Assessment of fleshy-fruited invasive alien plants in eastern South African grasslands using community perceptions, seed germination and dispersal, and repeat photography

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ABSTRACT

Invasive fleshy-fruited trees and shrubs have been an increasing problem in many grassland systems over the past few decades because they change vegetation structure and threaten native plant diversity. However, forest ecosystems have received more attention than grasslands because fleshy-fruited plants are relatively dominant in the forest. This study aimed to address gaps in knowledge of fleshy-fruited invasive alien plants in montane grassland ecosystems of South Africa by studying socio-economic and environmental impacts, community perceptions, potential animal seed dispersal and population dynamics over time of dominant fleshy-fruited invasive alien plants. In the grassland biome of South Africa, the dominant fleshy-fruited invasive species come from the Rosaceae family and include *Cotoneaster pannosus*, *Pyracantha angustifolia*, and *Rosa rubiginosa*, which were the focus species for this study. These are widespread and damaging invasive plants within the grassland biome of many other countries, so understanding how each spread may assist in managing the species regionally and internationally. In Chapter 2, I reviewed the research efforts on fleshy-fruited invasive alien plants in grassland ecosystems and mosaics. The systematic review showed seed dispersal was the most studied concept of fleshy-fruited invasive alien plants in grasslands. In Chapter 3, this multifaceted study collated data from communities living within areas invaded by the species on their perceptions of these species through in-person, online and telephonic questionnaires to understand the socio-economic context of invasions and how people contribute to both spread and control. Questionnaire surveys showed that the general public does not regard *P. angustifolia* as a problem, while landowners and conservationists regard the species as a problem. The community has attempted to use herbicides, fire, and mechanical control, but the population of these invasives is still increasing, and the community has requested clearing assistance from the government. In Chapter 4, the rate of spread

was assessed by comparing recent photographs with historical ones. Repeat photography showed that fleshy-fruited invasive alien plants have increased in the grasslands over the past 12 years. In Chapter 5, I also assessed bird potential preference using choice trials. Fruit selection trials revealed significant differences among plant species by various frugivorous birds. In Chapter 6, the collection of excreta and subsequent seedling emergence from mammalian faecal samples assessed the involvement of mammals in the seed dispersal of fleshy-fruited invasive alien plants. Mammalian faeces collection showed medium to large-sized mammals to be effective seed dispersal agents of these invasive plants.

The study introduced a novel approach using Google Street View archives to assess vegetation population changes and provide a cost-effective means to study vegetation dynamics and ecosystem responses to environmental change. By identifying factors influencing fruit selection by frugivorous birds and locally occurring terrestrial mammalian species as effective seed dispersers, the research offers insights into the ecological mechanisms driving the spread of these invasive plants. Understanding these dynamics informs targeted intervention strategies for managing invasive plants more effectively, contributing to conservation efforts and biodiversity preservation. This study also highlights the need for further collaborative research to address the multifaceted challenges posed by invasive plant species.

PREFACE

The data described in this thesis were collected in the Eastern Cape, Free State and KwaZulu-Natal Provinces, Republic of South Africa, from February 2021 to December 2023. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof Colleen T. Downs, Prof Sandy-Lynn Steenhuisen (University of the Free State) and Dr Grant Martin (Rhodes University). This thesis, submitted for the degree of Doctor of Philosophy in Science 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.

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Lehlohonolo Donald Adams

April 2024

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

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Prof Colleen T. Downs

Supervisor

April 2024

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DECLARATION 1 - PLAGIARISM

I, Lehlohonolo Donald Adams, 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:
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DECLARATION 2 - PUBLICATIONS

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

PUBLICATION 1 (Provisionally accepted)

Role of local medium to large mammalian species in seed dispersal of fleshy-fruited invasive alien plants in the montane Grassland Biome of South Africa

Lehlohonolo D. Adams, Grant. D. Martin, Sandy-Lynn Steenhuisen and Colleen T. Downs

Author contributions:

LDA conceived the paper with CTD. LDA collected and analysed data and wrote the paper. CTD, SS and GDM contributed valuable comments to the manuscript.

PUBLICATION 2 (In prep- Not submitted)

Fleshy-fruited invasive alien plants in grasslands: A systematic review

Lehlohonolo D. Adams, Grant. D. Martin, Sandy-Lynn Steenhuisen and Colleen T. Downs

Author contributions:

LDA conceived the paper with CTD. LDA collected and analysed data and wrote the paper. CTD, SS and GDM contributed valuable comments to the manuscript.

PUBLICATION 3 (In prep- Not submitted)

Community perceptions of a fleshy-fruited alien plant *Pyracantha angustifolia* in South African grasslands

Lehlohonolo D. Adams, Grant. D. Martin, Sandy-Lynn Steenhuisen and Colleen T. Downs

Author contributions:

LDA conceived the paper with CTD. LDA collected and analysed data and wrote the paper. CTD, SS and GDM contributed valuable comments to the manuscript.

PUBLICATION 4 (In prep- Not submitted)

Drivers of fleshy-fruited plant invasions and change over time in the grasslands of South Africa along roadsides

Lehlohonolo D. Adams, Grant. D. Martin, Sandy-Lynn Steenhuisen and Colleen T. Downs

Author contributions:

LDA conceived the paper with CTD. LDA collected and analysed data and wrote the paper. CTD, SS and GDM contributed valuable comments to the manuscript.

PUBLICATION 5 (In prep- Not submitted)

The role of fruit colour and size in fruit selection by frugivorous birds of selected fleshy-fruited invasive alien plants

Lehlohonolo D. Adams, Grant. D. Martin, Sandy-Lynn Steenhuisen and Colleen T. Downs

Author contributions:

LDA conceived the paper with CTD. LDA collected and analysed data and wrote the paper. CTD, SS and GDM contributed valuable comments to the manuscript.

Signed: ……… [redacted] ……………

Lehlohonolo Donald Adams

April 2024

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This thesis is dedicated to the 14-old Lehlohonolo Donald Adams, who got excited when he learned that a person could study anything until they are called a Dr. He then vowed to study anything in nature until he is called a Dr. Dear Donny this is for you *mfanaka*.

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CHAPTER 1

INTRODUCTION

1.1 Biological invasions

To thrive, native species and ecological systems must withstand numerous anthropogenic threats, including climate change, habitat loss, and the introduction of alien species (Carwardine et al., 2018). Over the past few decades, researchers across various disciplines globally have been increasingly focusing on biological invasions (Nuñez et al., 2021), driven by the adverse effects associated with various types of invasions (van Wilgen et al., 2022). Alien species travel across geographical barriers mainly because of human transportation. When alien species become invasive, they impact native species' abundance and diversity, heightening their risk of extinction, altering the genetic makeup of native populations, and reshaping species community phylogenetic diversity while modifying trophic networks (Pyšek et al., 2020). These invasions are linked to both immediate and long-term impacts (van Wilgen et al., 2022), often becoming noticeable and problematic only after the alien species establish and expand their ranges (Pyšek et al., 2020). By disrupting nutrient and contaminant cycles, habitat structure, disturbance regimes, hydrology, and other factors, many alien invasive species can disrupt ecosystem function and the delivery of ecosystem services (Vilà and Hulme, 2017; Castro-Díez et al., 2019). These impacts on ecosystems and biodiversity are escalating and are expected to accelerate in the future (Duffy et al., 2017; Hughes et al., 2020).

South Africa is renowned for its rich biodiversity, characterised by high levels of floral and faunal endemism (van Wilgen et al., 2022). The country is home to three globally recognised biodiversity hotspots: the Cape Floristic Region, Maputaland-Pondoland Albany, and the Succulent Karoo (Mittermeier et al., 2004; Slingsby et al., 2023). However, for decades, ecologists have expressed concerns about the increasing threats posed by invasive species to the country's biodiversity, water resources, and the productivity of rural farming areas (van Wilgen et al., 2020). In response to these concerns, national programs have been implemented to mitigate the impacts of alien species on natural ecosystems and their services to humans (van Wilgen and Wannenburgh, 2016). Nonetheless, these national strategies require species-specific studies to better understand the invasion processes and enhance the effectiveness of invasive species control efforts. As many as 559 terrestrial plant species, 446 terrestrial invertebrate species, 77 freshwater fauna, and 56 marine species have been recorded as invasive species in South Africa (van Wilgen et al., 2020).

Trees and shrubs account for at least 50% of the terrestrial alien invasive plant species studied, particularly prevalent in Australia, southern Africa, and North America because of horticultural activities (Richardson and Rejmánek, 2011; van Wilgen et al., 2022). These woody species pose significant threats to rangelands, encroaching upon grassland ecosystems and reducing the carrying capacity for livestock (Carbutt, 2012; Yapi et al., 2018; O'Connor and van Wilgen 2020; Chikowore et al., 2021). Additionally, they alter thermal landscapes and food resources for small animal communities (Schreuder, 2016). Contrary to previous beliefs, high mountain regions are susceptible to alien plant invasions, with the richness of invasive species decreasing with increasing elevation (Vicente et al., 2013; Zefferman et al., 2015; Tecco et al., 2016; Pauchard et al., 2016; McDougall et al., 2018; Schickhoff et al., 2021). These invaders at high elevations tend to be generalists, and anthropogenic factors play a significant role in their distribution (Steyn et al., 2017; Fuentes-Lillo et al., 2021; Iseli et al., 2023).

1.2 Focal species

This study collated data on fleshy-fruited invasive alien plants (Figure 1.1). *Cotoneaster pannosus, P.angustifolia,* and *R. rubiginosa* were the main focal species of the study. Although other fleshy-fruited invasive alien and native fleshy-fruited plants were included in different chapters of this thesis. All these three focal species are category 1b invasive plants under the Alien and Invasive Species Regulations of the National Environmental Management: Biodiversity Act (NEM:BA) (South African Department of Environmental Affairs, 2014). Species in this category have the following restrictions: (a) importing into the country, (b) growing, breeding or in any other way propagating or causing the species to multiply, (c) conveying, moving, or otherwise translocating and (d) selling or otherwise trading of the specimen (DEA, 2014). Such species should be eradicated if possible or controlled.

