below and slightly above the long-term average in the first, second- and third years following rabbit control and increased to moderately above average in the fourth. *Avena fatua* and *C. africanum* are winter annuals that survive seasonal summer stress as dormant seeds (Stubbendieck, et al. 1992, Halvorson, et al. 2003a, Gess, et al. 2014). The seeds germinate during winter after the first autumn rains (Halvorson and Guertin 2003a, Magee, et al. 2009). The absence of *A. fatua* and *C. africanum* from inland dune sites during the first three years following rabbit control was clearly a result of their inability to germinate because of inadequate winter rainfall.

Avena fatua and *C. africanum* require open, sunny sites for germination and growth (Parker and Muller 1982, Halvorson and Guertin 2003a, Magee, et al. 2009). Like the ephemerals *A. arvensis*, *E. peplus*, *H. glabra* at strand sites they would most likely have been restricted to areas with shallower soils where larger and more competitive species could not establish. Shallow soils usually experience drier than normal soil moisture conditions due to enhanced evaporation. As a result, the rise of winter rainfall to slightly above average in the third year following rabbit control could have been insufficient to raise soil moisture to levels suitable for the species to germinate. Only increase in winter rainfall to moderately above the long-term average in the fourth year following rabbit control would have sufficiently raised soil moisture to levels suitable for their germination. The palatable *A. fatua* was absent Robben Island in 1933 and 1934 while the less palatable *C. africanum* occurred in small quantities on coastal-blown sand on the eastern section of the island (Adamson 1934). The alien grass *A. fatua* , which is native to the Mediterranean and Eurasia (Halvorson and Guertin 2003a), could have been absent either because it had not yet been introduced to the island or had been temporarily extirpated by heavy rabbit herbivory. However, *A. fatua* seeds can stay dormant in the soil for 7-8 years, and occasionally over 10 years (Halvorson and Guertin 2003a). *Capnophyllum africanum* is endemic to the Cape Floristic Region where it is confined to deep sandy coastal soils (Magee, et al. 2009). Therefore, the annuals *A. fatua* and *C. africanum* would most likely not have occurred at inland dune sites before and after rabbit control as moisture conditions at the microhabitats available to them would have been too dry for the germination of the plants.

Wahlenbergia androsacea, *Emex australis*, *Ornithoglossum viride*, *Trachyandra* sp., and *Zantedeschia aethiopica*

The disappearance of the five species – *W. androsacea*, *E. australis*, *O. viride*, *Trachyandra* sp. and *Z. aethiopica* – in the first year following rabbit control was clearly linked to cessation of herbivory. This was because, unlike the annual grass *E. longiflora* that disappeared temporarily in the second year following rabbit control and re-emerged afterwards, the six species never re-emerged following their disappearance. Although the species could have initially disappeared in response to worsening drought conditions in the second year following rabbit control, they did not re-emerge like *E. longiflora* once the drought was over. It is therefore reasonable to deduce that their disappearance or failure to re-emerge was directly linked to rabbit control.

While *O. viride* and *Z. aethiopica* are unpalatable to herbivores (Vahrmeijer 1981, Simmonds, et al. 2000, El Mokni and Hédi El Aouni 2012), *W. androsacea*, *E. australis*, and *Trachyandra* sp. are palatable but not well grazed (Shearing, et al. 1994, Simmonds, et al. 2000, du Toit 2002). All five plant species were present at inland dune sites between 1933 and 1934 when the island was overrun with rabbits and the vegetation heavily degraded (Adamson 1934). *Emex australis* and *Trachyandra* sp. occurred widely and abundantly while *O. viride* was equally widespread but less abundant. Although well represented, *Z. aethiopica* occurred in much lower densities, becoming exceedingly abundant in hollows and depressions, and especially at the base of slopes formed by sand dunes. *Wahlenbergia androsacea* occurred rarely, being confined to extremely shallow soils. *Wahlenbergia androsacea*, *E. australis*, *O. viride* and *Trachyandra* sp. are poor competitors for light and as a result require open, disturbed environments to germinate and grow (Adamson 1934, Anon , b, 2022). Likewise, although *Z. aethiopica* is shade tolerant (Adamson 1927, Meek, et al. 2013), it is a poor interspecies competitor for soil moisture (Jackson 1986, Perry 1989, Corr 1993) and also requires open environments for establishment and growth. As a result, the species would have been outcompeted and replaced from inland dune sites by re-emerging and more competitive palatable species following rabbit control.

Sporobolus virginicus

The disappearance of the perennial grass *S. virginicus* in the first year following rabbit control was likely an indirect and transient artifact of prevailing drought conditions. Adamson (1934) did not observe *S. virginicus* in 1933 and 1934 when Robben Island was under heavy rabbit herbivory. *Sporobolus virginicus* is palatable to herbivores (Mfitumukiza 2004) and would have thus been suppressed by heavy rabbit herbivory prior to rabbit control. The palatable grass would have re-emerged during the first year following rabbit control in response to reduced herbivore pressure. However, *S. virginicus* is a poorly competitive pioneer species (Naidoo, et al. 1993). The species' brief emergence following rabbit control was probably facilitated by prevailing drought conditions that would have delayed the response of more competitive palatable species such as the woody shrub *T. fruticosa* and the perennial grass *Ehrharta villosa* to rabbit herbivore control. Therefore, given constant and average inter-annual rainfall, *S. virginicus* would not have occurred at inland dune sites before and after rabbit control. The grass would have been suppressed by herbivory prior to rabbit control and by re-establishing more competitive palatable plant species afterwards.

Phyllobolus canaliculatus and *Asparagus capensis*

The transient emergence of the perennial herb *P. canaliculatus* and woody shrub *A. capensis* in the second year following rabbit control was clearly in response to decline in TWR to moderately below the long-term average. Total winter rainfall was slightly and moderately below and slightly above the long-term average in the first, second- and third years following rabbit control and increased to moderately above average in the fourth. *Phyllobolus canaliculatus* is a deciduous winter-growing perennial succulent that sheds leaves and stems in summer (UWC Cape Flats Indigenous Nursery 2020), while *A. capensis* is a small spiny shrub whose seeds germinate in autumn and winter (Cowell 2013). Although, *P. canaliculatus* and *A. capensis* are drought-resilient, they are poor inter-specific competitors that can only become established on open sunlit ground (Adamson 1934, Fredericks 1998, UWC Cape Flats Indigenous Nursery 2020). The drop in TWR to moderately below the long-term average evidently facilitated the transient occurrence of drought-tolerant *P. canaliculatus* and *A. capensis* plants by inhibiting the growth of other more competitive but drought-intolerant species. *Asparagus capensis* is unpalatable to herbivores (van Breda, et al. 1990) while *P. canaliculatus* is palatable but not well grazed (UWC Cape Flats Indigenous Nursery 2020). However, both species were absent from inland dune sites in 1933 and 1934 when the island was overrun with rabbits and the vegetation heavily degraded (Adamson 1934). Even under conditions of heavy rabbit herbivory the two species appear to have been suppressed by inter-specific competition from other more competitive herbivore-tolerant species. Therefore, given constant and average inter-annual rainfall, *P. canaliculatus* and *A. capensis* would most likely not have occurred at inland dune sites before and after rabbit control because of being outcompeted by co-occurring plant species.

Vulpia myuros, *Isolepis* sp., *Torilis arvensis* and *Anagallis arvensis*

The transient emergence of the annual grass *V. myuros* and annual herbs *Isolepis* sp., *T. arvensis* and *A. arvensis* in the third year following rabbit control was clearly in response to increase in TAUR to moderately above the long-term average. Total autumn rainfall was considerably below the long-term average during the first- and second years following rabbit control and briefly rose to moderately above average in the third year before declining to slightly below average in the fourth year. *Vulpia myuros*, *Isolepis* sp., *T. arvensis* and *A. arvensis* are winter annuals that germinate in autumn (DiTomaso, et al. 2013, Akhter, et al. 2020). Seed germination in *V. myuros*, *T. arvensis* and *A. arvensis* is triggered by sufficient soil moisture, while in *Isolepis* sp. it requires standing water on waterlogged soils (Tshiila 2012, DiTomaso, et al. 2013, Anon 2017a). All four species are short-statured ruderals that occur in open disturbed habitat (Hyde, et al. 2014, South African National Biodiversity Institute 2014, Anon 2017a, Akhter, et al. 2020). As a result, the species were most likely restricted to areas of shallow soil (such as troughs at the bases of sand dunes) where larger and more competitive species could not establish. Shallow soils experience drier than normal soil moisture conditions because of high evaporation rates. Consequently, only the rise of autumn rainfall to moderately above the long-term average in the third year following rabbit control would have been sufficient to raise soil moisture to levels sufficient for the four ruderal species to germinate. *Vulpia myuros T. arvensis* and *A arvensis* were absent from inland dune sites in 1934 while *Isolepis* sp. occurred in small quantities (Adamson 1934). Therefore *V. myuros*, *T. arvensis* and *A. arvensis* would most likely not have occurred at inland dune sites before and after rabbit control given constant and average inter-annual rainfall. *Isolepis* sp., which would have been able to take advantage of temporary water pools after rainfall events, would have maintained low cover before and after rabbit control. The most likely *Isolepis* species to have been present on the island are *Isolepis antarctica* (L.) Roem. Schult. and *Isolepis incomtula* Nees (Adamson 1934).

Ehrharta longiflora

The brief disappearance of the annual grass *E. longiflora* in the second year following rabbit control was clearly in response to decline in TWR to moderately below the long-term average. Total winter rainfall was slightly and moderately below and slightly above the long-term average in the first, second- and third years following rabbit control and increased to moderately above average in the fourth. *Ehrharta longiflora* is a shallow rooted winter annual (Moore and Moore 2007a, Winston, et al. 2014) that reproduces entirely from seeds that germinate following autumn and winter rainfall (Western Australian Herbarium 1998, Bossard, et al. 2000, Moore and Moore 2007a). As the germination of *E. longiflora* seeds is controlled by soil moisture, the failure of their seeds to germinate because of extremely low TWR in the second year following rabbit control would have led to its complete absence.

Ehrharta longiflora, which is palatable to herbivores (Germishuizen, et al. 2003, van Oudtshoorn 2012), was not observed by Adamson (1934) at inland dune sites in 1933 and 1934 when the island was overrun with rabbits. The grass was most likely absent from the sites due to rabbit herbivory and would have re-emerged following rabbit control in response to reduced grazing pressure. However, the positive response of *E. longiflora* to rabbit control would have most likely been limited by availability of suitable microhabitat. The annual grass requires disturbed open sites for successful establishment (Winston, et al. 2014) and such microhabitats were not readily available at inland dune sites following rabbit control. Therefore *E. longiflora* would have been absent from inland dune sites before rabbit control and would have emerged and maintained low cover following their control given constant and average inter-annual rainfall.

Oncosiphon suffruticosum, *Conocosia pugioniformis*, *Ehrharta villosa*, *Tetragonia fruticosa* and *Cissampelos capensis*

Like at strand sites, the five species that occurred persistently - the annual herb *O. suffruticosum*, perennial herb *C. pugioniformis*, perennial grass *E. villosa* and woody shrubs *T. fruticosa* and *C. capensis* - were clearly able to do so because of their ability to withstand the drought conditions of the first two years following rabbit control. The perennial herb *C. pugioniformis* and woody shrub *T. fruticosa* are succulents that are able to store water in their tissue and alternate between CAM and C3 photosynthesis which would allow for growth during periods of high temperature and low water availability (Schmalzer and Hinkle 1987, van Breda and Barnard 1991, Hoffman, et al. 2009). *Tetragonia fruticosa* has a fairly well-developed root system (van Breda and Barnard 1991) while *C. pugioniformis* has large, fleshy taproots (Schmalzer and Hinkle 1987). The perennial grass *E. villosa*, annual herb *O. suffruticosum* and woody shrub *C. capensis* are also adapted to withstand drought conditions (Adamson 1934, Rudman 2003, Anon 2014). *Ehrharta villosa* regenerates from rhizome fragments and has deep root systems that access soil moisture from deep below the soil surface (Hodder 1997, Harrington, et al. 1998). *Oncosiphon suffruticosum* is well adapted to semi-arid conditions (Anon 2014). Late germinating *O. suffruticosum* plants remain vegetative and survive the summer to flower in the following season (Moore and Moore 2007b). *Cissampelos capensis* is a drought resistant shrub (Hoot, et al. 2009) that retains its leaves throughout the year (Adamson 1934) and has deep rooted rhizomes (de Wet, et al. 2002). As a result, the change in cover of the species following rabbit control most likely reflected direct response to cessation of rabbit herbivory pressure.

Oncosiphon suffruticosum, *C pugioniformis*, *E. villosa*, *T. fruticosa* and *C. capensis* occurred at inland dune sites on Robben Island in 1933 and 1934 when the island was overrun with rabbits (Adamson 1934). *Oncosiphon suffruticosum*, which is unpalatable to herbivores (Le Roux 2005, Anon 2014, Western Australian Herbarium 2022) and *C. pugioniformis*, which is less palatable (Louw and Beukes 1988, South African National Biodiversity Institute 2022), occurred abundantly at the sites. *Tetragonia fruticosa* which is highly palatable (Gillham 1963, van Breda and Barnard 1991, Todd 2000) and *E. villosa*, and *C. capensis* which are palatable but not well grazed (Louw and Beukes 1988, van Breda and Barnard 1991, de Villiers, et al. 2001, Germishuizen and Meyer 2003) were sparse (Adamson 1934). *Oncosiphon suffruticosum*, *C. pugioniformis*, and *C. capensis* are poor inter-species competitors that occur in disturbed open localities where grasses or perennial vegetation has been reduced, especially by heavy grazing (Schmalzer and Hinkle 1987, Anon 2014). *Ehrharta villosa* and *T. fruticosa* are aggressive inter-species competitors on deep sandy habitats. *Ehrharta villosa* is a coastal dune specialist (Verboom, et al. 2003) that reacts positively to sand burial (Hertling 1997). The deep rhizome system of *E. villosa* allows it to access water from deep below the soil surface (Harrington, et al. 1998). *Tetragonia fruticosa* also has a well-developed root system with a tap root that penetrates the soil to a considerable depth (van Breda and Barnard 1991). Furthermore, *Ehrharta villosa* has long stems (often to a height of 2 m or more) which allow the plant to overshadow surrounding vegetation (Harrington, et al. 1998). Release from herbivory following control or eradication of herbivores would have allowed *E. villosa* and *T. fruticosa* to recover their competitive ability and increase in cover. The increase in cover of *E. villosa* and *T. fruticosa* would have led to a decrease in abundance of O. *suffruticosum* and *C. pugioniformis* and prevented an increase in cover of *C. capensis* in response to rabbit control. Therefore, given constant and average inter-annual rainfall, the cover of *E. villosa* and *T. fruticosa* would have increased, while that of *O. suffruticosum* and *C. pugioniformis* decreased following rabbit control. *Cissampelos capensis* would have maintained a low constant cover.

References

Adamson RS. 1927. The plant communities of Table Mountain: preliminary account. *Journal of Ecology* 15: 278-309.

Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

Akhter MJ, Jensen PK, Mathiassen SK, Melander B, Kudsk P. 2020. Biology and management of *Vulpia myuros* - An emerging weed problem in No-Till Cropping Systems in Europe. *Plants (Basel, Switzerland)* 9: 715.

Anon 2014. Declared Plant Policy under the Natural Resources Management Act 2004. Calomba daisy (*Oncosiphon suffruticosum*). Government of South Australia.

Anon. 2017a. *Anagallis arvensis* (scarlet pimpernel). CABI Invasive Species Compendium. Available at http://www.cabi.org/isc/datasheet/5352. [accessed 15 September 2017]

Anon. 2017b. *Emex australis* (Doublegee). CABI Invasive Species Compendium. Available at http://www.cabi.org/isc/datasheet/20826. [accessed 15 September 2017]

Anon. 2017c. *Euphorbia peplus*. Identic Pty Ltd. Available at https://keyserver.lucidcentral.org/weeds/data/media/Html/euphorbia_peplus.htm. [accessed 15 September 2017]

Anon. 2017d. Flora of North America. *Hypochaeris glabra* Linnaeus. eFlora.org. Available at http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=250005015. [accessed 15 September 2017]

Anon. 2017e. *Moraea collina* (Cape tulip). CABI. Available at http://www.cabi.org/isc/datasheet/110455. [accessed 15 September 2017]

Anon. 2017f. *Sonchus oleraceus* (common sowthistle). CABI Invasive Species Compendium. Available at http://www.cabi.org/isc/datasheet/50584. [accessed 15 September 2017]

Anon. 2017g. *Wahlenbergia androsacea* A. DC.: Encyclopedia of Life. Available at http://www.eol.org/pages/5134842/overview. [accessed 15 September 2017]

Anon. 2022. Bihrmann's Caudiforms: *Ornithoglossum viride*. Available at http://www.bihrmann.com/caudiciforms/subs/orn-vir-sub.asp. [accessed 20 June 2022]

Anon. n.d.-a. *Asparagus capensis*. JSTOR Global Plants. Available at https://plants.jstor.org/compilation/asparagus.capensis. [accessed 15 September 2017]

Anon. n.d.-b. *Moraea collina*. Hortipedia. The GardenInfoPortal. Available at http://en.hortipedia.com/wiki/Moraea_collina#Characteristics. [accessed 15 September 2017]

Anon. n.d.-c. *Spergula arvensis* (corn spurry). CABI Invasive Species Compendium. Available at http://www.cabi.org/isc/datasheet/50838. [accessed 15 September 2017]

Arnone II JA, Kestenholz C. 1997. Root competition and elevated CO_2: effects on seedling growth in *Linum usitatissimum* populations and *Linum–Silene cretica* mixtures. *Functional Ecology* 11: 209-214.