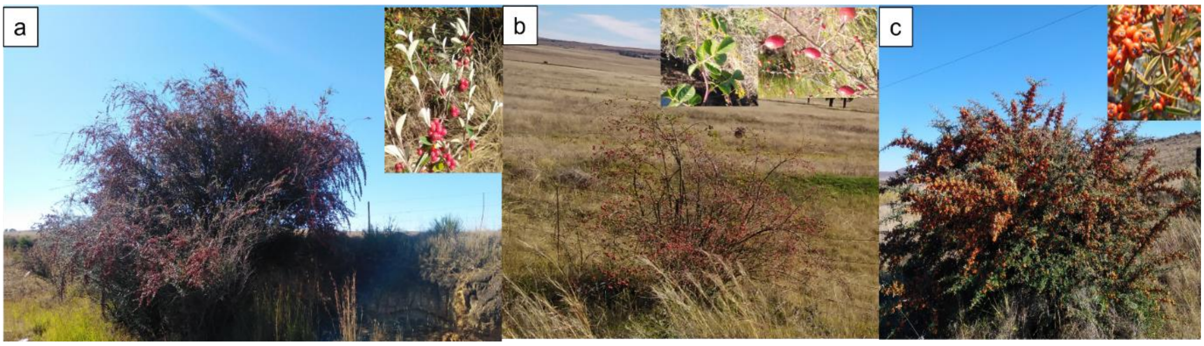

Figure 1.1: Three common fleshy-fruited invasive alien plants investigated in the study. (Note: letters show plant species a. *Cotoneaster pannosus*, b. *Rosa rubiginosa*, and c. *Pyracantha angustifolia*).

Cotoneaster pannosus (silver-leaf cotoneaster) is a semi-evergreen shrub that grows up to three meters high with berry-like fruits. It invades forest margins, rocky outcrops, and riverbanks. It originates from southwest China. It is cultivated as an ornamental species, a source of pollen for bees and hedging (Henderson, 2020). *Cotoneaster pannosus* has escaped cultivation and become invasive together with its congener species orange cotoneaster *C. franchetii* Bois and glaucous cotoneaster *C. glaucophyllus* Franch, at least in Argentina, South Africa, Spain, Hawai'i, California, Kenya and Australia (Starr et al., 2003; Mugo et al., 2015; Aymerich and Sáez, 2019; Moreschi et al., 2019). Although *C. pannosus* is initially dispersed in long distances via horticultural trade, further spread is aided by local seed dispersal through birds and mammals (Starr et al., 2003). Other species in this study also use the same mode of seed dispersal to increase their ability to invade. The seedlings sprout along fence lines, in pastures, roads, grasslands, woodlands and native shrublands (Starr et al., 2003; Henderson, 2020).

Pyracantha angustifolia (yellow firethorn) is an evergreen shrub that grows up to 6 m high and also produces pome fruits that are orange-red or orange-yellow (Adams, 2020). The sharp-pointed woody spines protect the plant from herbivores and make it difficult to handle. It also invades forest margins, rocky outcrops and riverbanks and originates from southwest China (Henderson, 2020). The plant and its congeners, red firethorn, *P. coccinea*, and Himalayan firethorn, *P. crenulata,* have naturalised in many countries and become invasive. This includes countries such as Argentina, Australia, Brazil, Canada, Columbia, England, and France (Guix, 2007; de Villalobos et al., 2010; Urcelay et al., 2019; Pereyra et al., 2022).

Rosa rubiginosa (eglantine or sweetbriar) is a compact, deciduous shrub that is 1-2 m high with slightly arching branches. Its branches have thorns and are interspersed with rusty, granular hairs and bristles. This plant is cultivated for hedging and ornament, and the fruits are harvested. The species have been introduced to North America (e.g., California, New York, Texas), South America (e.g., Argentina Northeast, Bolivia, Chile Central), Africa (e.g., Cape Provinces, KwaZulu-Natal, Lesotho), Australia (e.g., New South Wales, Queensland, Tasmania), and more. It invades high-altitude grasslands, riverbanks, moist valleys, rocky outcrops and overgrazed land, and it originates from Asia and Europe (Henderson, 2020).

All these invasive alien plant species are prospects for biological control in South Africa (Martin, 2021). These are widespread and damaging invasive plants in South Africa and many other countries, so understanding how they spread is an important aspect of the ecology of the species and how it is invasive.

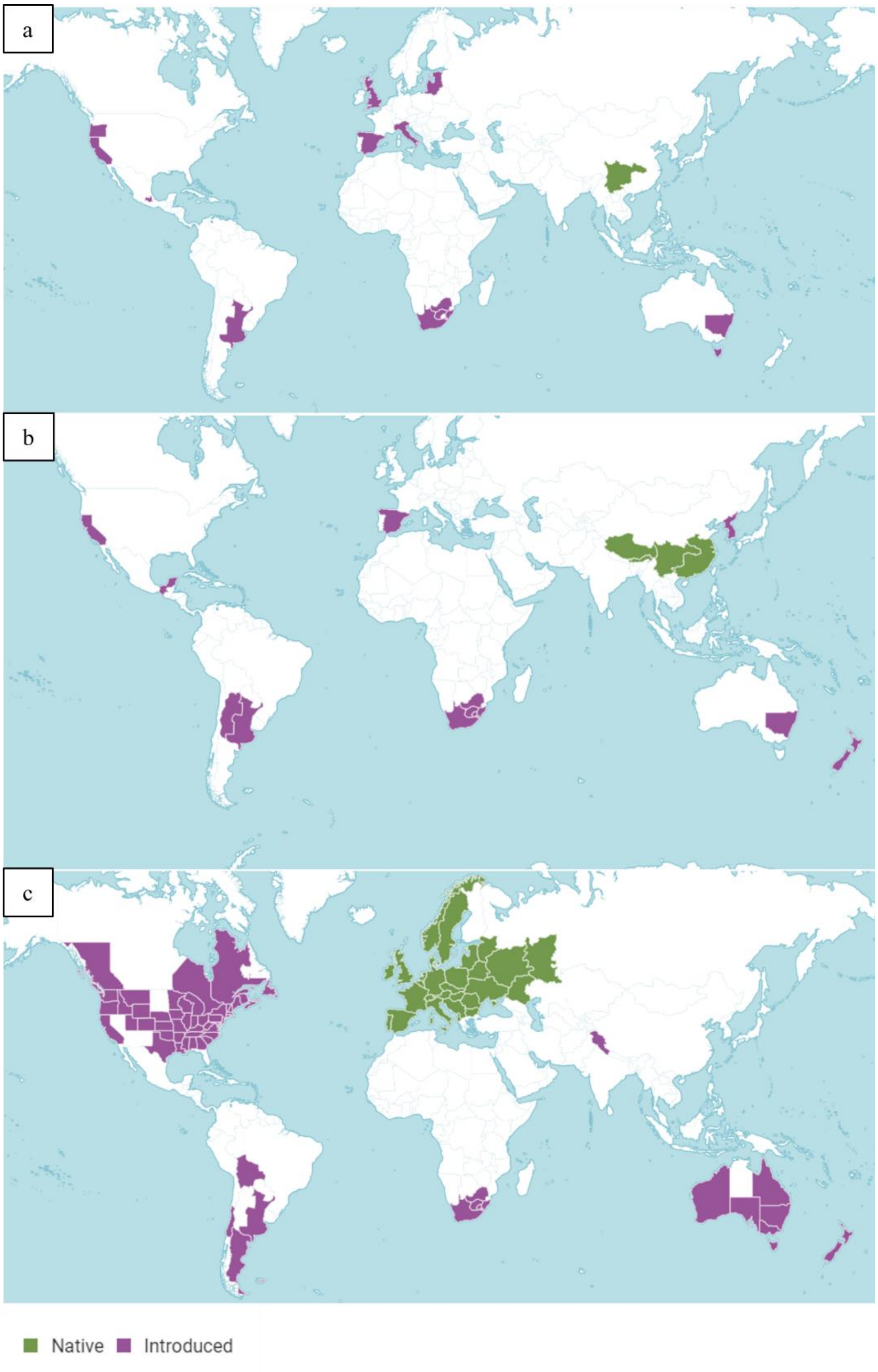

Figure 1.2: Global distribution of the three common fleshy-fruited invasive alien plants investigated in the study. (Note: letters show plant species a. *Cotoneaster pannosus*, b. *Pyracantha angustifolia*, and c. *Rosa rubiginosa*. Colour purple shows the introduced range of the species, and green shows the native distribution. Map source: Plants of the World 2024).

1.3 Study area

Globally, grasslands cover approximately 40% of the Earth's surface, of which 69% is agricultural land (O'Mara, 2012). They are the most widespread vegetation type and are found everywhere except Antarctica. (Figure 1.2). Temperate grasslands are more common in the Northern Hemisphere and are geographically associated with regions experiencing temperate climates (Allaby, 2006; O'Mara, 2012). The most extensive distribution of temperate grasslands is in North America, Eastern Europe, and portions of Asia encompassing Turkey, northern Iran, and southern China (Allaby, 2006). Due to the comparatively diminished landmass south of the Tropic of Capricorn in the Southern Hemisphere, temperate grasslands are restricted to specific areas within Argentina, Peru, and South Africa.

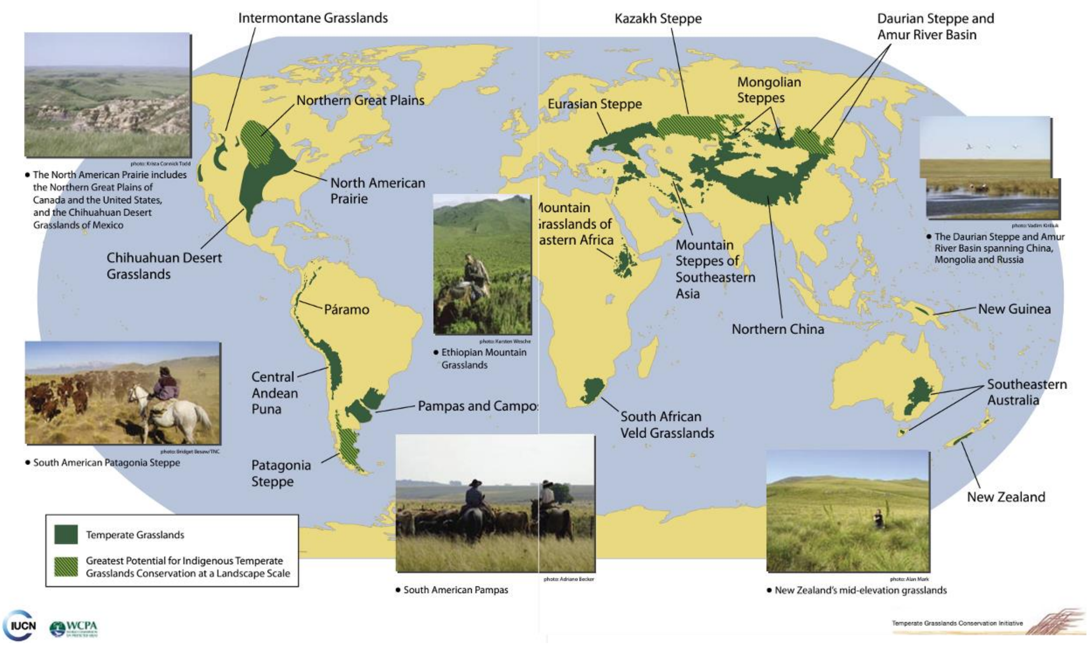

Figure 1.3: Map showing the distribution of grasslands. (Note: pictures on the map shows how particular grasslands look like, Source: IUCN, 2024).

Grasslands act as important biodiversity reservoirs and provide humans with material and non-material benefits. These benefits include ecosystem services like food production, water regulation and supply, climate mitigation, pollination and a host of cultural services (O'Mara, 2012; Bardgett et al., 2021). Despite the important benefits, grassland degradation is widespread and becoming worse in many parts of the world, with at least 49% of the total grassland area being degraded to some extent (Gibbs and Salmon, 2015; Lark et al., 2020). For this reason, grasslands need to be preserved, but they remain one of the least conserved ecosystems, and only about 2% have been conserved (Bardgett et al., 2021).

1.4 Motivation for the study

Fleshy-fruited trees and shrubs have been an increasing problem over the past decades in the montane grasslands in southern Africa (Carbutt, 2012; Canavan et al., 2021). Fleshy-fruited invasive plant species have been a problem in South Africa (Bitani et al., 2020, 2022; Mbobo, 2022). These species are predominantly bird-dispersed in forest systems, and as a result, the invasion of bird-dispersed species in forest ecosystems has received much more attention than other ecosystems like grasslands (Henderson, 2007; Bitani et al., 2020). This underrepresentation is not exclusive to South Africa; drivers of invasion and ecology of fleshy-fruited invasive alien plants have been underrepresented in literature globally in grasslands (Gosper et al., 2005; Adams, 2020; Bellis et al., 2020; Vergara-Tabares et al., 2022; Plenderleith et al., 2022; Dáttilo et al., 2023; Zhu et al., 2023). This study aimed to address gaps in knowledge on the effects of fleshy-fruited invasive alien plants in grassland ecosystems by studying socio-economic and environmental impacts, community perceptions, population dynamics over time and animal seed dispersal.

1.5 Aims and objectives

The primary aim of the study was to determine the main drivers of invasion of fleshy-fruited invasive alien plants in the montane grasslands of South Africa. The study examined the socio-economic and environmental impacts associated with these fleshy-fruited invasive alien plants. To achieve this aim, the objectives addressed included (1) reviewing research conducted on fleshy-fruited invasive alien plants in grasslands, (2) assessing the impact of invasion on montane grassland vegetation and landscapes using repeat photography of historical photographs and vegetation surveys, (3) determining the involvement of animals in seed dispersal of these invasives by assessing seed composition in animal faeces, and conducting germination trials and field observations, (4) determining the conflict of interest in management and the effect of humans on spreading these invasives by conducting questionnaires, and (5) evaluating the role of birds on seed dispersal through conducting fruit choice trials in with captive frugivorous birds.

1.6 Structure of the thesis

The central part of this thesis is structured as manuscripts intended for publication in peer-reviewed journals as scientific articles. Chapter 1 serves as the introduction, offering a literature review of the concepts explored in this study. Following this, Chapters 2 through 5 each present empirical findings related to specific objectives formatted in accordance with the respective target journals. Despite some unavoidable repetition, particularly in the methods section because of the thesis format, this repetition is considered minor as it allows readers to approach each chapter independently while maintaining the overall context of the thesis. Chapter 2 reviews research on fleshy-fruited invasive alien plants in grassland ecosystems and mosaic grasslands to assess existing efforts in this area. Chapter 3 examines community perceptions of a selected fleshy-fruited invasive alien plant *P. angustifolia* in the Free State Province, compiling data on its uses, management efforts, and control effectiveness. Chapter 4 analyses vegetation changes over time and identifies drivers of invasion along roadsides and farms using repeat photography. Chapter 5 investigates seed dispersal by birds, focusing on fruit selection by captive aviary birds. The role of mammals in the seed dispersal of fleshy-fruited invasive alien plants in montane grasslands is examined in Chapter 6. Finally, Chapter 7 comprises a comprehensive discussion, conclusions, and recommendations drawn from the study.

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CHAPTER 2

Fleshy-fruited invasive alien plants in grasslands: A systematic review

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Running header: Systematic review of fleshy-fruited invasive alien plants

2.1 Abstract

Grasslands are found across various biogeographic regions, encompassing a substantial portion of terrestrial landscapes. They are crucial hubs of biodiversity and integral providers of essential ecosystem services such as pollination, seed dispersal and carbon sequestration. However, despite their ecological significance, grasslands face multiple threats, such as invasion by alien plants. While these invasions have historically been dominated by large invasive trees such as *Eucalyptus* species, more recently, an increase in fleshy-fruited shrubs and trees has been noted. Existing research on fleshy-fruited plants has mainly focused on forest ecosystems, with reviews emphasising seed dispersal dynamics. Our review explores existing peer-reviewed literature on fleshy-fruited invasive alien plants within grassland ecosystems and their mosaics. Grassland mosaics refers to study areas where the grassland had patches of other ecosystems or other ecosystems having patches of grasslands We systematically searched articles from databases (Google Scholar, Scopus, Web of Science, and ScienceDirect), and developed Boolean search strings derived from scoping searches. This method led us to identify and include 32 articles that met the defined criteria on 50 species. Our findings reveal that the most frequently studied plant families in this context were Rosaceae and Solanaceae, and Argentina and South Africa emerged as the leading contributors to research on this topic. The most frequently mentioned plant species were *Lantana camara*, *Ligustrum lucidum*, *Melia azedarach*, *Morus alba* and *Pyracantha angustifolia*. This synthesis of research underscores the importance of continued research collating empirical data on fleshy-fruited invasive alien plants in the grasslands and other treeless ecosystems to address knowledge gaps and mitigate their escalating threats. This review shows research gaps that could direct future research on fleshy-fruited invasive alien plants in the grasslands.

Keywords: biological invasions, fruit-bearing plants, woody invasion, global review

2.2 Introduction

Grasslands are found across various biogeographic regions, and they cover a significant portion (~40%) of the total terrestrial landscape (Neary and Leonard, 2020). They host rich biodiversity, supporting a multitude of organisms (Murphy et al., 2016). Furthermore, these grasslands are not just biodiversity hotspots; they offer crucial ecosystem services. They provide high-quality forage for herbivores (Boval and Dixon, 2012), serve as habitats for pollinators crucial for both crops and native species (Bendel et al., 2019; Bengtsson et al., 2019), and play a significant role in carbon sequestration (Eze et al., 2018; Bai and Cotrufo, 2022). Additionally, they serve as spaces for recreational and cultural activities, enhancing human well-being (Gómez-Limon and de Lucio, 1995). They also afford many other environment-stabilising services, such as soil erosion control and mitigation of floodwaters (Bengtsson et al., 2019).

Grasslands, despite their ecological significance, are among the most altered landscapes globally, demanding urgent action to restore their vital services (Stanton et al., 2018; Bernath-Plaisted et al., 2023). Multiple factors contribute to this decline, including habitat degradation because of energy development and infrastructure (Daniel and Koper, 2019; Shaffer et al., 2019; Ott et al., 2021), intensified agriculture and pesticide use (Case and Staver, 2016; Stanton et al., 2018; Moreau et al., 2022; Douglas et al., 2023), ongoing challenges in fire and grazing management (Duquette et al., 2022; Raynor et al., 2022), the escalating threat of climate change (Wilsey et al., 2019; Maresh Nelson et al., 2023), and shrub encroachment from both native and invasive species (Van Auken, 2009; Scholtz et al., 2018; Andersen and Steidl, 2019). Collectively, these factors pose significant challenges to the conservation and sustainability of these essential ecosystems and their associated biodiversity. It is also worth noting that the grasslands are one of the least conserved biomes (Bernath-Plaisted et al., 2023).

Invasive alien species threaten grasslands, impacting their grazing capacity and altering vegetation structure (Yapi et al., 2018; Humphries et al., 2020). Of particular concern are invasive shrubs and trees (Richardson and Rejmánek, 2011; Richardson et al., 2014). Many of these invasive woody species act as 'transformers' (Richardson et al., 2000), significantly altering ecosystems by directly affecting numerous functions and indirectly influencing the characteristics of indigenous species and their ecosystems (Aerts et al., 2017).