Barrett-Lennard. 2003. *Saltland Pastures in Australia*. Canberra: Land & Water Australia.

Bidwell S, Attiwill PM, Adams MA. 2006. Nitrogen availability and weed invasion in a remnant native woodland in urban Melbourne. *Austral Ecology* 31: 262-270.

Blasi C, Capotorti G, Copiz R, Guida D, Mollo B, Smiraglia D, Zavattero L. 2014. Classification and mapping of the ecoregions of Italy. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* 148: 1255-1345.

Bossard CC, J.M. R, Hoshovsky MC. 2000. *Invasive plants of California's wildlands*. Berkeley: University of California Press.

Brown K, Brooks K. 2002. *Bushland weeds. A practical guide to their management. With case studies from the Swan Coastal Plain and beyond*. Perth: Environmental Weeds Action Network (Inc).

Bullock AA. 1952. South African poisonous plants. *Kew Bulletin* 7: 117-129.

Burrows CJ, Wilson HD, Meurk CD. 1999. The ecological restoration of Otamahua/Quail Island 2. The vascular land flora and vegetation. *New Zealand Natural Sciences* 24: 127-150.

Cheam AH. 1986. Patterns of change in seed dormancy and persistence of *Bromus diandrus* Roth. (Great brome) in the field. *Australian Journal of Agricultural Research* 37 471-481.

Christodoulakis D. 1996. The Flora of Ikaria (Greece, E. Aegean Islands). *Phyton (Horn, Austria)* 36: 63-91.

Coetzee K. 2008. Blaauwberg Conservation Area: management guidelines for larger wildlife and their habitats. *Report prepared for the Biodiversity Management Branch, City of Cape Town*.

Corr BE. 1993. *Zantedeschia* research in the United States: past, present and future. *Acta Horticulturae* 337: 177-188.

Cowan IA. 1945. The ecological relationship of the food of the Columbian black-tailed deer, *Odocoileus hemionus columbianus* (Richardson), in the coast forest region of Southern Vancouver Island, British Columbia. *Ecological Monographs* 15: 109-139.

Cowell CR. 2013. Investigating the most favourable seed establishment methods for restoring Sand Plain Fynbos on old fields. MTH, Cape Peninsula University of Technology, Cape Town.

Crawley MJ. 1990. Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology* 27: 803-820.

de Villiers AJ, van Rooyen MW, Theron GK. 2001. Seedbank phytosociology of the Strandveld Succulent Karoo, South Africa: a pre-mining benchmark survey for rehabilitation. *Land Degradation and Development* 12: 119-130.

de Wet H, Tilney PM, van Wyk BE. 2002. Vegetative morphology and anatomy of *Cissampelos* in South Africa. *South African Journal of Botany* 68: 181-190.

DiTomaso JM, Kyser GB, Oneto SR, Wilson RG, Orloff SB, Anderson LW, Wright SD, Roncoroni JA, Miller TL, Prather TS (eds). 2013. *Weed control in natural areas in the Western United States*. Weed Research and Information Center, University of California. Davis.

du Toit PCV. 2002. Objektiewe weidingswaardes van Nama-Karooplantegroei, grasse en bossies van die Karoo. *Grootfontein Agric* 4: 8-18.

El Mokni R, Hédi El Aouni M. 2012. *Zantedeschia aethiopica* (Araceae) a new species naturalized in the Northwest of Tunisia. *Flora Mediterranea* 22: 191-196.

Esler AE. 1980. Botanical features of Motutapu, Motuihe, and Motukorea, Hauraki Gulf, New Zealand. *New Zealand Journal of Botany* 18: 15-36.

Esler AE. 1987. The naturalisation of plants in urban Auckland, New Zealand 3. Catalogue of naturalised species. *New Zealand Journal of Botany* 25: 539-558.

Farrow EP. 1917. On the ecology of the vegetation of Breckland. III. General effects of rabbits on the vegetation. *Journal of Ecology* 5: 1-18.

Fisher JL, Loneragan WA, Dixon K, Veneklaas EJ. 2009. Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. *Biological Conservation* 142: 256-269.

Fredericks F (ed). 1998. *Vegetation of Robben Island*. University of the Western Cape.

Freeman D, Balcom J, Chmielewski J. 2021. Genus: *Phyllobolus*. Available at https://www.succulentguide.com/cactus/?genus=Phyllobolus [accessed 22 March 2021]

Germishuizen G, Meyer NL. 2003. *Plants of southern Africa: an annotated checklist*. Pretoria: National Botanical Institute.

Gess SK, Gess FW. 2014. *Wasps and bees in southern Africa*. Pretoria: South African National Biodiversity Institute.

Gill GS, Blacklow WM. 1985. Variations in seed dormancy and rates of development of Great Brome, *Bromus diandru*s Roth., as adaptations to the climates of southern Australia and implications for weed control. *Australian Journal of Agricultural Research* 36: 295-304.

Gillham ME. 1963. Some interactions of plants, rabbits and sea-birds on South African islands. *Journal of Ecology* 51: 275-294.

Halvorson WL, Guertin P. 2003a. Factsheet for: *Avena fatua* L. . *USGS Weeds in the West project: status of introduced plants in Southern Arizona parks*. Tucson: U.S. Geological Survey / Southwest Biological Center.

Halvorson WL, Guertin P (eds). 2003b. *Factsheet for: Cynodon dactylon (L.) Pers.* U.S. Geological Survey / Southwest Biological Center. Tucson.

Harrington KC, Hodder LM, Outred HA. 1998. Biology and control of pypgrass. Paper presented at the Proceedings of the 51st New Zealand Plant Protection Conference.

Hertling UM. 1997. *Ammophila arenaria* (l.) Link (Marram grass) in South Africa and its potential invasiveness. DPhil, Rhodes University, Grahamstown.

Hodder LM. 1997. The biology and control of *Ehrharta villosa*, South African pypgrass. MSc, Massey University.

Hoffman MT, Carrick PJ, Gillson L, West AG. 2009. Drought, climate change and vegetation response in the succulent karoo, South Africa. *South African Journal of Science* 105: 54-61.

Hoot SB, Zautke H, Harris DJ, Crane PR, Neves SS. 2009. Phylogenetic patterns in Menispermaceae based on multiple chloroplast sequence data. *Systematic Botany* 34: 44-56.

Hyde IIA, Wursten BT, Ballings P. 2014. *Torilis arvensis* (Huds.) Link Available at http://www.zimbabweflora.co.zw/speciesdata/species.php?speciesid=143050 [accessed 22 January 2023]

Jackson N, Cudney D, DiTomaso J, C. B, Lee V, Drewitz J, Bossard S, Randall L, Hansen-Winter B, Faber P, *et al.* 2006. *Invasive plants of California's wildland*. California Invasive Plant Council.

Jackson WPU. 1986. The Cape white arum lily, *Zantedeschia aethiopica*. *Veld & Flora* 72: 44-45.

Jones K, Hanna E. 2004. Design and implementation of an ecological engineering approach to coastal restoration at Loyola Beach, Kleberg County, Texas. *Ecological Engineering* 22: 249-261.

Knevel IC. 2001. The life history of selected coastal foredune species of South Africa. DPhil, Rhodes University.

Kon KF, Blacklow WM. 1988. Identification, distribution and population variability of Great brome (*Bromus diandrus* Roth) and Rigid brome (*Bromus rigidus* Roth). *Australian Journal of Agricultural Research* 39 1039-1050.

Latzel V, Malíková L, Klimešová J. 2011. Compensatory growth of *Euphorbia peplus* regenerating from a bud bank. *Botany* 89: 313-321.

Le Roux A. 2005. *Namaqualand – South African Wild Flower Guide 1*. Cape Town: Botanical Society of South Africa.

Lloyd JW, Linger MT. 1986. Report on the vegetation of Robben Island. *'n Natuurbewaringsondersoek van Robbeneiland*. Cape Town: Cape Nature

Louw G, Beukes T. 1988. Ken ons veldplante. *Die Noordwester*: 6-12.

Magee AR, van Wyk BE, Tilney PM, Downie SR. 2009. A taxonomic revision of *Capnophyllum* (Apiaceae: Apioideae). *South African Journal of Botany* 75: 283-291.

Manning J, Paterson-Jones C. 2008. *Field Guide to Fynbos* (2nd edn). Cape Town: Struik Publishers Ltd.

Marcum KB, Murdoch CL. 1992. Salt tolerance of the coastal salt marsh grass, Sporobolus virginicus (L.) kunth. *New Phytologist* 120: 281-288.

Martin GR, Twigg LE, Lena Z. 2007. Seasonal changes in the diet of the European rabbit (*Oryctolagus cuniculus*) from three different Mediterranean habitats in south-western Australia. *Wildlife Research* 34: 25-42.

Masters DG, Benes SE, Norman HC. 2007. Biosaline agriculture for forage and livestock production. *Agriculture, Ecosystems & Environment* 119: 234-248.

Meek CS, Richardson DM, Mucina L. 2013. Plant communities along the Eerste River, Western Cape, South Africa: Community descriptions and implications for restoration. *Koedoe* 55: 1-14.

Menke JW. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia* 20: 22-25.

Mfitumukiza D. 2004. Evaluating rangeland potentials for cattle grazing in a mixed farming system. MSc, International Institute for Geo-Information Science and Earth Observation, Enschede.

Moore CB, Moore JH. 2007a. Annual veldgrass: *Ehrarta longiflora* Smith. HerbiGuide - The Pesticide Expert on a Disk Available at http://www.herbiguide.com.au/Descriptions/hg_Annual_Veldtgrass.htm. [accessed 25 September 2017]

Moore CB, Moore JH. 2007b. Colombia Daisy: *Oncosiphon suffruticosum* (L.) Kallersjo. HerbiGuide - The Pesticide Expert on a Disk. Available at http://www.herbiguide.com.au/Descriptions/hg_Colomba_Daisy.htm. [accessed 25 September 2017]

Myers K, Poole WE. 1963. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations IV. The effects of rabbit grazing on sown pastures. *Journal of Ecology* 51: 435-451.

Naidoo G, Mundree SG. 1993. Relationship between morphological and physiological responses to waterlogging and salinity in *Sporobolus virginicus* (L.) Kunth. *Oecologia* 93: 360-366.

Papini A, Signorini MA, Foggi B, Della Giovampaola E, Ongaro L, Vivona L, Santosuosso U, Tani C, Bruschi P. 2017. History vs. legend: Retracing invasion and spread of *Oxalis pes-caprae* L. in Europe and the Mediterranean area. *PLOS ONE* 12: e0190237.

Parker VT, Muller CH. 1982. Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. *American Midland Naturalist* 107: 69-81.

Perry PL. 1989. A new species of *Zantedeschia* (Araceae) from the western Cape. *South African Journal of Botany* 55: 447-451.

Rivero R, Zabala A, Gianneechini R, Gil J, Moraes J. 2001. *Anagallis arvensis* poisoning in cattle and sheep in Uruguay. *Veterinary and Human Toxicology* 43: 27–30.

Rothwell JT, Marshall DJ. 1986. Suspected poisoning of sheep by *Anagallis arvensis* (scarlet pimpernel). *Australian veterinary journal* 63: 316–316.

Rudman T 2003. Tasmanian beach weed strategy for marram grass, sea spurge, sea wheatgrass, pyp grass and beach daisy. Nature Conservation Branch, Department of Primary Industries, Water and Environment, Tasmania.

Schmalzer PA, Hinkle CR (eds). 1987. *Species biology and potential for controlling four exotic plants (Ammophila Arenaria, Carpobrotus Edulis, Cortaderia Jubata, And Gasoul Crystallinum) on Vandenberg Air Force Base, California*. National Aeronautics and Space Administration, John F. Kennedy Space Center. Florida.

Scott JK, Neser S. 1996. Prospects for the biological control of the environmental weed, *Zantedeschia aethiopica* (arum lily). Paper presented at the Proceedings of the 11th Australian Weeds Conference, Melbourne, Australia, 30 September-3 October.

Shearing D, van Heerden K. 1994. *Karoo: South African wild flower guide 6*. Kisternbosch: Botanical Society of South Africa.

Sherley RB. 2016. Unusual foraging behaviour in two introduced mammals following degradation of their island habitat. *Biodiversity Observations* 7: 1-10.

Simmonds H, Holst P, Bourke C. 2000. *The palatability, and potential toxicity of Australian weeds to goats*. Kingston: Rural Industries Research and Development Corporation.

South African National Biodiversity Institute. 2014. *Isolepis* R.Br. Available at https://www.plantzafrica.com/planthij/isolepsis.html. [accessed 25 May 2022]

South African National Biodiversity Institute. 2022. *Conicosia pugioniformis* (L) N.E.Br subsp. *pugioniformis*. SANBI. Available at http://pza.sanbi.org/. [accessed 12 January 2022]

Struik GJ. 1967. Growth habits of dandelion, daisy, catsear, and hawkbit in some New Zealand grasslands. *New Zealand Journal of Agricultural Research* 10: 331-344.

Stubbendieck J, Hatch SL, Butterfield CH. 1992. *North American Range Plants*. Lincoln, Nebraska: University of Nebraska Press.

Tainton NM, Bransby DI, Booysen Pd. 1990. *Common veld and pasture grasses of Natal* (2nd edn). Pietermaritzburg: Shuter and Shooter.

Todd SW. 2000. Patterns of seed production and shrub association in two palatable Karoo shrub species under contrasting land use intensities. *African Journal of Range and Forage Science* 17: 22-26.

Toelken HR. 1981. The species of *Crassula* L. in Australia. *Journal of the Adelaide Botanic Garden* 3: 57-90.

Tshiila AA. 2012. Systematics of *Finicia* clade (Cyperaceae). MSc, University of Cape Town, Cape Town.

UWC Cape Flats Indigenous Nursery. 2020. UWC Nature Reserve: *Phyllobolus canaliculatus*. Available at https://uwccfnursery.blogspot.com/2020/05/phyllobolus-canaliculatus [accessed 13 January 2022]

UWC Cape Flats Indigenous Nursery. 2021. Propagating *Phyllobolus canaliculatus* (Vingerkanna). Available at https://www.pinterest.co.uk/pin/593490057135262691/ [accessed 22 March 2021]

Vahrmeijer J. 1981. *Gifplante van Suider-Afrika wat veeverliese veroorsaak*. Kaapstad: Tafelberg Uitgewers Beperk.

van Breda PAB, Barnard SA. 1991. *100 veld plants of the winter rainfall region: A guide to the use of veld plants for grazing*. Pretoria: Department of Agricultural Development.

van Breda PAB, Nel EJ, Bayer MB (eds). 1990. *Palatability of plant species – winter rainfall region: Little Karoo and Ceres Karoo* Elsenburg Agricultural Development Institute

van Dyne GM, Heady HF. 1965. Botanical composition of sheep and cattle diets on a mature annual range. *Hilgardia* 36: 465-492.

van Leeuwen CG, van der Maarel E. 1971. Pattern and process in coastal dune vegetations. *Acta Bot. Neerl.* 20 191-197.

van Oudtshoorn F. 2012. *Guide to grasses of southern Africa*. Pretoria: Briza Publications.

Verboom GA, Linder HP, Stock WD. 2003. Pylogenetics of the grass genus *Ehrarta*: evidence for radiation in the summer-arid zone of the South African Cape. *Evolution* 57: 1008-1021.

Verdaguer D, Sala A, Vilà M. 2010. Effect of environmental factors and bulb mass on the invasive geophyte *Oxalis pes-caprae* development *Acta Oecologica* 36: 92–99.

Vilà M, Bartomeus I, Gimeno I, Traveset A, Moragues E. 2006. Demography of the invasive geophyte *Oxalis pes-caprae* across a Mediterranean island. *Annals of Botany* 97: 1055–1062.

Vural M, Dönmez AA. 2002. Two new taxa of *Silene* (Caryophyllaceae) from Turkey. *Annales Botanici Fennici* 39: 153-158.

Western Australian Herbarium. 1998. FloraBase - the Western Australian Flora. Department of Parks and Wildlife. Available at https://florabase.dpaw.wa.gov.au. [accessed 22 March 2021]

Western Australian Herbarium. 2022. *Oncosiphon suffruticosum* (L.) Kallersjo. Available at https://florabase.dpaw.wa.gov.au [accessed 12 January 2022]

Williams AR. 2007. *Puccinellia* (Poaceae) in Western Australia. *Nuytsia* 16: 435-467.

Williams B, Wells TCE, Wells DA. 1974. Grazing management of Woodwalton Fen: seasonal changes in the diet of cattle and rabbits. *Journal of Applied Ecology* 11: 499-516.

Winston R, DesCamp W, Andreas J, Randall CB, Milan J, Schwarzländer M. 2014. *New invaders of the Southwest*. Washington, DC: Forest Health Technology Enterprise Team, United States Department of Agriculture.

ANNEXURE VIII: CHAPTER 5 — SUPPLEMENTARY MATERIAL 1

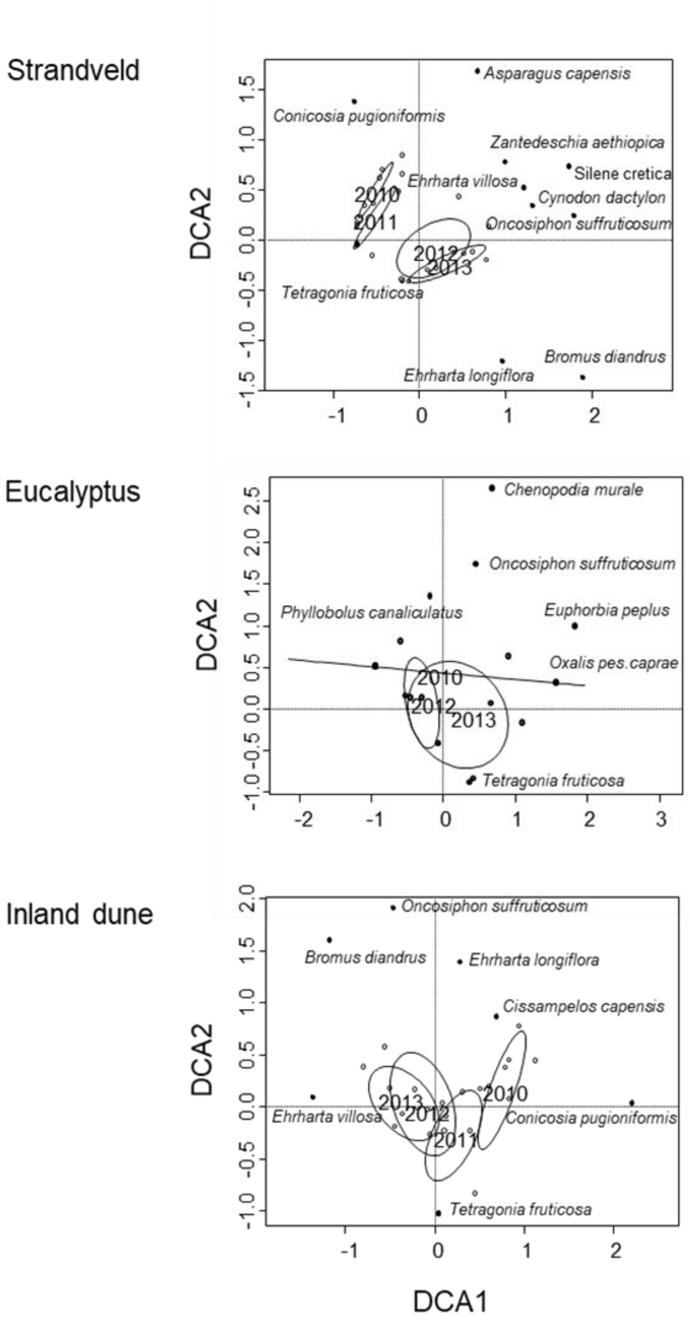
Table S1 Palatability classes for plant species sampled from Robben Island following the control of invasive alien European rabbits.

Species	Family	Growth Form	Palatability	References
Anagallis arvensis L.	Primulaceae	Annual herb	Unpalatable	(Rothwell, et al. 1986, Rivero, et al. 2001, Germishuizen, et al. 2003)
Asparagus capensis L.	Asparagaceae	Perennial shrub	Unpalatable	(van Breda, et al. 1990)
Atriplex cinerea Poir.	Amaranthaceae	Perennial erect to spreading shrub	Less palatable	(Simmonds, et al. 2000, Moore 2001, Western Australian Herbarium 2022a)
Avena fatua L.	Poaceae	Annual erect, tufted, or ascending grass	Palatable	(van den Berg, et al. 2009, van Oudtshoorn 2012, BioNet-EAFRINET 2022a)
Bromus diandrus Roth.	Poaceae	Annual graminoid	Unpalatable	(van Breda, et al. 1990, Germishuizen and Meyer 2003, Coetzee 2008)
Capnophyllum africanum (L.) Gaertn.	Apiaceae	Annual herb	Less palatable	(Germishuizen and Meyer 2003, Western Australian Herbarium 2022b)
Cissampelos capensis L.f.	Menispermaceae	Perennial climber herb shrub	Less palatable	(van Breda, et al. 1990, Germishuizen and Meyer 2003)
Cynodon dactylon (L.) Pers.	Poaceae	Perennial graminoid	Less palatable	(van Breda, et al. 1990, Simmonds, et al. 2000, Germishuizen and Meyer 2003)
Chenopodium murale L.	Amaranthaceae	Annual herb	Unpalatable	(Heneidy 2002)
Crassula natans Thunb.	Crassulaceae	Annual (occ. perennial) hydrophyte succulent	Unpalatable	(Gillham 1963, van Breda, et al. 1990, Germishuizen and Meyer 2003)

Conicosia pugioniformis (L.) N. E. Br.	Aizoaceae	Perennial tufted succulent herb	Less palatable	(Louw, et al. 1988, South African National Biodiversity Institute 2022)
Crassula sp.	Crassulaceae	Annual (occ. perennial) hydrophyte succulent	Unpalatable	(Gillham 1963, van Breda, et al. 1990, Germishuizen and Meyer 2003)
Dittrichia graveolens (L.) Greuter	Compositae	Annual erect, bushy, viscid aromatic herb	Unpalatable	(Brownsey, et al. 2013, Western Australian Herbarium 2022c)
Emex australis Steinh.	Polygalaceae	Annual herb	Less palatable	(Simmonds, et al. 2000, Germishuizen and Meyer 2003)
Ehrharta longiflora Sm.	Poaceae	Annual graminoid	Palatable	(Germishuizen and Meyer 2003, van Oudtshoorn 2012)
Euphorbia peplus L.	Euphorbiaceae	Annual (occ. Perennial) herb	Unpalatable	(Bullock 1952, Gillham 1963, Simmonds, et al. 2000, Germishuizen and Meyer 2003)
Ehrharta villosa Schult.f.	Poaceae	Perennial graminoid	Less palatable	(Louw and Beukes 1988, Germishuizen and Meyer 2003)
Helichrysum patulum (L.) D. Don	Compositae	Perennial straggling shrublet	Unpalatable	(BioNet-EAFRINET 2022b)
Hypochaeris glabra L.	Compositae	Annual rosette herb	Less palatable	(Cowan 1945, van Dyne, et al. 1965, Struik 1967, Global Biodiversity Information Facility (GBIF) 2022)
Isolepis sp. (I. antartica/I. incomtula)	Cyperaceae	Annual helophyte herb	Less palatable	(Germishuizen and Meyer 2003)
Moraea collina Thunb.	Iridaceae	Perennial geophyte herb	Unpalatable	(van Breda, et al. 1990, Germishuizen and Meyer 2003)

Oxalis pes-caprae L.	Oxalidaceae	Perennial geophyte	Less palatable	(Simmonds, et al. 2000, Germishuizen and Meyer 2003, Vilà, et al. 2006)
Oncosiphon suffruticosum (L.) Kallersjo	Compositae	Annual erect, aromatic herb	Unpalatable	(Le Roux 2005, Western Australian Herbarium 2022d)
Ornithoglossum viride (L.f.) Dryland. Ex W.T.Aiton	Colchicaceae	Perennial geophyte	Unpalatable	(Vahrmeijer 1981, Germishuizen and Meyer 2003)
Phyllobolus canaliculatus (Haw.) Bittrich	Aizoaceae	Perennial branched succulent geophyte	Less palatable	(UWC Cape Flats Indigenous Nursery 2020)
Spergula arvensis L.	Caryophyllaceae	Annual herb	Unpalatable	(Reader, et al. 1981, Native Plant Trust 2022)
Silene cretica L.	Caryophyllaceae	Annual herb	Less palatable	(Germishuizen and Meyer 2003)
Sonchus oleraceus (L.) L.	Compositae	Annual herb	Palatable	(Lewin 1948, Simmonds, et al. 2000)
Sporobolus virginicus (L.) Kunth	Poaceae	Perennial graminoid	Palatable	(Germishuizen and Meyer 2003, Mfitumukiza 2004)
Torilis arvensis (Huds.) Link	Apiaceae	Annual herb	Palatable	(Esler 1980, Germishuizen and Meyer 2003)
Tetragonia fruticosa L.	Aizoaceae	Perennial dwarf shrub	Highly palatable	(van Breda, et al. 1990, Germishuizen and Meyer 2003)
Trachyandra sp.	Xanthorrhoeaceae	Perennial tuberous or rhizomatous succulent shrublets	Less palatable	(Shearing, et al. 1994, Simmonds, et al. 2000)
Vulpia myuros (L.) C.C.Gmel	Poaceae	Annual graminoid	Less palatable	(Scott, et al. 1987)
Wahlenbergia androsacea A.DC.	Campanulaceae	Annual herb	Less palatable	(du Toit 2002, Germishuizen and Meyer 2003)

Zantedeschia aethiopica (L.) Spreng.	Araceae	Perennial geophyte herb	Unpalatable	(Simmonds, et al. 2000, Germishuizen and Meyer 2003, El Mokni, et al. 2012)



Strandveld

Eucalyptus

Inland dune

Figure S1 Detrended Correspondence Analysis (DCA) plots showing change in plant species composition on Robben Island following the control of European rabbits. Axes units are standard deviations (SD) of compositional change (4 SD units represent a complete compositional turnover; see Correa-Metrio, et al. 2014 for more details).

Table S2 Change in mean plant species forage production (kg DM ha^{-1} y^{-1}) following the control of invasive alien European rabbits on Robben Island. Only species with significant ($P \leq 0.05$) differences across years and contributed ≥ 5 kg DM ha^{-1} y^{-1} to overall change in actual forage production shown. Significant differences determined using Friedman/Wilcoxon two-sample paired tests. FDR-adjusted *P* values (classical one-stage method) provided for reference.

Sites	Species	Years				Test static Chi^2/W	*P* value	FDR adjusted *P*
		2010	2011	2012	2013			
Strand	**Annual grasses**							
	Ehrharta longiflora	0	0	68.58 ± 14.81	102.87 ± 12.91	17.00	0.219	0.306
	Perennial grasses							
	Sporobolus virginicus	8.30 ± 5.67	0	0	0	-	-	-
	Ehrharta villosa	0	1.11 ± 1.11	14.38 ± 9.45	16.59 ± 12.09	1.65	0.162	0.283
	Annual herbs							
	Silene cretica	0	0	12.17 ± 7.55	9.96 ± 4.77	4.00	0.750	0.875
	Perennial herbs							
	Conicosia pugioniformis	29.86 ± 6.35	6.64 ± 3.43	7.74 ± 4.34	9.96 ± 6.35	9.70	0.002	0.013
	Woody shrubs							
	Tetragonia fruticosa	338.48 ± 37.51	597.32 ± 87.92	627.18 ± 110.14	577.40 ± 114.03	7.95	0.035	0.122
Eucalyptus	**Annual grasses**							
	Ehrharta longiflora	0	0	2.77 ± 2.77	5.53 ± 5.53	2.00	1.000	1.000
	Annual herbs							
	Oxalis pes-caprae	1.11 ± 1.11	0	1.11 ± 1.11	9.96 ± 3.37	4.25	0.042	0.083
	Perennial herbs							
	Phyllobolus canaliculatus	2.21 ± 1.40	2.21 ± 2.21	28.76 ± 10.93	27.65 ± 19.94	9.35	0.003	0.013
	Woody shrubs							
	Tetragonia fruticosa	0	0	89.60 ± 40.07	199.10 ± 108.69	14.00	0.531	0.708

Inland dune	**Annual grasses**							
	Ehrharta longiflora.	8.30 ± 8.30	0	2.77 ± 2.77	24.89 ± 11.13	4.25	0.042	0.058
	Avena fatua	0	0	0	16.59 ± 10.49	-	-	-
	Perennial grasses							
	Ehrharta villosa	3.32 ± 3.32	19.91 ± 9.39	67.48 ± 29.85	120.57 ± 47.13	6.95	0.033	0.058
	Perennial herbs							
	Conicosia pugioniformis	38.71 ± 5.79	8.85 ± 5.33	8.85 ± 7.60	11.06 ± 4.74	7.80	0.029	0.058
	Woody shrubs							
	Tetragonia fruticosa	243.90 ± 97.67	562.47 ± 141.65	721.75 ± 131.64	627.18 ± 103.17	13.95	< 0.001	0.002

Table S3 Relationship between inter-annual rainfall variation and plant species actual forage production following the control of invasive alien European rabbits on Robben Island. Significant differences ($P \leq 0.05$) determined using Rao's *F* statistic and *t*-tests.

Site	Life form/Species	Multivariate Multiple Regressions														
		Overall Rainfall			TSUR				TAUR				TWR			
		R^2	*F*	*P*	R^2	Coeff	*t*	*P*	R^2	Coeff	*t*	*P*	R^2	Coeff	*t*	*P*
Strand	**Annual grasses**															
	Ehrharta longiflora	1.00	2070.00	< 0.001	0.79	-2.305	-7.64	< 0.001	0.95	7.201	35.45	< 0.001	0.65	21.106	14.22	< 0.001
	Perennial grasses															
	Sporobolus virginicus	0.27	2.49	0.090	-	-	-	-	-	-	-	-	-	-	-	-
	Ehrharta villosa	0.14	1.05	0.394	-	-	-	-	-	-	-	-	-	-	-	-
	Annual herbs															
	Silene cretica	0.33	3.27	0.042	0.26	-0.870	-0.27	0.791	0.31	3.052	1.40	0.177	0.21	8.327	0.52	0.607
	Perennial herbs															
	Conicosia pugioniformis	0.27	2.42	0.096	-	-	-	-	-	-	-	-	-	-	-	-
	Woody shrubs															
	Tetragonia fruticosa	0.30	2.79	0.067	-	-	-	-	-	-	-	-	-	-	-	-
Eucalyptus	**Annual grasses**															
	Ehrharta longiflora	0.09	0.67	0.580	-	-	-	-	-	-	-	-	-	-	-	-
	Annual herbs															
	Oxalis pes-caprae	0.39	4.20	0.019	0.15	-3.267	-1.74	0.097	0.09	1.617	1.15	0.263	0.29	14.490	2.77	0.012
	Perennial herbs															
	Phyllobolus canaliculatus	0.47	5.93	0.005	0.40	2.433	1.06	0.301	0.44	1.343	0.78	0.443	0.22	-5.411	-0.85	0.407
	Woody shrubs															
	Tetragonia fruticosa	0.61	10.48	< 0.001	0.48	-3.073	-1.20	0.245	0.53	4.867	2.53	0.020	0.44	13.338	1.86	0.077
Inland dune	**Annual grasses**															

Ehrharta longiflora	0.33	3.33	0.040	0.13	-4.316	-1.46	0.160	0.07	1.735	0.83	0.415	0.25	27.531	2.40	0.026
Avena fatua	0.42	4.91	0.010	0.09	-5.389	-2.62	0.016	0.07	2.665	1.84	0.081	0.22	27.000	3.39	0.003
Perennial grasses															
Ehrharta villosa	0.28	2.55	0.085	-	-	-	-	-	-	-	-	-	-	-	-
Perennial herbs															
Conicosia pugioniformis	0.39	4.18	0.019	< 0.01	1.252	0.43	0.674	0.14	-5.088	-2.46	0.023	0.01	10.668	0.94	0.358
Woody shrubs															
Tetragonia fruticosa	0.21	1.72	0.194	-	-	-	-	-	-	-	-	-	-	-	-

Table S4 Durbin-Watson tests for serial autocorrelation in relationships between inter-annual rainfall variation, grazing capacity change and plant species actual forage production following control of invasive alien European rabbits on Robben Island. Durbin-Watson (DW) statistics close to 0 represent positive autocorrelation, 2- no autocorrelation and 4- negative autocorrelation. Only results for significant ($P \leq 0.05$) regressions (see Table 5.3 in the main text and Table S3 above) shown.