In recent decades, shrub and tree invasions have attracted more research attention, with an increase in the number of species, expanded invaded areas, diverse impacts, and mounting challenges in management strategies (Richardson and Rejmánek, 2011; Richardson et al., 2014; van Wilgen et al., 2022). These invasions often detrimentally affect biodiversity, economic prospects, and water yield (Pejchar and Mooney, 2009; Pyšek et al., 2012; Vítková et al., 2017; Vilà and Hulme, 2017; Yapi et al., 2018; Nuñez et al., 2021). Among the most frequently cited invasive alien plant species causing severe environmental and socioeconomic problems is the fleshy-fruited invasive alien plant *Lantana camara* L. (Verbaneaceae) (Henderson, 2007; Boy and Witt, 2013). Its presence alters ecosystem processes, earning it the classification of an ecosystem engineer (Richardson and van Wilgen, 2004).

Most fleshy-fruited shrubs and trees are primarily dispersed by birds and there is a growing body of research on invasion by these plants (Richardson and Rejmánek 2011; Bitani and Downs, 2022; Adams et al., 2022; Juncosa-Polzella et al., 2023, Palacio et al., 2023). There are few reviews of the literature published on fleshy-fruited invasive plants (Gosper, 2005; Buckley et al., 2006; Aslan and Rejmánek, 2012; Wotton and McAlpine, 2015; Vanderhoff and Rentsch, 2022; Cordero et al., 2023). However, most of these reviews focus on seed dispersal (Aslan and Rejmánek, 2012; Wotton and McAlpine, 2015; Vanderhoff and Rentsch, 2022; Cordero et al., 2023). While some reviews on fleshy-fruited invasive alien plants are species-specific (e.g. Taconi and Pires, 2021), others are genus-specific or family-focused (e.g. Mbobo et al., 2022). In our systematic review, we focused on all fleshy-fruited invasive alien plants species rather than specific plant families or genera. This allowed us to identify the most studied concepts and identify the research gaps. Our study aimed to assess research efforts on fleshy-fruited invasive alien plants in grassland ecosystems and mosaics through a global review of peer-reviewed publications.

2.3 Methods

2.3.1 Research question, scoping search and literature mapping

Foo's (2001) practical guide for ecologists and evolutionary biologists on formulating a question for a systematic review and finding a representative sample of research findings was used. This ensured that question formulation and locating relevant literature was standardised (Purssell and McCrae, 2020). The initial question for the study was about fleshy-fruited invasive alien plants. This question aimed to address the research on fleshy-fruited invasive alien plants without limitation to specific ecosystems, but the scope was too large, and thus, the focus was narrowed to grasslands. To assess the topics studied most about fleshy-fruited invasive alien plants in grasslands and whether there is enough primary research done on the topic for a systematic review (Purssell and McCrae, 2020), we searched "Fleshy-fruited invasive alien plants in grasslands" in February 2022 using Google Scholar without any restrictions and the search resulted in 842 results (see Foo, 2021 for scoping review methods).

We scanned the first five pages of the search for empirical studies to download relevant papers. The first 20 articles reporting on empirical studies where data were collected from the field on fleshy-fruited invasive alien plants were downloaded (Foo, 2021). The presence of the latter empirical studies indicated that there is enough information on the topic for synthesis (Foo, 2021). We used the 20 empirical studies to map out the literature in two ways. From these articles, we (1) extracted author keywords and organised them into categories and (2) generated word clouds from abstracts and titles using MonkeyLearn (MonkeyLearn Inc, 2023) (Figure 2.1). The scoping search indicated that seed dispersal, reproductive traits, and plant-animal interactions were the most studied aspects. Environmental impacts and human involvement in dispersal were less studied. From author key-words showed that the categories of topics studied were plant-animal interactions, reproductive traits, seed dispersal, plant form and environmental impacts.

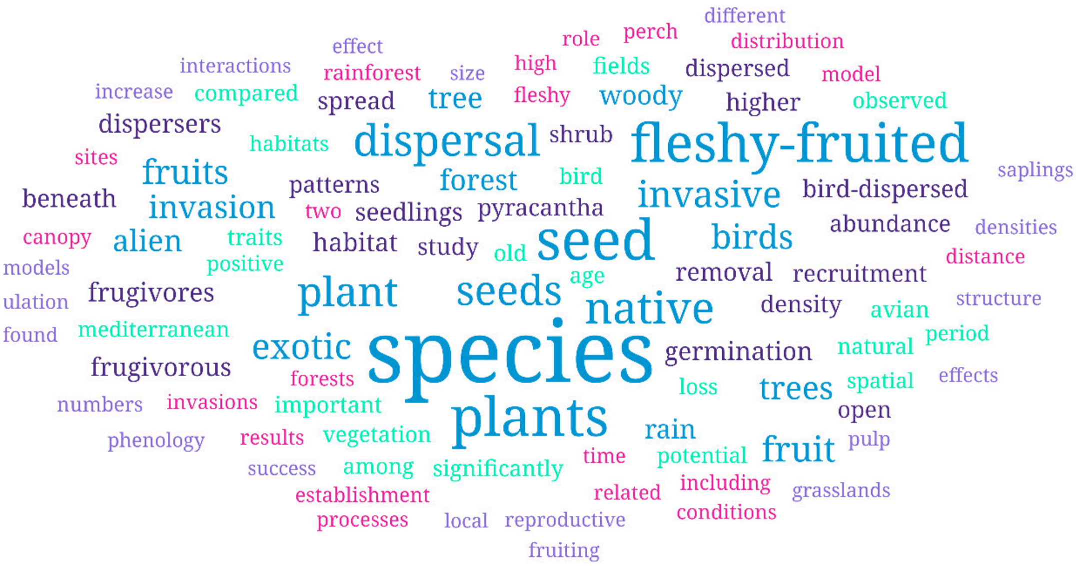


Figure 2.1: Word cloud generated from abstracts and titles of the first 20 articles on empirical studies from Google Scholar using MonkeyLearn. (Note: The number of times the term appeared on the title and abstracts is indicated by the font size. The bigger the font, the higher the frequency. Different colours have been grouped to arrange words of similar size).

2.3.2 Literature search

We included records of studies that collected empirical data in the field on one or more fleshy-fruited invasive alien plants in a grassland or mixed habitat that had grassland patches. We used the phrases "fleshy-fruited" OR "fleshy fruited" AND "alien" OR "Non-native" AND "grassland" to search in Science Direct on 08 February 2022. The search resulted in 4074 records. The search was refined by limiting publication titles to Agriculture, Ecosystems and Environment, Basic and Applied Ecology, Biological Conservation, Ecological Indicators, Ecological Modelling, Flora, Global Ecology and Conservation, Journal of Arid Environments, Journal of Environmental Management, Land Use Policy, Perspectives in Plant Ecology, Evolution and Systematics, Plant Science, Rangeland Ecology and Management, Rangelands, Remote Sensing of Environment, South African Journal of Botany and Trends in Ecology and Evolution. We were left with 1408 records after limiting publication titles. We searched the following combinations: (All fields = (invasi* OR invader OR alien OR exotic OR ruderal OR weed OR non-native OR introduced OR naturalis* OR non-indigenous) AND All fields = (plant OR flora OR ecolog*) AND All fields = (grassland) AND All fields = (fruit* OR bird OR frugi* OR fleshy*)); on Web of Science and received 410 records. We used the Boolean search: (ALL ((invasi* OR invader OR alien OR exotic OR ruderal OR weed OR non-native OR introduced OR naturaliz*) AND topic = (plant OR flora) AND topic = (grassland))) AND (fruit OR fleshy-fruited) AND (LIMIT-TO (SUBJAREA, "AGRI") OR LIMIT-TO (SUBJAREA, "ENVI")); to search for records from Scopus. The search string resulted in 490 records refined to limit the search to the subject areas of Agricultural and Biological Sciences, and Environmental Science from an otherwise 644 unrestricted records. Different search strings were used according to program specifics. "Fleshy-fruited" OR "fleshy fruited" AND "alien" OR "non-native" OR "invasive" AND "grassland*" were searched on Google Scholar. All record titles were listed on an Microsoft® Excel® spreadsheet, and duplicates were removed using the duplicate function. We undertook record screening in two phases guided by the screening flowchart (Figure 2.2). The initial phase included assessing relevant records by reading the title, abstract and author keywords. The second phase included screening the full text, where we scanned the whole document for inclusion/exclusion. Search alerts were created in ScienceDirect, Scopus and Web of Science and were screened for inclusion or exclusion.

2.3.3 Inclusion and exclusion criteria

For a study to be included in this review, it had to meet the following criteria: 1) It must be an original research article collecting data in the field, 2) it had to include or focus on invasive alien plants that bear fleshy fruit pulp, and 3) it must have collected the data in a grassland biome or mosaic grassland microhabitat. The search did not exclude studies based on publication year.

2.3.4 Data analyses

Data obtained from the original articles were analysed using descriptive statistics. Microsoft® Excel® for Microsoft 365 was used to generate frequencies and percentages to present trends.

2.4 Results

2.4.1 Peer-reviewed publications

Only 32 peer-reviewed publications ranging from 1994 to 2023 met the selection criteria and were included in the review (Figure 2.2). The oldest study dated back to 1994, and publication records started increasing in 2016 and reached a peak in 2022 (Figure 2.3).

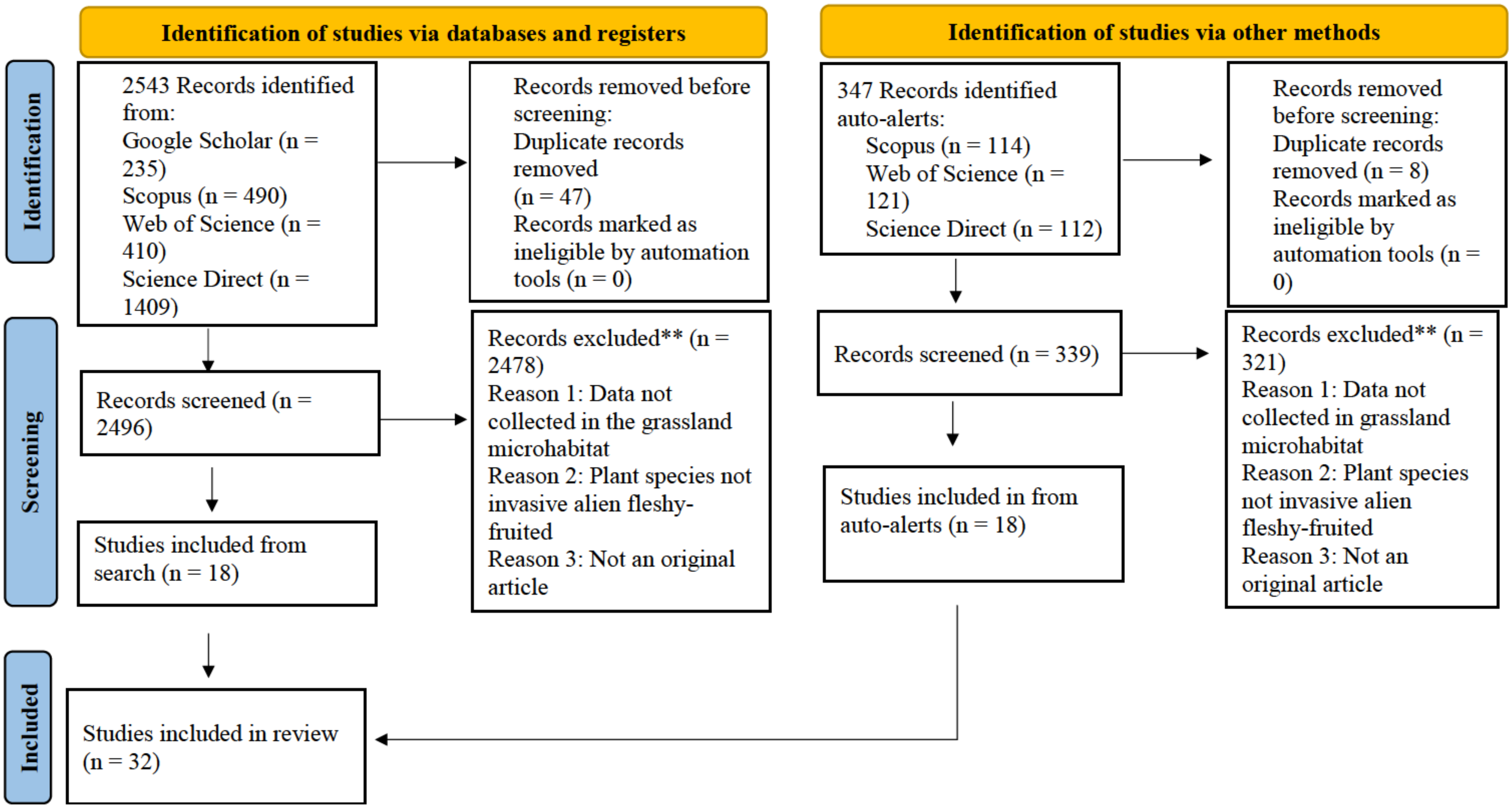


Figure 2.2: Modified PRISMA model showing the screening process used to search and select relevant articles for the study.

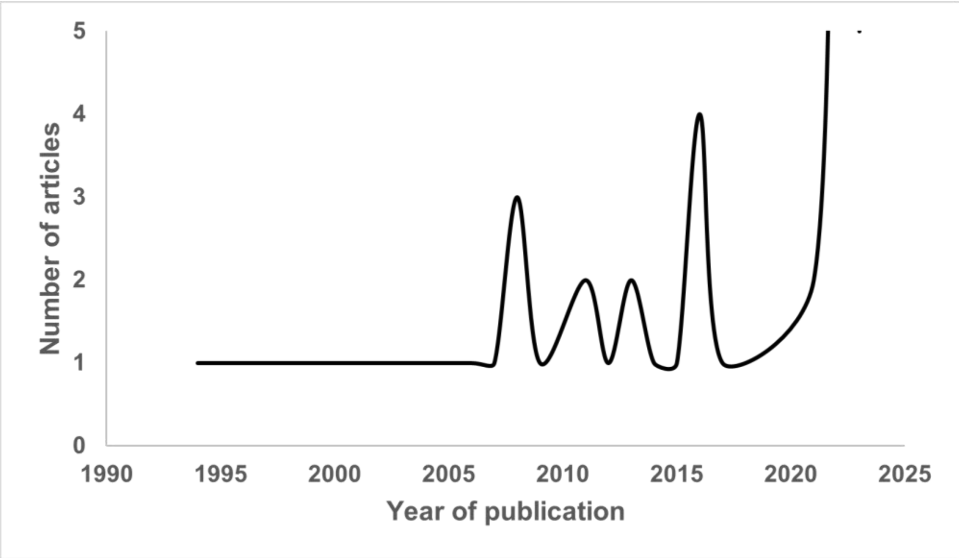


Figure 2.3: Number of published original research articles between 1994 - 2023 on fleshy-fruited invasive alien plants globally that met the selection criteria in the present study.

2.4.2 Concepts studied

Many concepts were covered in the publications. However, the Word cloud showed that seed dispersal was the most studied concept (Figure 2.4).

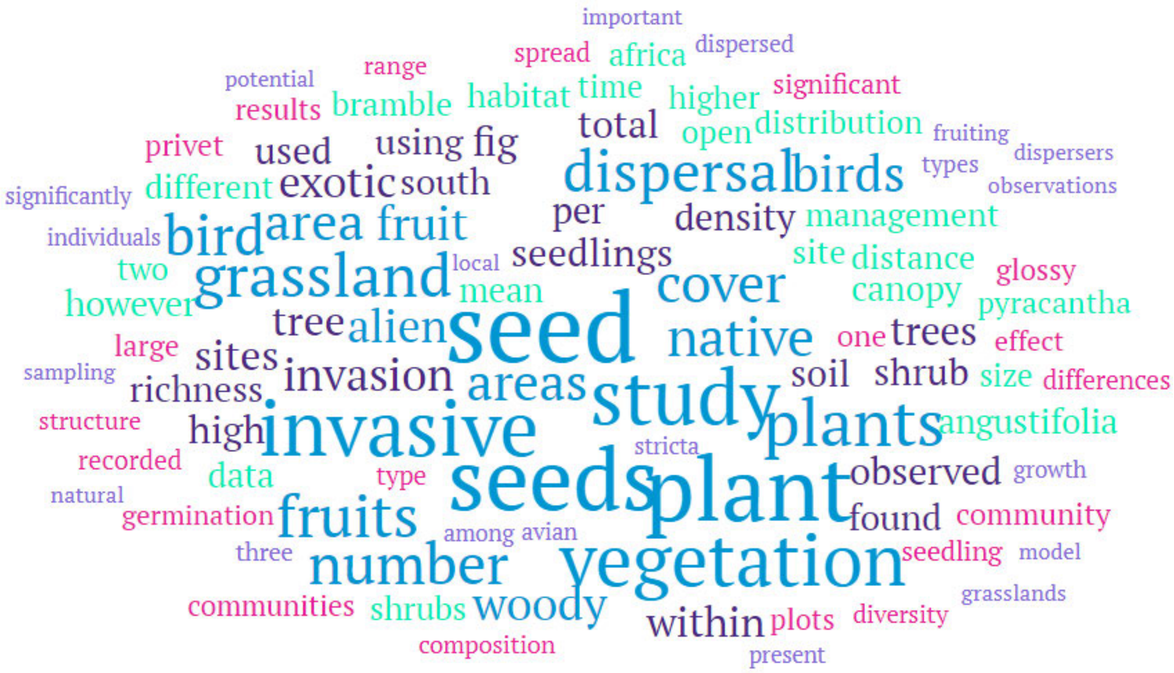


Figure 2.4: Word cloud showing word frequencies from original articles excluding references, authors' names and addresses. (Note: The number of times the term appeared on the title and abstracts is indicated by the font size. The bigger the font, the higher the frequency. Different colours have been used to arrange words of similar size).

2.4.3 Geographic location

Studies included in the review collected data from Argentina, Belgium, Canada, China, Czech Republic, France, Hungary, India, Kenya, Silicy, South Africa, the United States of America and Zimbabwe. Most studies were conducted in South Africa (43.8%), followed by Argentina (18.8%) (Figure 2.5).