Sites	Life form/species	Rainfall					
		TSUR		TAUR		TWR	
		DW	*P*	DW	*P*	DW	*P*
Strand		-	-	2.05	0.541	-	-
	Annual grasses						
	Ehrharta longiflora	0.71	< 0.001	0.68	< 0.001	0.70	<0.001
Eucalyptus		-	-	1.62	0.159	1.78	0.290
	Annual herbs						
	Oxalis pes-caprae	-	-	-	-	0.73	<0.001
	Woody shrubs						
	Tetragonia fruticosa	-	-	0.67	< 0.001	-	-
Inland dune		-	-	2.79	0.979	-	-
	Annual grasses						
	Ehrharta longiflora	-	-	-	-	2.09	0.583
	Avena fatua	1.36	0.047	-	-	1.51	0.103
	Perennial grasses						
	Conicosia pugioniformis	-	-	1.95	0.439	-	-

Table S5 Plant species presence-absence and mean species cover (%) following the control of invasive alien European rabbits on Robben Isand. Data organised for optimal interpretation using constrained seriation (Brower, et al. 1988).

Sites	Species	Year			
		2010	2011	2012	2013
Strand	*Sporobolus virginicus* (L.) Kunth	1.00 ± 0.68			
	Sonchus oleraceus (L.) L.	0.33 ± 0.33		0.33 ± 0.33	
	Conicosia pugioniformis (L.) N. E. Br.	9.00 ± 1.91	2.00 ± 1.03	2.33 ± 1.31	3.00 ± 1.91
	Asparagus capensis L.	3.67 ± 2.09	5.67 ± 2.80	6.00 ± 3.10	4.00 ± 2.00
	Tetragonia fruticosa L.	22.70 ± 2.51	40.00 ± 5.89	42.00 ± 7.38	38.70 ± 7.64
	Oncosiphon suffruticosum (L.) Kallersjo	0.33 ± 0.33	0.33 ± 0.33	4.33 ± 2.33	7.00 ± 3.75
	Zantedeschia aethiopica (L.)	0.67 ± 0.42		0.67 ± 0.42	0.67 ± 0.67
	Cynodon dactylon (L.) Pers.	0.33 ± 0.33		1.33 ± 0.99	1.67 ± 0.61
	Vulpia myuros (L.) C.C.Gmel			0.67 ± 0.67	
	Isolepis sp.			1.00 ± 0.68	
	Crassula sp.			0.33 ± 0.33	
	Ehrharta villosa Schult.f.		0.33 ± 0.33	4.33 ± 2.85	5.00 ± 3.64
	Moraea collina Thunb.			1.33 ± 0.99	
	Spergula arvensis L.			0.33 ± 0.33	
	Ehrharta longiflora Sm.			20.70 ± 4.46	31.00 ± 3.89
	Bromus diandrus Roth.			0.67 ± 0.42	1.33 ± 1.33
	Silene cretica L.			3.67 ± 2.28	3.00 ± 1.44
	Euphorbia peplus L.				0.67 ± 0.67
	Anagallis arvensis L.				0.33 ± 0.33
	Phyllobolus canaliculatus (Haw.) Bittrich				0.33 ± 0.33
	Hypochaeris glabra L.				0.33 ± 0.33
Eucalyptus	*Phyllobolus canaliculatus* (Haw.) Bittrich	1.33 ± 0.67	0.67 ± 0.67	8.67 ± 3.29	8.33 ± 6.01
	Oxalis pes-caprae L.	0.67 ± 0.67		0.33 ± 0.33	3.00 ± 1.13
	Ehrharta longiflora Sm.			0.33 ± 0.33	0.67 ± 0.67
	Crassula natans Thunb.			0.33 ± 0.33	0.33 ± 0.33

	Tetragonia fruticosa L.			6.00 ± 2.68	13.30 ± 7.28
	Oncosiphon suffruticosum (L.) Kallersjo			0.67 ± 0.42	1.33 ± 0.67
	Chenopodium murale L.			0.33 ± 0.33	0.33 ± 0.33
	Torilis arvensis (Huds.) Link				0.33 ± 0.33
	Euphorbia peplus L.				1.67 ± 1.67
	Conicosia pugioniformis (L.) N. E. Br.				0.33 ± 0.33
Inland Dune	*Ornithoglossum viride* (L.f.) Dryland. Ex W.T.Aiton	0.33 ± 0.33			
	Wahlenbergia androsacea A.DC	0.33 ± 0.33			
	Emex australis Steinh.	0.33 ± 0.33			
	Sporobolus virginicus (L.) Kunth	0.33 ± 0.33			
	Trachyandra sp.	0.67 ± 0.42			
	Zantedeschia aethiopica (L.)	0.33 ± 0.33			
	Phyllobolus canaliculatus (Haw.) Bittrich		0.33 ± 0.33		
	Asparagus capensis L.		0.33 ± 0.33		
	Ehrharta villosa Schult.f.	1.00 ± 1.00	6.00 ± 2.83	20.30 ± 9.00	36.30 ± 14.20
	Cissampelos capensis L.f.	25.00 ± 6.57	21.70 ± 4.88	26.70 ± 6.01	19.30 ± 4.02
	Oncosiphon suffruticosum (L.) Kallersjo	1.33 ± 1.33	0.33 ± 0.33	5.67 ± 2.28	1.33 ± 0.99
	Conicosia pugioniformis (L.) N. E. Br.	11.70 ± 1.74	2.67 ± 1.61	2.67 ± 2.29	3.33 ± 1.43
	Tetragonia fruticosa L.	16.30 ± 6.54	37.70 ± 9.49	48.30 ± 8.82	42.00 ± 6.91
	Isolepis sp.			0.33 ± 0.33	
	Torilis arvensis (Huds.) Link			3.33 ± 1.69	
	Ehrharta longiflora Sm.	1.00 ± 1.00		0.33 ± 0.33	3.00 ± 1.34
	Vulpia myuros (L.) C.C.Gmel			1.33 ± 0.42	
	Anagallis arvensis L.			0.33 ± 0.33	
	Bromus diandrus Roth.			10.70 ± 4.43	13.00 ± 5.26
	Avena fatua L.				2.00 ± 1.26
	Capnophyllum africanum (L.) Gaertn.				1.33 ± 0.84

REFERENCES

BioNet-EAFRINET. 2022a. Factsheet - *Avena fatua* (Common Wild Oat). Available at https://keys.lucidcentral.org/keys/v3/eafrinet/weeds/key/weeds/Media/Html/index.htm [accessed 22 January 2022]

BioNet-EAFRINET. 2022b. Factsheet - *Helichrysum patulum*. Available at https://keys.lucidcentral.org/keys/v3/eafrinet/weeds/key/weeds/Media/Html/index.htm [accessed 12 January 2022]

Brower JC, Kile KM. 1988. Seriation of an original data matrix as applied to palaeoecology. *Lethaia* 21: 79-93.

Brownsey R, Kyser GB, DiTomaso JM. 2013. Stinkwort is rapidly expanding its range in California. *California Agriculture* 67: 110-115.

Bullock AA. 1952. South African poisonous plants. *Kew Bulletin* 7: 117-129.

Coetzee K. 2008. Blaauwberg Conservation Area: management guidelines for larger wildlife and their habitats. *Report prepared for the Biodiversity Management Branch, City of Cape Town*.

Correa-Metrio A, Dechnik Y, Lozano-García M, Caballero M. 2014. Detrended correspondence analysis: A useful tool to quantify ecological change from fossil data sets. *Boletín de la Sociedad Geológica Mexicana* 66: 135-143.

Cowan IA. 1945. The ecological relationship of the food of the Columbian black-tailed deer, *Odocoileus hemionus columbianus* (Richardson), in the coast forest region of Southern Vancouver Island, British Columbia. *Ecological Monographs* 15: 109-139.

du Toit PCV. 2002. Objektiewe weidingswaardes van Nama-Karooplantegroei, grasse en bossies van die Karoo. *Grootfontein Agric* 4: 8-18.

El Mokni R, Hédi El Aouni M. 2012. *Zantedeschia aethiopica* (Araceae) a new species naturalized in the Northwest of Tunisia. *Fl. Medit.* 22: 191-196.

Esler AE. 1980. Botanical features of Motutapu, Motuihe, and Motukorea, Hauraki Gulf, New Zealand. *New Zealand Journal of Botany* 18: 15-36.

Germishuizen G, Meyer NL. 2003. *Plants of southern Africa: an annotated checklist*. Pretoria: National Botanical Institute.

Gillham ME. 1963. Some interactions of plants, rabbits and sea-birds on South African islands. *Journal of Ecology* 51: 275-294.

Global Biodiversity Information Facility (GBIF). 2022. *Hypochaeris glabra* L. Available at https://www.gbif.org [accessed 12 January 2022]

Heneidy SZ. 2002. Role of indicator range species as browsing forage and effective nutritive source in Matruth, a Mediterranean coastal region, NW-Egypt. *Online Journal of Biological Sciences* 2: 136-142.

Le Roux A. 2005. *Namaqualand – South African Wild Flower Guide 1*. Cape Town: Botanical Society of South Africa.

Lewin RA. 1948. Biological flora of the British Isles: Sonchus L. (*S. oleraceus L.* and *S. asper* (L.) Hill). *Journal of Ecology* 36 203-223.

Louw G, Beukes T. 1988. Ken ons veldplante. *Die Noordwester*: 6-12.

Mfitumukiza D. 2004. Evaluating rangeland potentials for cattle grazing in a mixed farming system. MSc, International Institute for Geo-Information Science and Earth Observation, Enschede.

Moore G. 2001. Soil guide. A handbook for understanding and managing agricultural soils. *Agriculture Western Australia Bulletin No. 4343*.

Native Plant Trust. 2022. *Spergula arvensis* (corn spurry): Go Botany. Available at https://gobotany.nativeplanttrust.org/species/spergula/arvensis/ [accessed 13 January 2022]

Reader PM, Southwood TRE. 1981. The relationship between palatability to invertebrates and the successional status of a plant. *Oecologia (Berl)* 51: 271-275.

Rivero R, Zabala A, Gianneechini R, Gil J, Moraes J. 2001. *Anagallis arvensis* poisoning in cattle and sheep in Uruguay. *Veterinary and Human Toxicology* 43: 27–30.

Rothwell JT, Marshall DJ. 1986. Suspected poisoning of sheep by *Anagallis arvensis* (scarlet pimpernel). *Australian Veterinary Journal* 63: 316–316.

Scott JM, Blair GJ. 1987. Competition from *Vulpia myuros* (L.) C.C. Gmelin in pastures, and its control by coating seeds with herbicides. *Australian Journal of Experimental Agriculture* 27: 367-375.

Shearing D, van Heerden K. 1994. *Karoo: South African wild flower guide 6*. Kisternbosch: Botanical Society of South Africa.

Simmonds H, Holst P, Bourke C. 2000. *The palatability, and potential toxicity of Australian weeds to goats*. Kingston: Rural Industries Research and Development Corporation.

South African National Biodiversity Institute. 2022. *Conicosia pugioniformis* (L) N.E.Br subsp. *pugioniformis*. SANBI. Available at http://pza.sanbi.org/. [accessed 12 January 2022]

Struik GJ. 1967. Growth habits of dandelion, daisy, catsear, and hawkbit in some New Zealand grasslands. *New Zealand Journal of Agricultural Research* 10: 331-344.

UWC Cape Flats Indigenous Nursery. 2020. UWC Nature Reserve: *Phyllobolus canaliculatus*. Available at https://uwccfnursery.blogspot.com/2020/05/phyllobolus-canaliculatus [accessed 13 January 2022]

Vahrmeijer J. 1981. *Gifplante van Suider-Afrika wat veeverliese veroorsaak*. Kaapstad: Tafelberg Uitgewers Beperk.

van Breda PAB, Nel EJ, Bayer MB (eds). 1990. *Palatability of plant species – winter rainfall region: Little Karoo and Ceres Karoo* Elsenburg Agricultural Development Institute

van den Berg L, van Lingen M (eds). 2009. *Weidingswaardes (WIW) vir Karoo plantspesies – Hersiene weergawe*. Grootfontein Agricultural Development Institute. Middelburg.

van Dyne GM, Heady HF. 1965. Botanical composition of sheep and cattle diets on a mature annual range. *Hilgardia* 36: 465-492.

van Oudtshoorn F. 2012. *Guide to grasses of southern Africa*. Pretoria: Briza Publications. [accessed

Vilà M, Bartomeus I, Gimeno I, Traveset A, Moragues E. 2006. Demography of the invasive geophyte *Oxalis pes-caprae* across a Mediterranean island. *Annals of Botany* 97: 1055–1062.

Western Australian Herbarium. 2022a. *Atriplex cinerea* Poir. Available at https://florabase.dpaw.wa.gov.au [accessed 12 January 2022]

Western Australian Herbarium. 2022b. *Chenopodium murale* L. Available at https://florabase.dpaw.wa.gov.au [accessed 12 January 2022]

Western Australian Herbarium. 2022c. *Dittrichia graveolens* (L.) Greuter Stinkwort. Available at https://florabase.dpaw.wa.gov.au [accessed 12 January 2022]

Western Australian Herbarium. 2022d. *Oncosiphon suffruticosum* (L.) Kallersjo. Available at https://florabase.dpaw.wa.gov.au [accessed 12 January 2022]

ANNEXURE IX: CHAPTER 5 — SUPPLEMENTARY MATERIAL 2

Overview

In this supplementary document we present details on how we used a pseudo before-after, control-impact (BACI) experimental design and correlative statistical rainfall–vegetation relationships to identify and cancel out the confounding effects of inter-annual rainfall variation on our study's results. As detailed in the Materials and Methods section of the main text, our study was based on an unplanned attempt to restore vegetation on Robben Island by removing alien invasive European rabbits. Due to the opportunistic nature of our study, we initiated vegetation monitoring a full year after the commencement of rabbit control activities. As a result, without a before-impact control, we could not implement the BACI design that is commonly used to assess impact in longitudinal observational studies. Additionally, because of our inability to design and implement planned treatments and randomisation, we were constrained to evaluating the influence of rainfall variation on vegetation response using correlative statistical control and thus could not directly demonstrate causality. To overcome the challenges, we used an earlier vegetation survey of the island by Adamson (1934) as a BACI-like control and strengthened, whenever possible, the interpretation of correlative rainfall–vegetation relationships in our results by providing plausible mechanisms, demonstrating links between putative causes and outcomes and sourcing supporting independent evidence from the published literature. Adamson (1934) surveyed vegetation on Robben Island in 1933-1934 when the island was overrun with rabbits. We used this survey's results as a BACI-like control by assuming that the conditions on the island in 1933-1934 were like those in the period preceding rabbit control in 2009 and 2010.

Below, we present for each of our three study sites (strand, eucalyptus, and inland dune) detailed accounts of how we used the above-mentioned approaches to: i) evaluate and cancel out the influence of inter-annual rainfall variation on vegetation response; and ii) determine how grazing capacity and underlying species cover would have changed given constant and average inter-annual rainfall. As our intention was to ensure that each of the sections of this document were as comprehensive and self–contained as possible, there is considerable repetitive use of information presented in the main text and separate parts of the document.

Strand sites

Statistical correlation indicates that interannual rainfall variation influenced a considerable amount (~36%) of the change in grazing capacity following rabbit control at strand sites. Grazing capacity increased moderately between the first- and second years following rabbit control, slightly more markedly between the second and third and decreased slightly between the third and fourth. Inter-annual variation in TAUR had the greatest influence (~35%) on grazing capacity change followed by TSUR (~1%). Total autumn rainfall was considerably below the long-term average during the first- and second years following rabbit control and rose to moderately above and slightly below average in the third- and fourth year. Total summer rainfall was moderately and considerably below the long-term average during the first- and second years following rabbit control and rose to moderately above and equal to the average in the third and fourth.

Based on our interpretation of underlying vegetation dynamics and correlative rainfall–vegetation relationships, we determined that given constant and average inter-annual rainfall, grazing capacity would have increased across strand sites following rabbit control given average and constant inter-annual rainfall. Mean grazing capacity across the sites would have increased between the first- and second years and remained stable (possibly at ~16 LSU 100 $ha^{-1}y^{-1}$) in the proceeding years. The increase in grazing capacity would have been driven by increased cover of *T. fruticosa* and *E. longiflora* and the emergence of *E. villosa*.

These increases would have been accompanied by a decline in the cover of *C. pugioniformis*. The increase in the cover of *T. fruticosa* would have been of major, *E. longiflora* intermediate and emergence of *E. villosa* minor importance in driving grazing capacity change while the decline in the cover of *C. pugioniformis* would have been of intermediate importance. Forage production by *T. fruticosa* and *E. longiflora* would have increased markedly between the first- and second years in response to rabbit control and, after that, remained constant. Additionally, forage production by *E. villosa* would have marginally increased between the first- and second years and remained steady in the proceeding years while *C. pugioniformis* decreased moderately between the first- and second years following rabbit control and constantly remain low in the proceeding years.

Below, we present details of our determination of how each of the species that underlay grazing capacity change at strand sites would have responded to rabbit control given constant and average inter-annual rainfall.