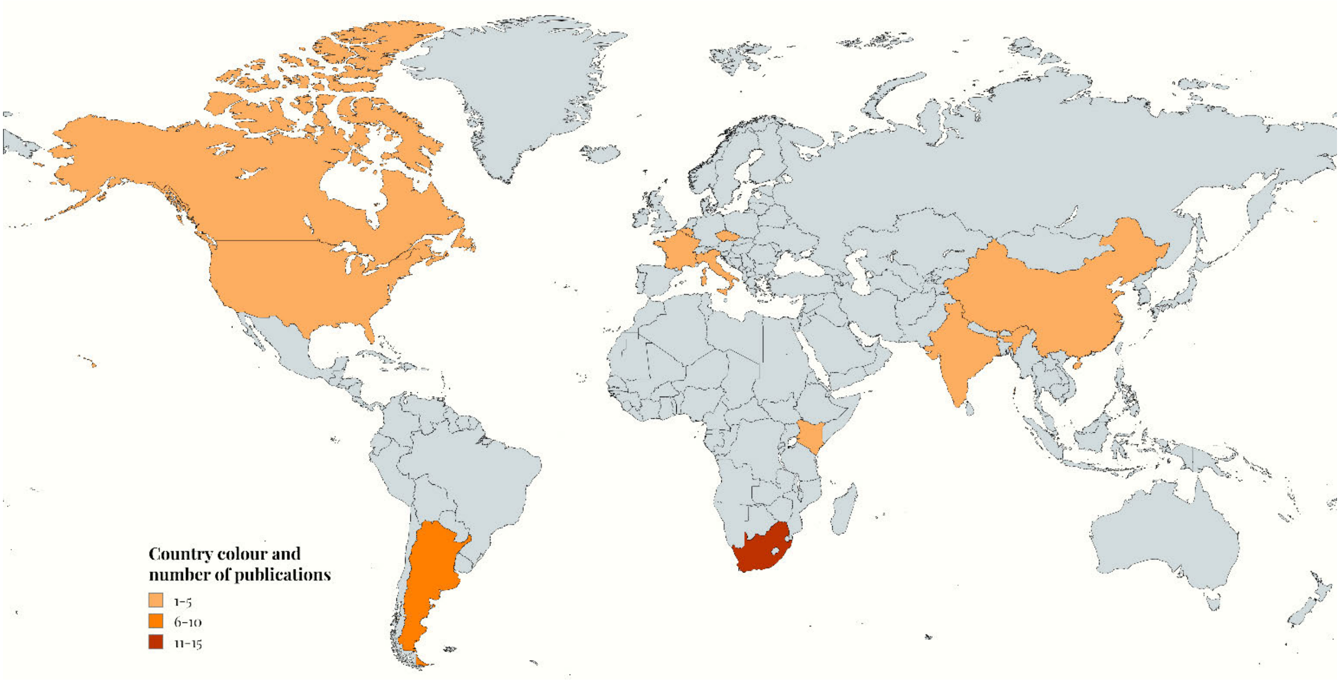


Figure 2.5: The number of studies per country on invasive fleshy-fruited invasive alien plants in grassland ecosystems and mosaics globally included in the present review up to November 2023.

2.4.4 Plant taxonomy

Out of 51 species studied, *Lantana camara* L. (Verbenaceae), *Ligustrum lucidum* W.T.Aiton (Oleaceae), *Melia azedarach* L. (Meliaceae), *Morus alba* L. (Moraceae), and *Pyracantha angustifolia* (Franch.) C. K. Schneid (Rosaceae) were the most frequently studied fleshy-fruited invasive alien plant species. There have been more studies on Rosaceae and Oleaceae in terms of the number of publications, but more species of Rosaceae and Solanaceae studies in terms of the diversity of species studied (Table 2.1). Fewer plant species studied were perennial subshrubs; most study species were woody shrubs and trees (Table 2.1).

Table 2.1: List of fleshy-fruited invasive alien plants that have naturalised in grassland habitats and mosaics globally.

Plant species/genus	Family	No. of studies	Growth form	References
Berberis julianae C.K.Schneid.	Berberidaceae	1	shrub	Masole et al., 2022
Chaenomeles speciosa (Sweet) Nakai	Rosaceae	1	shrub	Moshobane et al., 2022
Cotoneaster pannosus Franch.	Rosaceae	1	shrub	Moshobane et al., 2022
Cotoneaster simonsii Baker	Rosaceae	1	shrub	Moshobane et al., 2022
Cotoneaster Medik.	Rosaceae	2	shrub	Moshobane et al., 2022; Giantomasi et al., 2008
Crataegus gracilior J. B. Phipp	Rosaceae	1	tree	Moshobane et al., 2022
Crataegus mexicana Moc. and Sesse ex DC.	Rosaceae	1	tree	Moshobane et al., 2022
Crataegus L.	Rosaceae	1	tree	Moshobane et al., 2022
Duranta erecta L.	Verbenaceae	1	shrub or tree	Moshobane et al., 2022
Lantana camara L.	Verbenaceae	6	subshrub or shrub	Ramaswami et al., 2016; Bhatt et al., 2021; Bitani and Downs, 2022; Moshobane et al., 2022; Jobin et al., 2023; Shiri et al., 2023
Ligustrum japonicum Thunb.	Oleaceae	2	shrub or tree	Moshobane et al., 2022; Vukeya et al., 2022
Ligustrum lucidum W.T.Aiton	Oleaceae	7	tree	Tecco et al., 2006; Tecco et al., 2007; Giantomasi et al., 2008; Aslan, 2011; Gavier-Pizarro et al., 2012; Bobadilla et al., 2016; Moshobane et al., 2022
Ligustrum ovalifolium Hassk.	Oleaceae	1	shrub or tree	Moshobane et al., 2022

Ligustrum sinense Lour.	Oleaceae	3	shrub or tree	Giantomasi et al., 2008; Moshobane et al., 2022; Bobadilla et al., 2016
Litsea glutinosa (Lour.) C.B.Rob.	Lauraceae	1	tree	Bhatt et al., 2021
Lycium barbarum L.	Solanaceae	1	shrub	Cubino et al., 2022
Malus domestica (Suckow) Borkh.	Rosaceae	1	tree	Kalwij et al., 2008
Melia azedarach L.	Meliaceae	6	tree	Giantomasi et al., 2008; Voigt et al., 2011; Bobadilla et al., 2016; Bhatt et al., 2021; Moshobane et al., 2022; Vukeya et al., 2022
Morus alba L.	Moraceae	6	tree	Debussche and Isenmann, 1994; Giantomasi et al., 2008; Pándi et al., 2014; Bobadilla et al., 2016; Bhatt et al., 2021; Moshobane et al., 2022
Morus nigra L.	Moraceae	1	tree	Moshobane et al., 2022
Olea europaea L.	Oleaceae	1	shrub or tree	Aslan, 2011
Opuntia tuna (L.) Mill.	Cactaceae	1	succulent shrub	Yang et al., 2022
Opuntia stricta (Haw.) Haw.	Cactaceae	1	succulent shrub	Strum et al., 2015
Physalis peruviana L.	Solanaceae	1	perennial	Moshobane et al., 2022
Phytolacca americana L.	Phytolaccaceae	1	perennial	Debussche and Isenmann, 1994
Potentilla indica (Andr.) Wolf	Rosaceae	1	perennial	Moshobane et al., 2022
Prunus avium (L.) L.	Rosaceae	1	tree	Badalamenti et al., 2022
Prunus mahaleb L.	Rosaceae	1	tree	Amodeo and Zalba, 2013

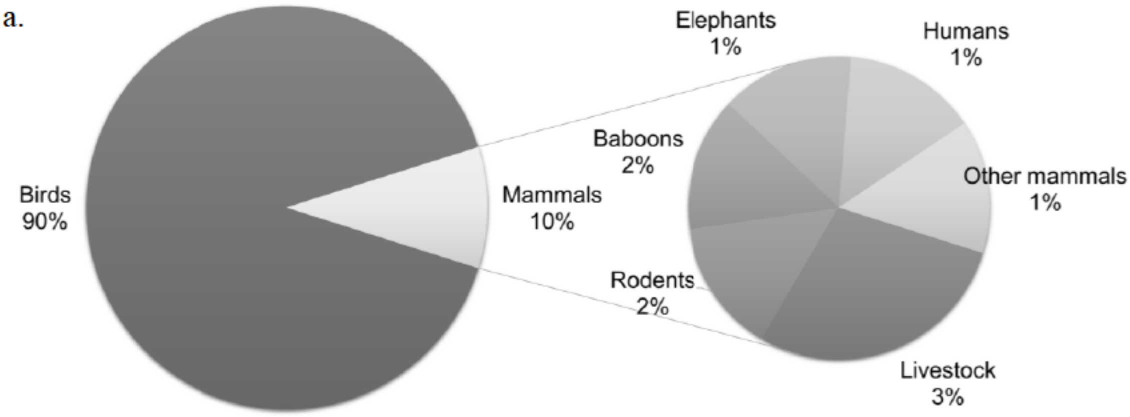
Prunus persica (L.) Batsch	Rosaceae	3	shrub or tree	Kalwij et al., 2008; Turner et al., 2021; Moshobane et al., 2022
Prunus serotina Ehrh.	Rosaceae	2	tree	Deckers et al., 2008; Moshobane et al., 2022
Prunus serotina var. salicifolia (Kunth) Koehne	Rosaceae	1	tree	Moshobane et al., 2022
Psidium guajava L.	Myrtaceae	1	tree	Moshobane et al., 2022
Pyracantha angustifolia (Franch.) C. K. Schneid.	Rosaceae	7	shrub	Tecco et al., 2006; Tecco et al., 2007; Giantomasi et al., 2008; Adams et al., 2022; Vukeya et al., 2022; Adams et al., 2023; Moshobane et al., 2022
Pyracantha crenulata (D. Don) M. Roemer	Rosaceae	1	shrub	Moshobane et al., 2022
Pyracantha M.Roem.	Rosaceae	1	shrub	Bobadilla et al., 2016
Pyrus calleryana Decne.	Rosaceae	1	tree	Woods et al., 2023
Ribes rubrum L.	Grossulariaceae	1	shrub	Cubino et al., 2022
Rosa bracteata J.C.Wendl.	Rosaceae	1	shrub	Saalfeld et al., 2016
Rosa rubiginosa L.	Rosaceae	1	shrub	Moshobane et al., 2022
Rubus armeniacus Focke	Rosaceae	1	scrambling shrub	Chance 2016
Rubus cuneifolius Pursh	Rosaceae	3	shrub	Reynolds and Symes, 2013; Moshobane et al., 2022; Theron et al., 2022
Rubus L.	Rosaceae	1		Moshobane et al., 2022
Schinus molle L.	Anacardiaceae	2	tree	Iponga et al., 2009; Bobadilla et al., 2016

Solanum aculeatissimum Jacq.	Solanaceae	1	shrub	Yang et al., 2022
Solanum mauritianum Scop.	Solanaceae	3	shrub or tree	Kalwij et al., 2008; Bhatt et al., 2021; Moshobane et al., 2022
Solanum pseudocapsicum L.	Solanaceae	1	subshrub or shrub	Moshobane et al., 2022
Solanum quitoense Lam.	Solanaceae	1	perennial shrub	Yang et al., 2022
Solanum sisymbriifolium Lam.	Solanaceae	1	annual or subshrub	Moshobane et al., 2022
Solanum L.	Solanaceae	1		Jobin et al., 2023
Triadica sebifera (L.) Small	Euphorbiaceae	2	tree	Aslan, 2011; Prather et al., 2017

2.4.5 Diversity of potential seed dispersers and predators

Seed dispersal by birds was the most frequent plant-animal interaction studied, with predation and seed dispersal by mammals being less frequent (Figure 2.6a). Birds, ants and mammals were potential seed predators, as reported from data collected through observations, fruit traps, vegetation surveys, modelling predictions and animal faeces (Figure 2.6b).

a.



b.

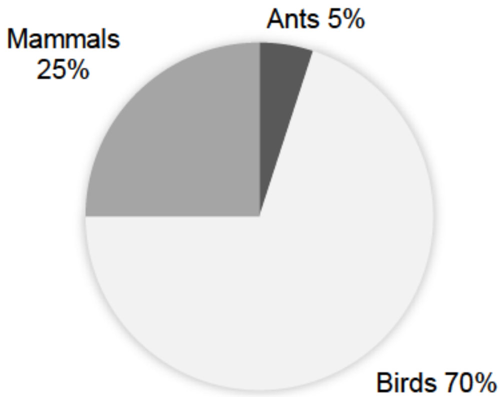


Figure 2.6: Seed dispersal and predation charts showing the event frequency from original articles that collected data on fleshy-fruited invasive alien plants in the grassland ecosystems and mosaics, where a. shows seed dispersal events while b. shows predation events. (Note: event referred to a count of vector and predator type per study).

2.5 Discussion

2.5.1 Peer-reviewed publications

Out of our comprehensive search, only 32 peer-reviewed publications spanning from 1994 to 2023 met the defined criteria. There has been a steady increase in articles published, particularly after 2016, peaking in 2022. This upward trajectory suggests an ongoing and anticipated rise in annual publications. Similar trends in escalating research output have been observed in diverse fields as demonstrated in other studies such as Wilkinson et al. (2023) on global research concerning Hyaenidae, Cordier et al. (2022) focusing on camera trap research in Africa, and Mariani et al. (2023) exploring artificial intelligence in innovation research. The increase in research publications in various fields can be attributed to several factors, including technological advancements, growing interest in specific topics, funding availability, evolving research methodologies, international collaborations, and improved research infrastructure (Zheng, 2015; Ahmad et al., 2021).

2.5.2 Geographic location

Only a handful of countries account for most published papers on the ecology of fleshy-fruited invasive alien plants in grassland ecosystems and grassland mosaics at large; this shows that bias exists in publication, and biological invasions as a subdiscipline of ecology is not an exception (Nuñez and Pauchard, 2010, Nuñez et al., 2021). Most of the studies were conducted in South Africa, followed by Argentina, thus giving Africa and South America the highest records of studies. This means most of the published data is from the temperate grasslands, particularly the Pampas and southern African grasslands. South Africa is a significant contributor to global research on biological invasions, contributing well over half of Africa's research output on biological invasions (Pyšek et al., 2008; Abrahams et al., 2019; Richardson, 2020). With a strong collaborative network of researchers, South Africa has maintained an active interest in studying biological invasions for more than 130 years (van Wilgen et al., 2020). Although South Africa owes its high number of peer-reviewed publications to research efforts in biological invasions, it is not the same for Argentina. Conversely, Argentina's focus on biological invasions has recently gained momentum. Over the past six years, the Argentine government has prioritised addressing biological invasions through a national strategy aimed at studying, controlling, and eradicating these species, as well as enhancing institutional capacities for managing biological invasions (Duboscq-Carra et al., 2021). The high number of publications on fleshy-fruited invasive alien plants is arguably because of the pioneering of the biological invasions discipline.

North American, Eurasian, Asian, Australian and New Zealand's grasslands were poorly represented. Although these areas have a large distribution of grasslands similar to Argentina and southern Africa, they do not have as many publications as the latter.

2.5.3 Plant taxonomy and growth form

The most frequent fleshy-fruited invasive alien plant species studied were *L. camara*, *L. lucidum*, *M. alba*, *M. azedarach*, and *P. angustifolia*. More research has been conducted on Rosaceae and Oleaceae based on publication volume, whereas studies have encompassed a greater diversity of species within Rosaceae and Solanaceae. Perennial subshrubs were less researched, while the majority were shrubs and trees. Many species of trees and shrubs have become naturalised or invasive (Richardson, 2011; Richardson and Rejmánek, 2011; Dyderski and Jagodziński, 2020). Invasive alien shrubs and trees are often associated with highly negative impacts (Hejda et al., 2017). Examples of impacts include changes in soil-nutrient cycling, affecting soil seed bank compositions and fire patterns (Gaertner et al., 2014; Gioria et al., 2014; Shackleton et al., 2018), along with modifications in microbial communities (Bowen et al., 2017). This might be why trees and shrubs were the most studied plant life forms in biological invasions.

2.4.4 Seed dispersal

We found seed dispersal and woody invasion to be the most studied concepts. Seed dispersal, one of the most important ecosystem functions globally, shapes plant populations and enhances succession (Beckman and Sullivan, 2023; Cordero et al., 2023). However, enhancement of succession from seed dispersal dynamics is also beneficial to alien plant invasions, thereby increasing their chances of invasion (Traveset and Richardson, 2021; Vergara-Tabares et al., 2022; Vélez et al., 2021; Cordero et al., 2023). Birds are the primary dispersers of many invasive alien plants, and thus, a thorough understanding of their role can aid agencies aiming to control the spread of invasive alien plants (Vanderhoff and Rentsch, 2022). Birds continue to be the primary seed dispersal agents of invasive trees (approximately 43%) and shrubs (about 61%) in grasslands (Richardson and Rejmánek, 2011). Although other dispersal modes have a lower representation, they can significantly contribute to invasions in specific habitats (Richardson and Rejmánek, 2011).

This review has shown that most of the work has been centred around seed dispersal, and previous reviews on fleshy-fruited invasive alien plants have addressed seed dispersal, particularly by birds, more than other subjects. We encourage future research to focus more on seed dispersal by other seed dispersal agents like mammals, pollination, environmental and socioeconomic impacts, management and potential control, rehabilitation of invaded systems and their use in cultural systems by different communities. Furthermore, some of the areas that are important in biological invasions but were not covered in these publications include climate change, management and conflict of interest. Thus, we recommend that these gaps be addressed through research.

2.6 Conclusions

This synthesis of research underscores the urgency for continued research on fleshy-fruited invasive alien plants in the grasslands and other treeless ecosystems to mitigate their escalating threats. The broader implications of these findings extend to conservation efforts, ecosystem management, and the preservation of global biodiversity. More research is needed on seed dispersal by other agents, pollination, environmental and socioeconomic impacts, management and potential control, rehabilitation, and their use in cultural systems by different communities.

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CHAPTER 3

Community perceptions of the fleshy-fruited alien plant, *Pyracantha angustifolia*, in South African grasslands

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Running header: Community perceptions of invasive alien plants

3.1 Abstract

Societal activities have driven biological invasions because of the economic and intrinsic benefits biological invasions provide. This shows the importance of including aspects of human perceptions in research to ensure effective management of invasive alien species by avoiding inefficiency, misunderstandings, and conflict when managing these species. However, many studies on human perceptions of invasive species consider only one or two influencing factors, lacking the development of more integrated and holistic understandings. In this study, we aimed to collate the understanding of communities of a fleshy-fruited invasive alien shrub *Pyracantha angustifolia*, in South African grasslands, through telephonic, in-person and online questionnaires between 2021 and 2023. Results showed that the fleshy orange-red fruits were predominantly consumed by children who acted as predators and seed dispersers by chewing or throwing the seeds away. The general urban public did not regard the species as a problem, but all farmers and conservationists regarded the plant as a problem. Reductions in grazing and recreation opportunities were the most frequent socio-economic impacts reported, while change in vegetation was the most reported environmental impact, thereby threatening indigenous vegetation. Regarding management options, fire was perceived as the least effective method, although moderate success through prescribed burning was also suggested. Government assistance in the form of funding and/or initiatives such as the Expanded Public Works Programme for clearing was the most desirable assistance the communities would like to receive from the government. Results from this study provided integrated and holistic offered comprehensive insights essential for understanding invasion processes and dynamics and showed the importance of collating data from the communities in southern Africa and abroad.

Keywords: invasion science, interviews, invasive alien plant, invasion control.

3.2 Introduction

Ecosystem services benefit humans, and societal human activities, such as harvesting of ecosystem resources, have long-driven ecosystem changes (Steffen et al., 2015; De Luca Peña et al., 2022). These activities are important for environmental management and conservation because they are central to shaping and responding to processes of environmental change (Bennett et al., 2017; Christie et al., 2017; Zhang et al., 2022). Since human activities have an influence on environmental change, it is efficient for environmental managers and scientists who work on socio-ecological changes such as biological invasions, climate change and land-use change to understand perceptions that drive environmental change to avoid inefficiency, misunderstandings, and conflict (Buijs et al., 2012; Woodford et al., 2016; Feng et al., 2022).