Tetragonia fruticosa

Inter-annual rainfall variation appears to have had no influence on the change in forage production by the woody shrub *T. fruticosa* following rabbit control. Forage production by the woody shrub increased markedly between the first- and second years following rabbit control (increased by 258.84 kg DM ha^{-1} y^{-1}), moderately between the second- and third (increased by 29.86 kg DM ha^{-1} y^{-1}) and decreased by 49.78 kg DM ha^{-1} y^{-1} between the third- and fourth (Annex VIII Table S2). *Tetragonia fruticosa* plants are highly adapted to conditions of low soil moisture. The shrub has succulent leaves and is able to use water stored in leaves to endure drought conditions (van Breda, et al. 1991, Hoffman, et al. 2009). Succulent plants are also able to alternate between CAM and C3 photosynthesis, which enables them to grow during periods of high temperature and low water availability. In addition, *T. fruticosa* plants have fairly well-developed root systems that can penetrate the soil to reasonable depths (van Breda and Barnard 1991). The ability of *T. fruticosa* to tolerate low soil moisture most likely explains why worsening drought conditions between the first- and second years following rabbit control did not negatively affect forage production by the woody shrub.

However, interannual variation in TAUR may have indirectly influenced change in forage production of *T. fruticosa* following rabbit control by suppressing germination of new plants. *Tetragonia fruticosa* seeds germinate intermittently in autumn following episodic leaching of salt from soil by rainwater (van Breda and Barnard 1991). Total autumn rainfall was considerably below the long-term average during the first- and second years following rabbit control and rose to moderately above and slightly below average in the third and fourth years, respectively. Considerably below average TAUR may have limited *T. fruticosa* forage production between the first- and second years following rabbit control by restricting *T. fruticosa* response to regrowth of existing adult plants. Although European rabbits can severely browse *T. fruticosa* plants to the base of their shoots, they usually have trouble consuming the woody shoots (Adamson 1934). Control of rabbit browsing therefore most likely allowed plants to re-grow from existing browsed stems. The moderate increase in forage production by *T. fruticosa* between the second- and third years following rabbit control may have been driven by the increase in TAUR to above the long-term average. Increase in TAUR would have led to increased leaching episodes and more germination events. Decline in TAUR to slightly below the long-term average could have driven the decrease in forage production between the third- and fourth years following rabbit control by decreasing germination success and recruitment of new plants.

Given constant and average inter-annual rainfall, increase in cover of *T. fruticosa* would have remained one of the main drivers of grazing capacity change following rabbit control. However, forage production by the woody shrub would most likely have increased markedly between the first- and second years following rabbit control and remained constant in the proceeding years.

Ehrharta longiflora

Inter-annual rainfall variation appears to have influenced all (~100%) of the change in forage production by the annual grass *E. longiflora* following rabbit control. Forage production by the grass increased moderately from zero between the second- and third years following rabbit control (increased by 68.58 kg DM ha^{-1} y^{-1}) and did not change between the third- and fourth (Annex VIII Table S2). Increase in TAUR and TWR from below to above the long-term average appears to have driven the emergence and most (~95%) of the increase in forage production by the grass between the second- and third years following rabbit control. Total autumn rainfall was considerably below the long-term average during the first- and second years following rabbit control and rose to moderately above and slightly below average in the third and fourth. Total winter rainfall was slightly and moderately below and slightly above the long-term average in the first-, second- and third years following rabbit control and increased to moderately above average in the fourth. An accompanying increase in TSUR from considerably below to moderately above the long-term average appears to have considerably suppressed (by ~79%) forage production by the grass. Total summer rainfall was moderately and considerably below the long-term average during the first- and second years following rabbit control and rose to moderately above and equal to the average in the third and fourth.

Ehrharta longiflora is a winter annual grass that survives summer stress as dormant seed (Moore, et al. 2007a, Fisher, et al. 2009, Winston, et al. 2014). The seeds become non-dormant at the end of summer to take advantage of favourable growing conditions in winter (Moore, et al. 2007b). Germination of *E. longiflora* is controlled by soil moisture and seeds germinate following autumn and winter rainfall (Western Australian Herbarium 1998, Bossard, et al. 2000, Moore and Moore 2007b). *Ehrharta longiflora* reproduces entirely from seed (Winston, et al. 2014) and the failure of plants to germinate would have led to its complete absence. Below average TAUR and TWR during the first two years proceeding rabbit control most likely suppressed germination of *E. longiflora* and resulted in its absence. The emergence and increase in forage production by *E. longiflora* between the second- and third years following rabbit control probably resulted from the increase in TAUR and TWR which raised soil moisture to levels suitable for germination and facilitated rapid growth in winter. Increase in TSUR may have limited increase in forage production by *E. longiflora* between the second- and third years following rabbit control by supporting more plant growth during the dry summer period and reducing the extent of open ground available for germination in autumn. *Ehrharta longiflora* requires open ground for germination (Winston, et al. 2014). Forage production by *E. longiflora* increased moderately after its emergence between the second and third years, reaching its upper equilibrium. Although the favourable wet conditions experienced in the third year stretched into the fourth year following rabbit control, forage production by *E. longiflora* remained constant. This was probably because the annual grass had covered all the available open ground.

Ehrharta longiflora is palatable (van Oudtshoorn 2012) and is favoured feed for rabbits on Robben Island (Gillham 1963). It does not persist under grazing as it often has creeping branched roots and rhizomes that are easily pulled up by herbivores (Moore and Moore 2007a). However, annual plants like *E. longiflora* that grow for a limited period may survive heavy rabbit herbivory even if they are subjected to heavy attack. Their short annual period of vegetation exposes them to attack for a considerably less period than is the case with most other plants such that some of them manage to survive the rabbit-attack and are able to flower (Farrow 1917). Adamson (1934) observed *E. longiflora* on rock outcrops on strand sites in 1934 when the island was overrun with rabbits and the vegetation heavily degraded. It is most likely that *E. longiflora* was continuously present before rabbit control albeit at low cover and would have been continuously present at strand sites after rabbit control if inter-annual rainfall had been constant and average.

Given constant and average inter-annual rainfall, increase in cover of *E. longiflora* would have been of intermediate importance in driving grazing capacity change following rabbit control. Forage production by the annual grass would most likely have instead increased moderately between the first- and second years following rabbit control and remained constant in the proceeding years.

Ehrharta villosa

Inter-annual rainfall variation appears to have had no influence on the change in forage production by the perennial grass *E. villosa* following rabbit control. Forage production by the perennial grass increased by 1.11 kg DM ha^{-1} y^{-1} between the first- and second years following rabbit control and did not change in the proceeding years (Annex VIII Table S2). The emergence and increase in forage production by *E. villosa* between the first- and second years following rabbit control clearly could not have been influenced by inter-annual rainfall variation as they occurred during worsening drought conditions. Total summer rainfall and TWR decreased from moderately and slightly below the long-term average to considerably and moderately below average between the first- and second years following rabbit control while TAUR remained considerably below average.

Ehrharta villosa can withstand drought conditions (Rudman 2003) by using its deep root systems to access water from deep below the soil surface (Harrington, et al. 1998). Additionally, *E. villosa* does not depend on seeds for reproduction, survival and spread (Hodder 1997). Seed production in *E. villosa* is very low and regeneration from rhizomes and rhizome fragments is the more important mode of reproduction and dispersal (Hodder 1997). Plants that regenerate from rhizomes can withstand drier conditions than those that depend on seed germination. The ability of *E. villosa* to tolerate low soil moisture most likely explains why worsening drought conditions between the first- and second years following rabbit control did not negatively affect forage production by the perennial grass. *Ehrharta villosa* requires fairly deep soil (Coetzee 2008). Soil at strand sites was generally shallow (3 to 5 cm (Adamson 1934)). As a result, areas with soil deep enough or underlying rocks with water-bearing fractures to support *E. villosa* plants were most likely limited at the sites. This explains why the grass reached its upper equilibrium in the second year following rabbit control. *Ehrharta villosa* is an aggressive competitor whose long stems (often growing to a height of two metres or more) allow it to grow over and overshadow competing vegetation (Harrington, et al. 1998).

Although precise information about rabbit preference for *E. villosa* on Robben Island is unavailable, herbivory appears to have a considerable effect on the abundance of the perennial grass on the island (Lloyd, et al. 1986, Sherley 2016). *Ehrharta villosa* is known to become more abundant when grassland is leniently grazed (Tainton, et al. 1990). Adamson (1934) did not find *E. villosa* at strand sites in 1934 when the island was under heavy rabbit herbivory. It is therefore most likely that *E. villosa* was absent from strand sites before rabbit control and only emerged after cessation of rabbit herbivory.

Given average and constant inter-annual rainfall, emergence of *E. villosa* would have remained of intermediate importance in driving grazing capacity change following rabbit control. Forage production by perennial grass would still have increased slightly from zero between the first- and second years following rabbit control and remained constant in the proceeding years.

Conicosia pugioniformis

Inter-annual rainfall variation appears to have had no influence on the change in forage production by the perennial herb *C. pugioniformis* following rabbit control. Forage production by the species decreased moderately between the first- and second years following rabbit control (decreased by 23.22 kg DM ha^{-1} y^{-1}) and increased slightly between the second-, third- and fourth (increase by 1.10 and 2.22 kg DM ha^{-1} y^{-1}; Annex VIII Table S2). Like the woody shrub *T. fruticosa*, *C. pugioniformis* is a perennial leaf-succulent that can tolerate low soil moisture (Schmalzer, et al. 1987). The decline in forage production by *C. pugioniformis* between the first- and second years following rabbit control was therefore most likely not driven by worsening drought conditions but by competition with more competitive drought-resistant plants like *T. fruticosa*.

However, a small portion of the decline in forage production by *C. pugioniformis* between the first- and second years following rabbit control was most likely caused by limited recruitment of new plants from seed to replace short-lived adult plants that died from senescence. *Conicosia pugioniformis* is short-lived and reproduces solely from seed (Schmalzer and Hinkle 1987). Germination occurs in late autumn and early winter. TAUR and TWR were below the long-term average during the first- and second years following rabbit control and may have suppressed germination from seed.

The slight increase in forage production by *C. pugioniformis* between the second, third- and fourth years following rabbit control probably resulted from the increase in TAUR and TWR which raised soil moisture to levels suitable for germination and recruitment of new plants from seed. Total autumn rainfall was considerably below the long-term average during the first- and second years following rabbit control and rose to moderately above and slightly below average in the third and fourth. Total winter rainfall was below the long-term average during the first- and second years following rabbit control and rose to above average in the third and fourth. The recruitment of new *C. pugioniformis* plants from seed was evidently limited by inter-specific competition with other co-occurring species such as the woody shrub *T. fruticosa* and annual grass *E. longiflora*. Both *T. fruticosa* and *C. pugioniformis* have root systems with deep taproots that can penetrate the soil to reasonable depths (Schmalzer and Hinkle 1987, van Breda and Barnard 1991). However, in *T. fruticosa* the root system is comparatively more developed and morphologically versatile — developing long spreading roots in shallow soil and deeper roots in deep or harder soil (van Breda and Barnard 1991). *Conicosia pugioniformis* probably also faced intense competition from the taller *E. longiflora* for light and germination space.

Conicosia pugioniformis is not well grazed by livestock because of the astringent and often salty quality of its succulent tissue (Louw, et al. 1988, de Villiers, et al. 2001). European rabbits also appear to avoid the perennial herb. Adamson (1934) observed abundantly occurring *C. pugioniformis* plants at strand sites in 1934 when the island was overrun with rabbits and the vegetation heavily degraded. The plants occurred most abundantly in areas where rabbits were observed to congregate (Adamson 1934). It is therefore most likely that *C. pugioniformis* would have had a higher cover in the years preceding rabbit control when more open spaces for germination would have been available.

Given average and constant inter-annual rainfall, the decline in cover of *C. pugioniformis* would have remained of intermediate importance in driving grazing capacity change following rabbit control. Forage production by the herb would most likely have decreased moderately between the first- and second years following rabbit control and remained low in the proceeding years.

Silene cretica

Inter-annual rainfall variation appears to have influenced some (~33%) of the change in forage production by the annual alien herb *S. cretica* following rabbit control. Forage production by the herb increased moderately from zero between the second- and third years following rabbit control (increased by 12.17 kg DM ha^{-1} y^{-1}) and did not change between the third- and fourth (Annex VIII Table S2). *Silene cretica* is an ephemeral weedy species from the Mediterranean (Vural, et al. 2002, Blasi, et al. 2014). Ephemerals germinate soon after good rainfall events and often complete their life cycle in less than one month. Below average TSR, TAUR and TWR during the first two years proceeding rabbit control most likely suppressed *S. cretica* germination.

The emergence and some of the increase in cover of the herb between the second- and third years following rabbit control was clearly in response to increased TSR, TAUR and TWR to above the long-term average after the drought conditions of the first two years following rabbit control. Like with the annual herb *O. suffruticosum*, the influence of inter-annual rainfall variation on change in cover of *S. cretica* following rabbit control was inter-seasonal. This was probably because of the ephemeral nature of the species. *Silene cretica* has large, fibrous and fast-growing root systems (Arnone II, et al. 1997). Soil at strand sites was generally shallow (3 to 5 cm: (Adamson 1934). As a result, areas with sufficiently deep soil or underlying rocks with water-bearing fractures to support *S. cretica* plants were most likely limited at the sites. This may explain why the species reached its upper equilibrium in the second year following rabbit control.

Silene cretica plants are short and hairy. Hairy species are not preferred by rabbits (van Leeuwen, et al. 1971, Williams, et al. 1974) and plants with shoots which grow close to the ground surface suffer less rabbit-attacks than plants with tall vertical shoots (Farrow 1917, Crawley 1990). Adamson (1934) observed widespread and fairly abundant *S. cretica* plants at inland and coastal dune sites in 1934 when the island was under heavy rabbit herbivory. No mention was made however about the occurrence *S. cretica* at strand sites. This was probably because Adamson (1934) could have overlooked the short ephemerals because of their extremely low cover at strand sites. It is therefore most likely that the species would have persisted at strand sites during the years preceding rabbit control. However, because of low availability of suitably deep soils to support *S. cretica* plants at strand sites, the cover of the alien annual herb would have been considerably low.

Given constant and average inter-annual rainfall, change in *S. cretica* cover would have been insignificant in driving grazing capacity change following rabbit control. Forage production by the species would have remained moderate and constant in the years following rabbit control.

Sporobolus virginicus

Inter-annual rainfall variation appears to have had no influence on the change in forage production by the perennial grass *S. virginicus* following rabbit control. Forage production by the species decreased to zero between the first- and second years following rabbit control (decreased by 8.30 kg DM ha^{-1} y^{-1}) and did not change in the proceeding years (Annex VIII Table S2). *Sporobolus virginicus* rarely sets seed but reproduces, survives and spreads through rhizomes (Marcum, et al. 1992, Knevel 2001, Masters, et al. 2007, Williams 2007). Plants that regenerate from rhizomes can withstand drier conditions than those that depend on seed germination. The grass also has deep rhizomatous roots and requires low moisture for growth (Jones, et al. 2004). As a result, the disappearance of *S. virginicus* in the second year following rabbit control was most likely not linked to worsening drought conditions between the first- and second years following rabbit control but was in response to cessation of rabbit herbivory. The perennial grass is palatable to herbivores (Mfitumukiza 2004) and is an important grazing plant during the dry season (Barrett-Lennard 2003, Jones and Hanna 2004) and should have increased in cover following rabbit control. However, *S. virginicus* is a pioneer species (Naidoo, et al. 1993) and most likely disappeared from strand sites as a result of competition from more competitive species such as the woody shrub *T. fruticosa* and the annual grass *E. longiflora*.

Sporobolus virginicus plants have relatively deep root systems that reach as deep as 46 cm in mature plants (Jones and Hanna 2004). Soil depth at strand sites was only 3 to 5 cm (Adamson 1934). As a result, shallow soil depth or absence of underlying rocks with water-bearing fractures may have limited *S. virginicus* plants at the sites. The disappearance of *S. virginicus* from strand sites probably occurred because of its low cover caused by limited suitable habitat and intense competition from more competitive deep-rooted plants such as the woody shrub *T. fruticosa*. *S. virginicus* was probably absent from strand sites during rabbit herbivory and only re-emerged briefly during the first year following rabbit control. Adamson (1934) did not observe *S. virginicus* on Robben Island when the island was under heavy rabbit herbivory. This was probably because *S. virginicus* – which reproduces, survives and spreads through rhizomes – was able to occupy deep soil patches left bare by the inability of competing *T.*

fruticosa and *E. longiflora* plants to germinate as a result of below average TAUR and TWR (see discussions on *T. fruticosa* and *E. longiflora* above).

Given constant and average inter-annual rainfall, the change in *S. cretica* cover would have been insignificant in driving grazing capacity change following rabbit control. Forage production by the perennial grass would have been zero as it would have remained absent from strand sites following rabbit control.

Eucalyptus sites

Grazing capacity did not change at eucalyptus sites following rabbit control. The lack of change clearly resulted from the inhibiting effect of the alien plantation trees on understory vegetation dynamics. *Eucalyptus* trees, with their high water consumption rate and dense near surface roots (del Moral, et al. 1969), rapidly deplete soil moisture (Le Maitre, et al. 2002, Dye, et al. 2004, Dye, et al. 2007) and soil nutrients (Bernhard-Reversat 1996, Guo, et al. 2001, Marchante, et al. 2008) from upper soil layers. This most likely led to less fertile and drier than normal conditions for plant growth at eucalyptus sites and limited the response of plants to inter-annual rainfall variation and rabbit control. The fluctuations and increases in forage production by the woody shrub *T. fruticosa*, annual grass *E. longiflora*, less palatable annual herb *O. pes-caprae* and perennial herb *P. canaliculatus* following rabbit control may have been dampened responses to inter-annual variation in TAUR and TWR.

Based on our interpretation of underlying vegetation dynamics and correlative rainfall–vegetation relationships, we determined that grazing capacity would still have not changed at eucalyptus sites following rabbit control in the absence of inter-annual rainfall variation. The lack of change in grazing capacity would have been caused by subdued responses of *T. fruticosa*, *E. longiflora, O. pes-caprae* and *P. canaliculatus* to rabbit control.

Below, we present details of our determination of how each of the species that underlay grazing capacity change at eucalyptus sites would have responded to rabbit control given constant and average inter-annual rainfall.

Tetragonia fruticosa

Inter-annual rainfall variation appears to have had considerable influence (~61%) on the change in forage production by the woody shrub *T. fruticosa* following rabbit control. Forage production by the plant increased moderately from zero between the second- and third years following rabbit control (increased by 89.60 kg DM ha^{-1} y^{-1}) but did not change between the third- and fourth (Annex VIII Table S2). The emergence of *T. fruticosa* and some (~53%) of the increase in forage production by the species between the second- and third years following rabbit control was evidently in response to the increase in TAUR to moderately above the long-term average following the drought conditions of the first two years. As stated in the section for strand sites above, *T. fruticosa* seeds germinate intermittently in autumn following episodic leaching of salt from soil by rainwater (van Breda and Barnard 1991). The increased TAUR may have provided sufficient water for germination. Total autumn rainfall was moderately above average in the third- but below average in the first-, second- and fourth years after rabbit control. Unlike at strand and inland dune sites where some adult *T. fruticosa* plants persisted during the drought conditions of the first two years following rabbit control, there were no plants at eucalyptus sites during this period. This was probably because of relatively greater herbivory pressure on the highly palatable woody shrub at the sites, coupled with the drier conditions caused by *Eucalyptus* trees. Heavy browsing, combined with drought, causes death of *T. fruticosa* individuals (Adamson 1934). Browsing pressure under *Eucalyptus* trees was probably exacerbated by low vegetation cover and the occurrence of fewer *T. fruticosa* individuals. The woody shrub produces relatively few large seeds and is thus particularly susceptible to deleterious effects of heavy summer grazing (Todd 2000). Under heavy grazing, the recruitment of palatable species is reduced due to the failure to set seed, eventually resulting in the loss of such species from the rangeland.

Given constant and average inter-annual rainfall, increase in cover of *T. fruticosa* would have been negligible in driving grazing capacity change following rabbit control. Forage production by the species would have remained consistently low because of poor germination due to depletion of soil moisture by *Eucalyptus* trees.

Ehrharta longiflora

Although inter-annual rainfall variation did not have a statistically significant effect on forage production by *E. longiflora* following rabbit control, variation in TWR probably had some impact. Forage production by the annual grass increased by 2.77 kg DM ha^{-1} y^{-1} between the second- and third years following rabbit control and did not change between the third- and fourth (Annex VIII Table S2). Total winter rainfall increased from slightly and moderately below the long-term average during the first- and second years following rabbit control to slightly and moderately above the long-term average in the third and fourth. *Ehrharta longiflora* is a winter annual that survives summer stress as dormant seed (Moore and Moore 2007a, Fisher, et al. 2009, Winston, et al. 2014). The seeds become non-dormant at the end of summer to take advantage of favourable growing conditions in winter (Moore and Moore 2007b). Germination of *E. longiflora* is controlled by soil moisture and seeds germinate following autumn and winter rainfall (Western Australian Herbarium 1998, Bossard, et al. 2000, Moore and Moore 2007b). The annual grass reproduces entirely from seed (Winston, et al. 2014) and the failure of plants to germinate because of below average TWR would have led to its complete absence during the first two years following rabbit control. The emergence of *E. longiflora* between the second- and third years following rabbit control probably resulted from the increase in TWR which raised soil moisture to levels suitable for germination and facilitated rapid growth in winter.

Given constant and average inter-annual rainfall, increase in cover of *E. longiflora* would have been negligible in driving grazing capacity change following rabbit control. Forage production by the annual grass would have remained near zero because of suppression of germination by depletion of soil moisture by *Eucalyptus* trees.

Oxalis pes-caprae

Inter-annual rainfall variation appears to have influenced some (~39%) of the change in forage production by the geophytic annual herb *O. pes-caprae* following rabbit control. Forage production by the plant decreased between the first- and second years following rabbit control but increased by 9.96 kg DM ha^{-1} y^{-1} between the third- and fourth (Annex VIII Table S2). The temporary disappearance of the herb in the second year was clearly in response to a decline in TWR to moderately below the long-term average. The herb reproduces both sexually by seeds and asexually through bulbils (Papini, et al. 2017). *Oxalis* bulbs remain dormant in the summer and sprout in the autumn (Vilà, et al. 2006, Verdaguer, et al. 2010). As a result, peak vegetative growth occurs during autumn and winter, after which flowering starts (Verdaguer, et al. 2010). The slight increases in forage production by *O. pes-caprae* between the second-, third- and fourth years following rabbit control would have been in response to the subsequent increase in TWR to above average levels. Additionally, the increase in cover between the third- and fourth years following rabbit control would have also been driven by reduced competition from the perennial herb *Phyllobolus canaliculatus* (see discussion on the dynamics of *P. canaliculatus* following rabbit control below). The herb is less palatable as it accumulates oxalic acid in its leaves, which is toxic to herbivores if eaten in large quantities (Sala, et al. 2007). As a result, the herb would have persisted during the years prior to rabbit control. Adamson (1934) observed abundant *O. pes-caprae* when the island was under heavy rabbit herbivory. However, the cover of *O. pes-caprae* at eucalyptus sites would have been kept low before and after rabbit control by intense competition for soil nutrients and sunlight by *Eucalyptus* trees. *Oxalis pes-caprae* performs poorly under conditions of low soil fertility and shade (Verdaguer, et al. 2010).

Given constant and average inter-annual rainfall, increase in cover of *O. pes-caprae* would have been negligible in driving grazing capacity change following rabbit control. Forage production by the annual herb would have remained low because of intense competition for soil nutrients and sunlight by *Eucalyptus* trees.

Phyllobolus canaliculatus

Inter-annual rainfall variation appears to have influenced ~47% of the change in forage production by the perennial herb *P. canaliculatus* following rabbit control. Forage production by the herb remained constant between the first- and second years following rabbit control, increased moderately between the second- and third years and decreased slightly between the third- and fourth years. Forage production by the herb remained constant between the first- and second years following rabbit control, increased by 26.55 kg DM ha^{-1} y^{-1} between the second- and third (increased) and then decreased slightly between the third- and fourth (Annex VIII Table S2). The increase in forage production by *P. canaliculatus* between the second- and third years was evidently in response to increased TAUR to moderately above the long-term average after the drought conditions of the first two years. The herb is a deciduous winter-growing caudiciform that sheds leaves and stems in summer (Freeman, et al. 2021). The plants are propagated through cuttings, rooted runners and seeds (Freeman, et al. 2021, UWC Cape Flats Indigenous Nursery 2021). Increase in TAUR would have led to more germination events. The decline in TAUR to below the average could have driven the decrease in forage production between the third- and fourth years following rabbit control by decreasing germination success and recruitment of new plants. *Phyllobolus canaliculatus* is drought tolerant (Freeman, et al. 2021) and grows well in open well-drained soil (UWC Cape Flats Indigenous Nursery 2021). However, the species requires sunny conditions for germination and optimal growth (UWC Cape Flats Indigenous Nursery 2021). Therefore, shading by *Eucalyptus* trees most likely played a significant role in maintaining low *P. canaliculatus* cover before and following rabbit control. Although Adamson (1934) does not mention the presence of the herb when the island was under heavy rabbit herbivory, it would have most likely persisted prior to rabbit control as it is also less palatable. The herb may have been overlooked during the survey by Adamson (1934) because of its low cover.

Given constant and average inter-annual rainfall, increase in cover of *P. canaliculatus* would have been negligible in driving grazing capacity change following rabbit control. Forage production by the perennial herb would have remained low because of shading by *Eucalyptus* trees.

Inland dune sites

Like at strand sites, the change in grazing capacity (~39%) following rabbit control may have been driven by inter-annual rainfall variation. Grazing capacity increased markedly between the first- and second years following rabbit control, moderately between the second and third and decreased slightly between the third and fourth. Inter-annual variation in TAUR appears to have influenced ~36% of the ~39% change in grazing capacity caused by inter-annual rainfall variation. Total autumn rainfall was below average during the first two years following rabbit control.

Based on our interpretation of underlying vegetation dynamics and correlative rainfall–vegetation relationships, we determined that given constant and average inter-annual rainfall, grazing capacity would have increased across inland dune sites in response to rabbit control. Mean grazing capacity across the sites would have increased between the first- and second years following rabbit control and increased slightly across the second, third and fourth (possibly to ~19 LSU 100 ha^{-1}y^{-1}). The increase in grazing capacity would have been driven by the increased coverage of *T. fruticosa*, *E. villosa*, and the emergence of *E. longiflora* and *A. fatua*. The increases would have been accompanied by a decline in cover of *C.*

pugioniformis. The increase in cover of *T. fruticosa* and *E. villosa* would have been of major importance in driving grazing capacity. The decline in cover of *C. pugioniformis* would have been of intermediate while the emergence of *E. longiflora* and *A. fatua* minor importance. Forage production by *T. fruticosa* would have increased markedly between the first- and second years in response to rabbit control and remained constant in the proceeding years. Forage production by *E. villosa* would have increased moderately across the years. Forage production by *E. longiflora* would have increased slightly from zero between the first- and second years and remained constant in the proceeding years. Forage production by the alien annual grass *A. fatua* would have increased slightly from zero between the first- and second years and remained constant in the proceeding years. Forage production by *C. pugioniformis* would have decreased moderately between the first- and second years and remained stable in the proceeding years.

Below, we present details of our determination of how each of the species that underlay grazing capacity change at inland dune sites would have responded to rabbit control given constant and average inter-annual rainfall.

Tetragonia fruticosa

Inter-annual rainfall variation appears to have had no influence on the change in forage production by the woody shrub *T. fruticosa* following rabbit control. Forage production by the species increased markedly (318.57 kg DM ha^{-1} y^{-1}) between the first- and second years following rabbit control, less markedly between the second- and third and decreased moderately between the third- and fourth (decrease by 94.57 kg DM ha^{-1} y^{-1}; Annex VIII Table S2). *Tetragonia fruticosa* is adapted to conditions of low soil moisture because of its succulent leaves and well-developed root systems (van Breda and Barnard 1991, Hoffman, et al. 2009). This may explain why forage production by the species did not change in the first two years after rabbit control (see discussion on *T. fruticosa* dynamics at strand sites above for more details).

Like at strand sites, interannual variation in TAUR may have indirectly influenced the change in forage production of *T. fruticosa* following rabbit control by suppressing germination of new plants (see discussion on *T. fruticosa* dynamics at strand sites). The increase in TAUR from below to above average may have been driven the marked increase in forage production by *T. fruticosa* between the second- and third years after rabbit control. The decline in TAUR to below average most likely influenced the moderate decline in forage production in the third- and fourth years.

Given constant and average inter-annual rainfall, increase in cover of *T. fruticosa* would have remined one of the main drivers of grazing capacity change following rabbit control. However, forage production by the plant would most likely have increased markedly between the first- and second years following rabbit control and remained constant in the proceeding years.

Ehrharta villosa

Inter-annual rainfall variation appears to have had no influence on the change in forage production by the perennial grass *E. villosa* following rabbit control. Forage production by the grass increased moderately after the first year and thereafter increased markedly. Forage production by the grass increased moderately (16.59 kg DM ha^{-1} y^{-1}) between the first- and second years following rabbit control and more markedly between the second-, third- and fourth (increased by 47.57 and 53.09 kg DM ha^{-1} y^{-1}, respectively; Annex VIII Table S2). The initial increase in forage production by *E. villosa* clearly could not have been influenced by inter-annual rainfall variation as it occurred during worsening drought conditions (see discussion on *E. villosa* dynamics at strand sites above for more details). *Ehrharta villosa* plants can withstand drought conditions because of their deep roots (Harrington, et al. 1998) and ability to regenerate from rhizomes and rhizome fragments (Hodder 1997). However, unlike at strand sites, the greater soil depth at inland dune sites could support deep-rooted *E. villosa* plants. As a result, grass cover continued to increase during all four proceeding years.

The greater increase in forage production by *E. villosa* in subsequent years following rabbit control probably resulted from increased TSUR which raised soil moisture to levels suitable for germination and recruitment of new plants from seed. Seed production is low in *E. villosa* (Hodder 1997). However, the limited seeds produced by the grass germinate between spring and early summer (Cowell 2013). Total summer rainfall was below average during the first- and second years following rabbit control and increased to average or above average in subsequent years. At strand sites, *E. villosa* cover reached its upper equilibrium in the second year following rabbit control because of limited availability of sites with suitably deep soil while it grew unhindered at inland dune sites.

Although precise information about rabbit preference for *E. villosa* on Robben Island is unavailable, herbivory appears to have a considerable effect on the abundance of the perennial grass on the island (Lloyd and Linger 1986, Sherley 2016). *Ehrharta villosa* is known to become more abundant when grassland is moderately grazed (Tainton, et al. 1990). However, unlike at strand sites where the species was absent, Adamson (1934) observed *E. villosa* at inland dune sites. However, grass seemed to be negatively affected by rabbit herbivory as it only occurred among bushes of the hard, spiny and unpalatable woody shrubs such as *Lycium afrum* L. and *Lycium ferocissimum* Miers (Adamson 1934).

Given average and constant inter-annual rainfall, increase in cover of *E. villosa* would have remained one of the main drivers of grazing capacity change following rabbit control. Forage production by perennial grass would still have increased moderately across the years following rabbit control.

Conicosia pugioniformis

Inter-annual rainfall variation appears to have influenced ~39% of the change in forage production by the perennial herb *C. pugioniformis* following rabbit control. Forage production by the herb decreased moderately (29.86 kg DM ha^{-1} y^{-1}) between the first- and second years following rabbit control, did not change between the second- and third and increased slightly (2.21 kg DM ha^{-1} y^{-1}) between the third- and fourth (Annex VIII Table S2). Like at strand sites, the decline in forage production by the species between the first- and second years was probably not driven by worsening drought conditions but by competition with more competitive and drought-resistant plants such as *T. fruticosa*. Likewise, part of the decline in forage production between the first- and second years may have been caused by limited recruitment of new plants from seed to replace short-lived adult plants that died from senescence (see discussion on *C. pugioniformis* dynamics at strand sites).

However, unlike at strand sites, increased TAUR and TWR between the second- and third years did not result in increased forage production. Instead, increased TAUR may have indirectly suppressed forage production by driving the increase in cover of the more competitive *T. fruticosa*. The slight increase in forage production by *C. pugioniformis* between the third- and fourth years may have been in response to the decline in *T. fruticosa* cover caused by the decline in TAUR to slightly below the long-term average.

Given average and constant inter-annual rainfall, the decline in cover of *C. pugioniformis* would have remained of intermediate importance in driving grazing capacity change following rabbit control. Forage production by the perennial herb would most likely have decreased moderately between the first- and second years following rabbit control and remained constantly low in the subsequent years.

Ehrharta longiflora

Inter-annual rainfall variation appears to have influenced ~33% of the change in forage production by the annual grass *E. longiflora* following rabbit control. Forage production by the species decreased by 8.30 kg DM ha^{-1} y^{-1} to zero between the first- and second years following rabbit control, increased slightly between the second- and third and increased moderately (22.12 kg DM ha^{-1} y^{-1}) between the third- and fourth (Annex VIII Table S2). *Ehrharta longiflora* is a shallow rooted winter annual (Moore and Moore 2007a, Winston, et al. 2014). Germination of *E. longiflora* is controlled by soil moisture and seeds germinate following autumn and winter rainfall (Western Australian Herbarium 1998, Bossard, et al. 2000, Moore and Moore 2007b). The decline in TWR to below average may have driven the disappearance of the grass between the first- and second years. Total winter rainfall decreased from slightly to moderately below the long-term average between the first- and second years following rabbit control before increasing to slightly and moderately above the long-term average in the third and fourth.

Ehrharta longiflora re-emerged in the third year following rabbit control perhaps in response to above average TWR. Some of the increase (~25%) in forage production by the species between the third- and fourth years following rabbit control was clearly in response to the subsequent above average increase in TWR in the fourth year. *Ehrharta longiflora* is palatable (van Oudtshoorn 2012) and is favoured feed for rabbits on Robben Island (Gillham 1963). A previous study (Adamson (1934) did not report *E. longiflora* at inland dune sites when the island vegetation was under heavy rabbit herbivory. The grass was probably absent from inland dune sites due to intense rabbit herbivory and only re-emerged during the first year following rabbit control although a positive response by the species to rabbit control may have been limited by availability of suitable habitat. *Ehrharta longiflora* requires disturbed open sites for successful establishment (Winston, et al. 2014). Such habitats were not readily available at inland dune sites.

Given average and constant inter-annual rainfall, emergence of *E. longiflora* would have remained of minor importance in driving grazing capacity change following rabbit control. However, forage production by the grass would have increased slightly from zero between the first- and second years following rabbit control and remained constant in the proceeding years.

Avena fatua

Inter-annual rainfall variation appears to have influenced part (~42%) of the change in forage production by *A. fatua* following rabbit control. Forage production by the grass increased moderately from zero between the third- and fourth years following rabbit control. Forage production by the grass increased moderately from zero between the third- and fourth years following rabbit control (increased by 16.59 kg DM ha^{-1} y^{-1}; Annex VIII Table S2). Like *E. longiflora*, *A. fatua* is a winter annual (Stubbendieck, et al. 1992) that germinates in late autumn and early winter. Inadequate winter rainfall in the first three years proceeding rabbit control may have suppressed *A. fatua* germination and resulted in the absence of the grass. Total winter rainfall fluctuated about the long-term average in the first three years following rabbit control and increased to moderately above average in the fourth, which may have driven *A. fatua* germination and drove some (~22%) of the increase in forage production by the alien annual grass.

Avena fatua is palatable to herbivores (van den Berg, et al. 2009, van Oudtshoorn 2012). The species is missing from Adamson (1934) probably as a result of herbivory pressure. The grass would have become re-established following control of rabbit herbivory. However, the positive response of *A. fatua* to rabbit control may have been limited by availability of suitable habitat. *Avena fatua* commonly occurs in damp, pen, sunny sites (Halvorson and Guertin 2003). The grass is shade-intolerant (Parker, et al. 1982), and exhibits reduced growth, delays flowering and maturation, and diminished competitive ability when grown under shade (Halvorson and Guertin 2003). Root growth in *A. fatua* is also severely inhibited under shade conditions (Halvorson and Guertin 2003).

Given average and constant inter-annual rainfall, increased cover of *A. fatua* would have remained of minor importance in driving grazing capacity change following rabbit control. However, forage production by the species would have increased slightly from zero between the first- and second years following rabbit control and remained constant in the proceeding years.

REFERENCES

Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

Arnone II JA, Kestenholz C. 1997. Root competition and elevated CO_2: effects on seedling growth in *Linum usitatissimum* populations and *Linum–Silene cretica* mixtures. *Functional Ecology* 11: 209-214.

Barrett-Lennard. 2003. *Saltland Pastures in Australia*. Canberra: Land & Water Australia.

Bernhard-Reversat F. 1996. Nitrogen cycling in tree plantations grown on a poor sandy savanna soil in Congo. *Applied Soil Ecology* 4: 161–172.

Blasi C, Capotorti G, Copiz R, Guida D, Mollo B, Smiraglia D, Zavattero L. 2014. Classification and mapping of the ecoregions of Italy. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* 148: 1255-1345.

Bossard CC, J.M. R, Hoshovsky MC. 2000. *Invasive plants of California's wildlands*. Berkeley: University of California Press.

Coetzee K. 2008. Blaauwberg Conservation Area: management guidelines for larger wildlife and their habitats. *Report prepared for the Biodiversity Management Branch, City of Cape Town*.

Cowell CR. 2013. Investigating the most favourable seed establishment methods for restoring Sand Plain Fynbos on old fields. MTH, Cape Peninsula University of Technology, Cape Town.

Crawley MJ. 1990. Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology* 27: 803-820.

de Villiers AJ, van Rooyen MW, Theron GK. 2001. Seedbank phytosociology of the Strandveld Succulent Karoo, South Africa: a pre-mining benchmark survey for rehabilitation. *Land Degradation and Development* 12: 119-130.

del Moral R, Muller CH. 1969. The allelopathic effect of *Eucalyptus camaldulensis American Midland Naturalist* 83: 254–282.

Dye P, Jacobs S, Drew D. 2004. Verification of 3-PG growth and water-use predictions in twelve *Eucalyptus* plantation stands in Zululand, South Africa *Forest Ecology and Management* 193: 197-218.

Dye P, Versfeld D. 2007. Managing the hydrological impacts of South African plantation forests: An overview. *Forest Ecology and Management* 251: 121-128.

Farrow EP. 1917. On the ecology of the vegetation of Breckland. III. General effects of rabbits on the vegetation. *Journal of Ecology* 5: 1-18.

Fisher JL, Loneragan WA, Dixon K, Veneklaas EJ. 2009. Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. *Biological Conservation* 142: 256-269.

Freeman D, Balcom J, Chmielewski J. 2021. Genus: *Phyllobolus*. Available at https://www.succulentguide.com/cactus/?genus=Phyllobolus [accessed 22 March 2021]

Gillham ME. 1963. Some interactions of plants, rabbits and sea-birds on South African islands. *Journal of Ecology* 51: 275-294.

Guo LB, Sims REH. 2001. Effects of light, temperature, water and meat works effluent irrigation on eucalypt leaf litter decomposition under controlled environmental conditions. *Applied Soil Ecology* 17: 229–237.

Halvorson WL, Guertin P. 2003. Factsheet for: *Avena fatua* L. . *USGS Weeds in the West project: status of introduced plants in Southern Arizona parks*. Tucson: U.S. Geological Survey / Southwest Biological Center.

Harrington KC, Hodder LM, Outred HA. 1998. Biology and control of pypgrass. Paper presented at the Proceedings of the 51st New Zealand Plant Protection Conference.

Hodder LM. 1997. The biology and control of *Ehrharta villosa*, South African pypgrass. MSc, Massey University.

Hoffman MT, Carrick PJ, Gillson L, West AG. 2009. Drought, climate change and vegetation response in the succulent karoo, South Africa. *South African Journal of Science* 105: 54-61.

Jones K, Hanna E. 2004. Design and implementation of an ecological engineering approach to coastal restoration at Loyola Beach, Kleberg County, Texas. *Ecological Engineering* 22: 249-261.

Knevel IC. 2001. The life history of selected coastal foredune species of South Africa. DPhil, Rhodes University.

Le Maitre DC, van Wilgen BW, Gelderblom C, Bailey C, Chapman R, Nel J. 2002. Invasive alien trees and water resources in South Africa: case studies of the costs and benefits of management *Forest Ecology Management* 160: 143-159.

Lloyd JW, Linger MT. 1986. Report on the vegetation of Robben Island. *'n Natuurbewaringsondersoek van Robbeneiland*. Cape Town: Cape Nature

Louw G, Beukes T. 1988. Ken ons veldplante. *Die Noordwester*: 6-12.

Marchante E, Kjoller A, Struwe S, Freitas H. 2008 Short- and long- term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. *Applied Soil Ecology* 40: 210–217.

Marcum KB, Murdoch CL. 1992. Salt tolerance of the coastal salt marsh grass, Sporobolus virginicus (L.) kunth. *New Phytologist* 120: 281-288.

Masters DG, Benes SE, Norman HC. 2007. Biosaline agriculture for forage and livestock production. *Agriculture, Ecosystems & Environment* 119: 234-248.

Mfitumukiza D. 2004. Evaluating rangeland potentials for cattle grazing in a mixed farming system. MSc, International Institute for Geo-Information Science and Earth Observation, Enschede.

Moore CB, Moore JH. 2007. Annual veldgrass: *Ehrarta longiflora* Smith. HerbiGuide - The Pesticide Expert on a Disk Available at http://www.herbiguide.com.au/Descriptions/hg_Annual_Veldtgrass.htm. [accessed 25 September 2017]

Naidoo G, Mundree SG. 1993. Relationship between morphological and physiological responses to waterlogging and salinity in *Sporobolus virginicus* (L.) Kunth. *Oecologia* 93: 360-366.

Papini A, Signorini MA, Foggi B, Della Giovampaola E, Ongaro L, Vivona L, Santosuosso U, Tani C, Bruschi P. 2017. History vs. legend: Retracing invasion and spread of *Oxalis pes-caprae* L. in Europe and the Mediterranean area. *PLOS ONE* 12: e0190237.

Parker VT, Muller CH. 1982. Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. *American Midland Naturalist* 107: 69-81.

Rudman T 2003. Tasmanian beach weed strategy for marram grass, sea spurge, sea wheatgrass, pyp grass and beach daisy. Nature Conservation Branch, Department of Primary Industries, Water and Environment, Tasmania.

Sala A, Verdaguer D, Villa M. 2007. Sensitivity of the invasive geophyte *Oxalis pes-caprae* to nutrient availability and competition. *Annals of Botany* 99: 637-645.

Schmalzer PA, Hinkle CR (eds). 1987. *Species biology and potential for controlling four exotic plants (Ammophila Arenaria, Carpobrotus Edulis, Cortaderia Jubata, And Gasoul Crystallinum) on Vandenberg Air Force Base, California*. National Aeronautics and Space Administration, John F. Kennedy Space Center. Florida.

Sherley RB. 2016. Unusual foraging behaviour in two introduced mammals following degradation of their island habitat. *Biodiversity Observations* 7: 1-10.

Stubbendieck J, Hatch SL, Butterfield CH. 1992. *North American Range Plants*. Lincoln, Nebraska: University of Nebraska Press.

Tainton NM, Bransby DI, Booysen Pd. 1990. *Common veld and pasture grasses of Natal* (2nd edn). Pietermaritzburg: Shuter and Shooter.

Todd SW. 2000. Patterns of seed production and shrub association in two palatable Karoo shrub species under contrasting land use intensities. *African Journal of Range and Forage Science* 17: 22-26.

UWC Cape Flats Indigenous Nursery. 2021. Propagating *Phyllobolus canaliculatus* (Vingerkanna). Available at https://www.pinterest.co.uk/pin/593490057135262691/ [accessed 22 March 2021]

van Breda PAB, Barnard SA. 1991. *100 veld plants of the winter rainfall region: A guide to the use of veld plants for grazing*. Pretoria: Department of Agricultural Development.

van den Berg L, van Lingen M (eds). 2009. *Weidingswaardes (WIW) vir Karoo plantspesies – Hersiene weergawe*. Grootfontein Agricultural Development Institute. Middelburg.

van Leeuwen CG, van der Maarel E. 1971. Pattern and process in coastal dune vegetations. *Acta Bot. Neerl.* 20 191-197.

van Oudtshoorn F. 2012. *Guide to grasses of southern Africa*. Pretoria: Briza Publications.

Verdaguer D, Sala A, Vilà M. 2010. Effect of environmental factors and bulb mass on the invasive geophyte *Oxalis pes-caprae* development *Acta Oecologica* 36: 92–99.

Vilà M, Bartomeus I, Gimeno I, Traveset A, Moragues E. 2006. Demography of the invasive geophyte *Oxalis pes-caprae* across a Mediterranean island. *Annals of Botany* 97: 1055–1062.

Vural M, Dönmez AA. 2002. Two new taxa of *Silene* (Caryophyllaceae) from Turkey. *Annales Botanici Fennici* 39: 153-158.

Western Australian Herbarium. 1998. FloraBase - the Western Australian Flora. Department of Parks and Wildlife. Available at https://florabase.dpaw.wa.gov.au. [accessed 22 March 2021]

Williams AR. 2007. *Puccinellia* (Poaceae) in Western Australia. *Nuytsia* 16: 435-467.

Williams B, Wells TCE, Wells DA. 1974. Grazing management of Woodwalton Fen: seasonal changes in the diet of cattle and rabbits. *Journal of Applied Ecology* 11: 499-516.

Winston R, DesCamp W, Andreas J, Randall CB, Milan J, Schwarzländer M. 2014. *New invaders of the Southwest*. Washington, DC: Forest Health Technology Enterprise Team, United States Department of Agriculture.

ANNEXURE X: AVAILABLE ISLAND-SPECIFIC INFORMATION ON THE ECOLOGY OF ROBBEN, DASSEN, JUTTEN, SCHAAPEN, SEAL AND VONDELING ISLANDS

Overview

This supplementary document presents island-specific ecological data used to explore potential vegetation responses to rabbit control on South African offshore islands beyond Robben Island, building upon the theoretical framework outlined in Section V of the main text. While not exhaustive, rigorous efforts were undertaken to locate relevant published and unpublished literature through online searches on Google and Google Scholar. General keywords such as "Robben" OR "DASSEN" OR "Jutten" OR "Seal Island" OR "Vondelling" were initially used to identify potential sources. Subsequently, all identified sources were imported into a single library within the Qiqqa Research and Reference Management platform (Graham 2013). A purposive analysis was then conducted to pinpoint relevant island-specific ecological information within each retrieved publication. This involved meticulously scanning all collected literature for pertinent details, which were then annotated, tagged, and compiled into individual island-specific annotation reports. The information gathered during this process is presented in the following tables: Robben Island (Table S1), Dassen Island (Table S2), Jutten Island (Table S3), Schaapen Island (Table S4), Seal Island (Table S5), and Vondeling Island (Table S6).

Each table has the following sections:

- Island characteristics: This section describes the island's isolation, size, habitat types, soil conditions, and pre-existing herbivores.
- Rabbit herbivory history: This section details the history of rabbit herbivory on the island, including the duration and intensity of grazing, fluctuations in herbivory pressure, and control measures implemented.
- Post-rabbit control management: This section describes the eradication methods used or planned for use to remove rabbits from the island and the ongoing monitoring and control efforts to prevent future population surges.
- Additional information: This section provides details about existing ecological data, including vegetation surveys, soil analyses, and historical records. It also mentions the presence of specific plant functional groups, such as palatable and unpalatable species, and early and late successional species.

Robben Island

Location: 33°48’S, 18°22’E

Responsible Institution; Robben Island Museum

Table S1 Available island-specific information on the ecology of Robben Island

Key Factors	Available Information
1. Island Characteristics:	• Isolation: 11 km from Cape Town, with the nearest source of propagules at Bloubergstrand, approximately 7 km away (de Villiers 1971, Brooke and Prins 1986, Crawford and Dyer 2000). • Size and Habitat Heterogeneity: o Total area: 507 ha (Crawford and Dyer 2000). o Habitat types: ▪ Low-lying and gently undulating to flat terrain (Adamson 1934, Nankivell 1934, de Villiers 1971). ▪ Coastal areas primarily rocky, with a small sandy beach on the eastern shore (Adamson 1934, Nankivell 1934, Miller 1991). ▪ Varied vegetation types, historically resembling Cape Flats Dune Strandveld and Cape Seashore Vegetation (Crawford and Dyer 2000, Mucina and Rutherford 2006, Robben Island Museum 2006). The island has suffered extensive and prolonged exploitation by both humans and alien invasive organisms. This historical burden is evident in the island's flora, with a significant portion of the prevalent vegetation consisting of elements introduced over four centuries of human habitation (Nankivell 1934, Robben Island Museum 2006). • Soil Conditions: o Average soil depth: Variable, ranging from coastal-blown sand to deeper soils over limestone, shale, or rubble banks. Sand over limestone covers most of the island and is 0–70 cm thick, pale (lacking humus), without stones or gravel and has no definite stratification (Adamson 1934, Miller 1991) o Nutrient availability: Variable, with some areas containing limestone, wind-eroded dune sands, and sandy or rocky soils. Specific nutrient content data not readily available (Adamson 1934). • Pre-existing Herbivory: o Other herbivores present include helmeted guinea fowl, chukar partridge, Indian peafowl, springbok, fallow deer, and steenbok capacity (Crawford and Dyer 2000, Sherley 2016, Philander 2017). Their abundance impacts vegetation dynamics.
2. Rabbit Herbivory History:	• Duration and Intensity of Herbivory: o Time period: European rabbits introduced in 1654, present on the island for ~367 years (Measey, et al. 2020). o Grazing intensity: Fluctuating, with periods of low numbers (due to trapping, hunting, and predation) and surges during uninhabited phases (e.g., 2008) (Adamson 1934, Nankivell 1934, de Villiers, et al. 2010, Sherley 2016). • Herbivory Pressure Variability:

	o Fluctuations: Increased when the island was uninhabited, particularly in 2008 after desertion in 1998. Intensified when predation by feral cats was minimal or absent. o Control measures: Culling exercises and other attempts to control rabbit populations.
3. Post-Rabbit Control Management:	• Eradication Method: o Extensive culling program begun in 2008 and ongoing monitoring and control efforts to prevent future population surges (Anon 2008a, b, de Villiers, et al. 2010, Sherley 2016, Davies, et al. 2020, Measey, et al. 2020). European rabbits have not been observed on the island since 2019 (Davies, et al. 2020, Measey, et al. 2020). • Restoration Interventions: No formal restoration plan currently in place. However, ongoing monitoring and research may inform future interventions, such as: o Planting extirpated late successional and palatable species. o Habitat manipulation to favour desired plant functional groups. o Seed bank restoration techniques.
4. Additional Information:	• Existing ecological data includes: o Vegetation surveys conducted before and after rabbit control. o Soil analyses from various locations on the island. o Historical records of rabbit populations and vegetation changes. • Specific plant functional groups present: o Palatable vs. unpalatable species: Early successional palatable species like *Tetragonia fruticosa* and *Ehrharta* spp. have recovered well, while late successional palatable species are largely absent following rabbit control. Unpalatable species like *Conicosia pugioniformis* have declined in abundance following rabbit control. o Early vs. late successional species: Early successional species dominate currently, with limited recovery of late successional species following rabbit control due to factors like seed dispersal limitations and competition.

Dassen Island

Location: 33º25'S, 18º05'E

Responsible Institution; CapeNature Conservation

Table S2 Available island-specific information on the ecology of Dassen Island

Key Factors	Available Information
1. Island Characteristics:	• Isolation: 9 km from the mainland source of propagules (Brooke and Prins 1986, Keswick, et al. 2006). Other sources state the distance as 10 km (Ramsay, et al. 2002) and 11 km (Visagie and de Villiers 2019). • Size and Habitat Heterogeneity: 220 ha (3.2 km long and 1.6 km wide) (Underhill, et al., Mwema, et al. 2010). Other sources state the area as being 212 (Visagie and de Villiers 2019), 222 (Brooke and Prins 1986) and 224 ha (Apps 1986, Berruti 1986); habitat types include: o Low-lying, flat terrain with sandy soil (Apps 1986, Berruti 1986, Brooke and Prins 1986). o Rocky outcrops (few and on the island's periphery) (Berruti 1986). o Boulders (numerous and on the island's periphery) (Berruti 1986). o No wetlands (Mwema, et al. 2010). • Soil Conditions: o Average depth: Information not explicitly provided but described as generally low-lying and sandy. o Nutrient availability: Sandy soils with patches enriched by guano from seabirds and seals, likely low in overall nutrients (Visagie and de Villiers 2019). • Pre-existing Herbivory: o Birds: Cape gannet (*Morus capensis*), kelp gull (*Larus dominicanus*), and other seabirds (Brooke and Crowe 1982, Apps 1986, Berruti 1986) graze on vegetation, but likely minimal impact compared to rabbits. o Rodents: House mice (*Mus musculus*) present (Apps 1986, Berruti 1986), but population size and impact on vegetation unknown.
2. Rabbit Herbivory History:	• Duration and Intensity of Herbivory: Introduced between 1662 and 1668 (Apps 1986), thrived until oil-refiners thinned their numbers in the late 20th century (Skead 2011). Intensity likely varied over time but described as significant, contributing to reduced vegetation cover and species composition changes. • Herbivory Pressure Variability: Rabbit populations likely fluctuated due to hunting, disease, and food availability.
3. Post-Rabbit Control Management:	• Eradication Method: Plans for rabbit control not explicitly mentioned in the available literature. • Restoration Interventions: o No active restoration interventions implemented so far. o Potential future interventions could include: ▪ Planting of extirpated native species, particularly those with important ecological roles (e.g., nitrogen fixers). ▪ Habitat manipulation to control invasive species and promote native vegetation growth.

        - Seed bank restoration techniques if necessary.

4. Additional Information:

- Existing ecological data: The available literature mentions vegetation surveys and historical records of rabbit populations and vegetation changes. Further details or specific data sources would be helpful for comprehensive analysis.
- Vegetation information: The vegetation on Dassen Island is modified strandveld (Ramsay, et al. 2002). The vegetation consists of large open areas with low-growing mosses and annuals interspersed with taller plants (c. 25–100 cm) (Keswick, et al. 2006). The vegetation is sparse and open (Apps 1986, Berruti 1986, Keswick, et al. 2006), and has a highly ephemeral component, resulting in dramatic seasonal changes in vegetation (Ramsay, et al. 2002). *Tetragonia fruticosa* and *Tetragonia decurnbens* form patches of low scrub, whilst clumps of *Trachyandra divaricata* account for much of the remaining perennial vegetation (Ramsay, et al. 2002).
- Plant functional groups: Information not explicitly provided, but the literature sources mention salt-tolerant and ammonia-tolerant species (e.g., *Mesembryanthemum crystallinum*, *Preniu pallens*) (Brooke and Prins 1986) as well as herbivory-resilient ephemerals (e.g., *Urtica urms* and *M. crystallinurn*) (Ramsay, et al. 2002) suggesting adaptations to abiotic conditions and herbivory pressure on the island. Additional data on dominant species, growth strategies, and palatability would be valuable.
- Limitations:
    - The ecological information on Dassen Island in the available literature focuses primarily on feral cats and their impact on birds. More detailed data on rabbits, vegetation, and soil conditions would be needed for a comprehensive assessment of rabbit herbivory and post-control management.

Jutten Island

Location: 33°05'S, 17°57'E

Responsible Institution; SANParks

Table S3 Available island-specific information on the ecology of Jutten Island

Key Factors	Available Information
1. Island Characteristics:	• Isolation: Jutten Island is located 0.8 km from the mainland (Brooke and Prins 1986). • Size and Habitat Heterogeneity: The island is 46 hectares in size (Brooke and Prins 1986). Habitat details not available. • Soil Conditions: Information about the average soil depth and nutrient availability is not available. • Pre-existing Herbivory: No information on other herbivores. However, other herbivores, such as birds and rodents, are likely present on the island.
2. Rabbit Herbivory History:	• Duration and Intensity: Rabbits have been present on Jutten Island for at least 300 years (Skead 2011). • Herbivory Pressure Variability: There is no information available about fluctuations in rabbit populations.
3. Post-Rabbit Control Management:	• Eradication Method: The information available does not specify the planned approach for rabbit control. The chosen method will need to be effective in removing or significantly reducing the rabbit population while minimising impacts on other species and the environment. • Restoration Interventions: Information about planned actions to accelerate vegetation recovery is also not available. Restoration interventions could include planting native species, controlling invasive species, and managing habitats to create suitable conditions for plant establishment and growth.
4. Additional Information:	• The information available about Jutten Island is limited, and additional data is needed to fully understand the island's ecology and the potential impacts of rabbit removal. This additional information could include: o Existing ecological data, such as vegetation surveys, soil analyses, and historical information about rabbit populations or vegetation changes. o Information about the specific plant functional groups present on the island, such as palatable vs. unpalatable species and early vs. late successional species. This information would be helpful for predicting how different plant species might respond to rabbit removal and for planning targeted restoration interventions. • By gathering more information and carefully considering the island's specific characteristics and ecological context, land managers can develop a more effective and sustainable plan for rabbit control and post-rabbit control restoration on Jutten Island.

Schaapen Island

(Also known as Skaapeiland or Schapen Island)

Location: 33º06'S, 18º01'E

Responsible Institution; SANParks

Table S4 Available island-specific information on the ecology of Schaapen Island

Key Factors	Available Information
1. Island Characteristics:	• Isolation: 0.5 km from the mainland (Brooke and Prins 1986). • Size and Habitat Heterogeneity: 41 hectares (Brooke and Prins 1986). Habitat information not mentioned in available literature. • Soil Conditions: Information on soil depth and nutrient availability not available. • Pre-existing Herbivory: No information provided on other herbivores on the island, but seabirds likely present and could potentially impact vegetation to some extent.
2. Rabbit Herbivory History:	• Duration and Intensity of Herbivory: Rabbits present since at least 1781 and likely earlier (Skead 2011). Grazing intensity described as "prodigious" and rabbits used as a protein resource for sailors (Skead 2011). Intensity likely fluctuated over time depending on population size. • Herbivory Pressure Variability: Evidence of population fluctuations with records from 1781, 1803, 1804, 1953, 1982, and 2010 (Skead 2011).
3. Post-Rabbit Control Management:	• Eradication Method: The available literature does not mention an intended eradication method. • Restoration Interventions: No information provided on planned restoration actions.
4. Additional Information:	• Existing ecological data: Limited data available. Brooke and Prins (1986) and Skead (2011) provide some information on past vegetation and rabbit populations. • Vegetation information: Schaapen Island has historically been characterised by its natural vegetation cover (Brooke and Prins 1986). This condition has persisted since the final retreat of the last glacial ice sheet, which elevated the sea to its current level and transformed the high points of the former coastal plain into distinct islands (Brooke and Prins 1986). Consequently, the insular nature of Schaapen Island could have enabled the preservation of the fauna and flora present at the time of isolation, albeit subject to the inherent stochastic events that pose risks to populations on small islands (Brooke and Prins 1986). • Plant functional groups: Information on specific plant functional groups not available.

Seal Island

Location: 34°08'S, 18º35'E

Responsible Institution; Eastern Cape Nature Conservation (Part of the Woody Cape Nature Reserve)

Table S5 Available island-specific information on the ecology of Seal Island

Key Factors	Available Information
1. Island Characteristics:	• Isolation: 6 km from the mainland (Brooke and Prins 1986), • Size and Habitat Heterogeneity: 2 ha in total area (Brooke and Prins 1986). Habitat information is not provided in the available literature, but it is likely a small island with limited habitat diversity. • Soil Conditions: No information is available on soil depth or nutrient availability. • Pre-existing Herbivory: Information on other herbivores is not provided in the available literature.
2. Rabbit Herbivory History:	• Duration and Intensity of Herbivory: Explicit data is not available on the exact period of rabbit presence. However, the island has a long history (over 3 centuries) of rabbit herbivory. • Herbivory Pressure Variability: No evidence of rabbit population fluctuations is provided in the available literature.
3. Post-Rabbit Control Management:	• Eradication Method: Information about the planned rabbit control method is not provided in the available literature. • Restoration Interventions: Data on planned restoration actions is absent.
4. Additional Information:	• Additional Information: • Existing Ecological Data: The data provided is limited to location and size. Detailed vegetation surveys, soil analyses, and historical information are missing. • Plant Functional Groups: Information about specific plant groups present on the island is unavailable. • Limitations: o While the available information offers some baseline characteristics of Seal Island, it is insufficient to fully understand the island's ecology and the potential impacts of rabbit removal. For effective management and restoration, further data collection and analysis are crucial. This should include detailed habitat mapping, soil characterisation, surveys of existing vegetation and potential seed banks, and information about past and present rabbit populations. Additionally, understanding the specific plant functional groups present will be essential for predicting and managing vegetation recovery after rabbit removal.

Vondeling Island

Location: 33º09'S, 17°59'E

Responsible Institution; CapeNature Conservation

Table S6 Available island-specific information on the ecology of Vondeling Island

Key Factors	Available Information
1. Island Characteristics:	- Isolation: At 0.8 km, Vondeling Island is relatively close to the mainland (Brooke and Prins 1986). - Size and Habitat Heterogeneity: 21 hectares (Brooke and Prins 1986). Information on specific habitat types is not provided. However, the island is small and likely lacks diverse habitats. - Soil Conditions: Data on soil depth and nutrient availability is absent. - Pre-existing Herbivory: Information on the presence and abundance of other herbivores is not provided in the available literature.
2. Rabbit Herbivory History:	- Duration and Intensity of Herbivory: Rabbits have been present on Vondeling Island since at least the 17th century (possibly longer). The intensity of grazing is unknown, but it could be significant considering the small island size. - Herbivory Pressure Variability: No evidence of fluctuations in rabbit populations is available.
3. Post-Rabbit Control Management:	- Eradication Method: Information on the planned approach for rabbit control is unavailable. - Restoration Interventions: No data is available on planned restoration actions. Planting native species, habitat manipulation, and seed bank restoration could be potential interventions to accelerate vegetation recovery, if required.
4. Additional Information:	- Existing ecological data for Vondeling Island seems limited. Vegetation surveys, soil analyses, and information about rabbit populations and vegetation changes are crucial for effective restoration planning. - Specific plant functional groups present on the island are unknown. Identifying palatable, unpalatable, and early/late successional species is essential for understanding herbivory impacts and predicting recovery patterns.

References

Adamson RS. 1934. The vegetation and flora of Robben Island. *Transactions of the Royal Society of South Africa* 22: 279-296.

Anon. 2008a. Rabbits a threat to Robben Island. 'Available at' https://www.iol.co.za/news/south-africa/rabbits-a-threat-torobben-island-420389 [accessed 8 February 2017]

Anon. 2008b. Robben Island's rabbits to be culled. 'Available at' https://www.iol.co.za/news/south-africa/robben-islands-rabbits-to-be-culled-420363 [accessed 8 February 2017]

Apps P. 1986. A case study of an alien predator (*Felis catus*) introduced on Dassen Island: selective advantages. *South African Journal of Antarctic Research* 16.

Berruti A. 1986. The predatory impact of feral cats *Felis catus* and their control on Dassen Island *South African Journal of Antarctic Research* 16: 123-127.

Brooke RK, Crowe TM. 1982. Variation in species richness among the offshore islands of the southwestern Cape. *South African Journal of Zoology* 17: 49-58.

Brooke RK, Prins AJ. 1986. Review of alien species on South African offshore islands. *South African Journal of Antarctic Research* 16: 102-109.

Crawford R, Dyer B. 2000. Wildlife of Robben Island. In: Underhill L editor. *Bright Continent Guide*. Cape Town: Avian Demography Unit.

Davies S, Jordaan M, Karsten M, Terblanche J, Turner A, van Wilgen N, Veldtman R, Zengeya T, Measey J. 2020. Experience and lessons from alien and invasive animal control projects in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology*. Cham: SpringerOpen. p. 1302-1381.

de Villiers MS, Mecenero S, Sherley RB, Heinze E, Kieser J, Leshoro TM, Merbold L, Nordt A, Parsons NJ, Peter HU. 2010. Introduced European rabbits (*Oryctolagus cuniculus*) and domestic cats (*Felis catus*) on Robben Island: Population trends and management recommendations. *South African Journal of Wildlife Research* 40: 139-148.

de Villiers SA. 1971. *Robben Island: Out of reach, out of mind. A history of Robben Island*. Cape Town: Struik.

Graham K. 2013. TechMatters:"Qiqqa" than you can say Reference Management: A Tool to Organize the Research Process. *LOEX Quarterly* 40: 1-3.

Keswick T, Henen BT, Hofmeyr MD. 2006. Sexual disparity in activity patterns and time budgets of angulate tortoises (*Chersina angulata*) on Dassen Island, South Africa. *African Zoology* 41: 224-233.

Measey J, Hui C, Somers MJ. 2020. Terrestrial vertebrate invasions in South Africa. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA editors. *Biological Invasions in South Africa*. *Invading Nature - Springer Series in Invasion Ecology* No. 14. Cham, Swtzerland: Springer Open. p. 115-151.

Miller D. 1991. A geological description of Robben Island. *South African Lapidary Magazine* 23: 5-8.

Mucina L, Rutherford M (eds). 2006. *Vegetation map of South Africa, Lesotho, and Swaziland*. Pretoria: South African National Biodiversity Institute.

Mwema MM, de Ponte Machado M, Ryan PG. 2010. Breeding seabirds at Dassen Island, South Africa: chances of surviving great white pelican predation. *Endangered Species Research* 9: 125-131.

Nankivell JW. 1934. Robben Island. *The South African Geographical Journal* 17: 29-34.

Philander R. 2017. Robben Island to cull deer. 'Available at' https://www.iol.co.za/capeargus/news/robben-island-to-cull-deer-9940208 [accessed 26 October 2017]

Ramsay SL, Hofmeyr MD, Joshua QI. 2002. Activity patterns of the angulate tortoise (*Chersina angulata*) on Dassen Island, South Africa. *Journal of Herpetology* 36: 161-169.

Robben Island Museum (ed). 2006. *Integrated Conservation Management Plan (ICMP) for the Robben Island World Heritage Site*. Robben Island Museum Cape Town.

Sherley RB. 2016. Unusual foraging behaviour in two introduced mammals following degradation of their island habitat. *Biodiversity Observations* 7: 1-10.

Skead CJ. 2011. Historical incidence of the larger land mammals in the broader Western and Northern Cape In: Boshoff AF, Kerley GIH, Lloyd PH editors. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.

Underhill L, Kemper J, Whittington P, Wolfaardt A. 2000. Egyptian Goose *Alopochen aegyptiacus* moulting on Dassen Island. *Marine Ornithology* 28: 121–122.

Visagie J, de Villiers P 2019. South Africa. Dassen Island Nature Reserve. Ramsar Information Sheet. .