Introduced species could lead to biological invasions, which is one of the major drivers of environmental change(Richardson et al., 2000; Manzoor et al., 2021). Introduced species have the potential to spread extensively in their new ranges and become invasive (Richardson et al., 2000; Pyšek et al., 2020). These species often affect biodiversity, ecosystem processes and human well-being (Pejchar and Mooney, 2009; Jeschke et al., 2014; Shackleton et al., 2018). However, these species may also offer economic and intrinsic benefits, which could lead to conflicts of interest in their management because some people may oppose specific control methods and want to continue deriving benefits from these species (Crowley et al., 2017; Vaz et al., 2017; Zengeya et al., 2017; Villatoro et al., 2019). This shows the importance of including aspects of human perceptions in research to ensure the effective management of invasive species (Shackleton, 2019). Many studies on human perceptions of invasive species consider only one or two influencing factors, lacking the development of more integrated and holistic understandings (Kueffer, 2013; Shackleton et al., 2019). In our study, we include five influencing factors because a comprehensive approach is beneficial for research, management, policy formulation, and governance as they include primary factors that shape perceptions (Shackleton et al., 2018; Kapitza et al., 2019). These factors were ecological conditions, social conditions, values and beliefs, impacts and benefits (see methods).

Globally, research on human perceptions of invasive species has gained momentum. Since 2010, the interdisciplinary approach to research has rapidly accelerated (Kapitza et al., 2019). North America (32%) and Europe (28%) have dominated in this research, followed by Africa (17%), Asia (8%), Oceania (9%) and South America (6%) (Kapitza et al., 2019). There is a clear gap in literature coverage for these latter regions. This study aimed to contribute knowledge from Africa, specifically South Africa. Our study aimed to collate a holistic understanding of the invasive alien plant *Pyracantha angustifolia* (Franch.) C. K. Schneid (Rosaceae) in South African grasslands from community members. Our objectives were to determine (1) possible conflicts by assessing plant uses by the communities, (2) potential seed or propagule dispersal, (3) socio-economic and environmental impacts, (4) present control methods used and their effectiveness, and (5) collate recommendations from the communities. Conflicts were regarded as any resistance by the community towards control of this plant because of the benefits that they could be getting from it. We predicted that there would be conflicts as the literature states that people use the plant for various purposes, and control methods attempted will be reported as not being successful because the species has been reported to spread more over time and become more invasive (Henderson, 2020).

3.3 Methods

3.3.1 Study sites

The study was conducted in the Grassland Biome of South Africa, which includes mainly the Drakensberg Escarpment and neighbouring foothills. The study was limited to this Biome as it is the most invaded by *P. angustifolia* in South Africa (Chari et al., 2020). Therefore, the study included communities in east and southern Gauteng, Western Cape, and Free State provinces, as well as north and eastern towns of the Eastern Cape Province (Figure 3.1). This study focused on the montane grassland areas, mainly near the Drakensberg. The area receives an average rainfall of about 1800 to 2000 mm during the rainfall season from September to April and has cold winters with occasional snow. The dominant vegetation in the study area is the Eastern Free State Sandy Grassland (Gm 4), which is part of the Mesic Highveld (Mucina and Rutherford, 2006). Grasses from the Poaceae family dominate the area with at least 55 genera, followed by forbs from the Asteraceae family with more than 51 genera (Carbutt and Edwards 2003; Daemane et al., 2010).

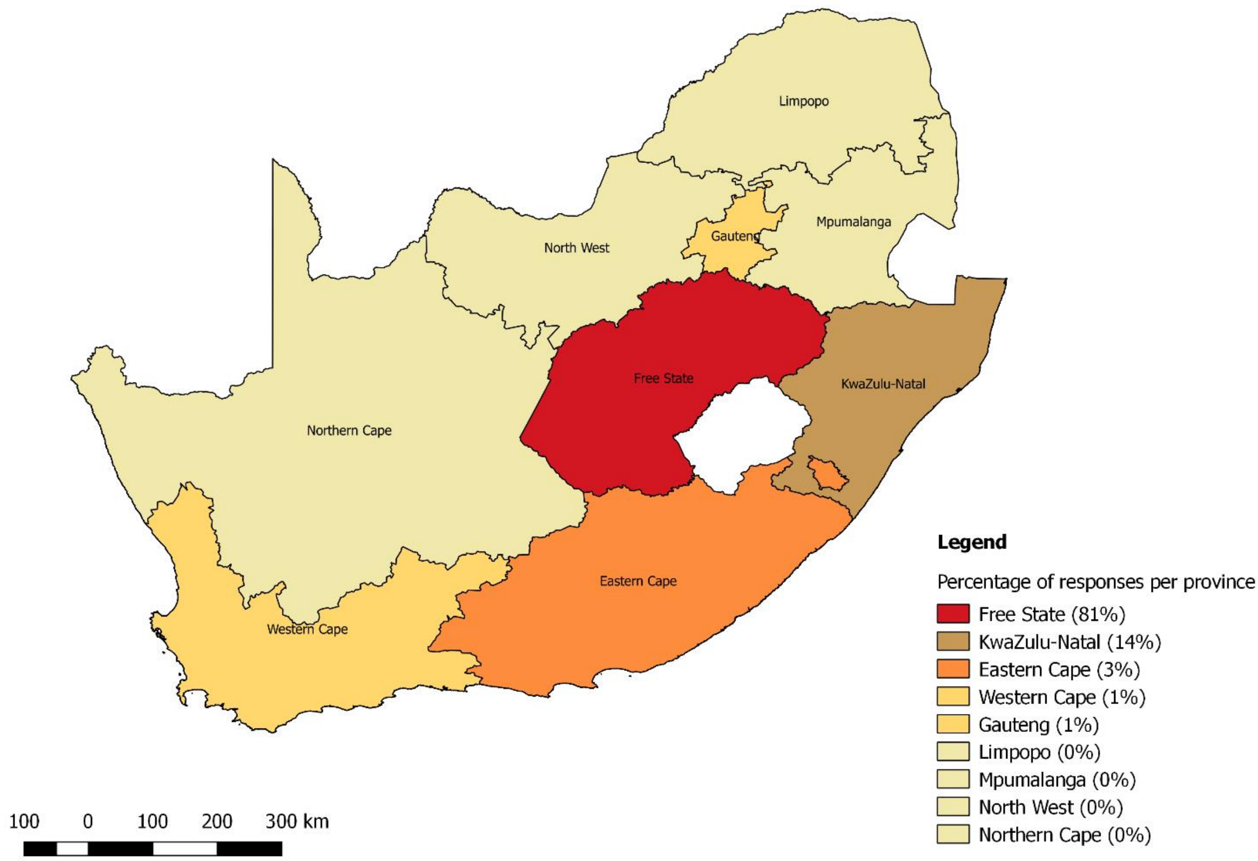

Figure 3.1: South African map showing respondents' provinces. Responses were administered online and in-person (N = 208).

3.3.2 Study species

Pyracantha angustifolia (Franch.) Schneid also known as the yellow firethorn or narrowleaf firethorn is native to southwest China and was introduced to South Africa as a hedging plant (Chari et al., 2020; Henderson, 2020). This plant has naturalised and has become invasive in many parts of the world, including Argentina (Vergara-Tabares et al., 2022), Australia (Swarbrick and Skarratt, 1992), Japan (Mito and Uesugi, 2004), the United States of America and some of its Hawaiian Islands (Nesom, 2010), Russia (Nobis et al., 2014) and South Africa (Henderson, 2020). The plant typically invades shrubland, forests and grasslands. In South Africa, *P. angustifiolia* began invading the grassland biome in the early 1980s (Henderson and Musil, 1984). The species then spread rapidly, forming dense stands in many high-altitude grasslands (Richardson et al., 2020). Although it has wide distribution with records in all nine provinces, *P.angustifolia* is predominantly abundant in Gauteng, Free State and Eastern Cape provinces (Figure 3.1, see Henderson 2020 for species distribution).

3.3.3 Data collection and analyses

Data on background information of the participant, species occurrences, attempted control methods, effectiveness of the control methods, suggestions for improvement and government involvement were collected using questionnaires (see questionnaire template in Supplementary information Survey 3.1). A total of 208 in-person (n = 202), telephonic (n = 2) and online questionnaires (n = 4) were completed. For in-person interviews, we walked around towns during the day between 09:00 and 15:00 and asked prospective participants if they would like to assist us with the study. Any adult was a prospect for participation in the study. We read the aims of the study and obtained their consent before we began with the questionnaire interview. Due to COVID-19 regulations, it was ideal for participants to provide verbal consent to minimise physical contact. It took two people to conduct the in-person interview: the interviewer and the scriber/field assistant. The interviewer asked the participant questions, and the scriber recorded the responses on a printed hard copy of the questionnaire. Online questionnaires were administered using Google Forms® and they were distributed through email to different research groups. The Google Forms® link was circulated to different research units and associations. Telephonic interviews were only conducted when the interested prospective participant could not access the online questionnaires and could not be interviewed in-person because of distance or different times of availability.

The questionnaires were translated into isiZulu, Sesotho and IsiXhosa, as these were the dominant languages spoken in the study areas. Humanities Ethical clearance was acquired (HSSREC/00003340/2021) through the University of KwaZulu-Natal, and all COVID-19 regulations were observed during data collection. To ensure that the data covered important areas of influence on the perception of invasive species, data collected included ecological conditions (i.e. invasion status), social conditions (socio-demographics and interests), values and beliefs (uses and perceptions), impacts, and benefits of the target species (Kapitza et al., 2019). Data were captured using Microsoft® Excel® for Microsoft 365 and analysed using multinomial regressions (Generalised Linear Models) in the IBM Statistical Package for Social Sciences v. 20 (SPSS, Tulsa, OK, USA). Chi-square tests and descriptive statistics were also conducted. A scoring system was used to identify conflict-generating species on the list of alien species to assess potential conflicts that may occur when *P. angustifolia* was controlled (Nentwig et al., 2016; Zengeya et al., 2017). The scoring system had two main categories: negative impacts (ecological and socio-economic) and benefits (economic and intrinsic). Each category was assessed on a scale of 1 to 3 (indicating little or no evidence), 4 to 6 (localised impacts), or 7 to 10 (widespread impacts). Final scores were calculated by selecting the highest scores from both negative impacts or benefits for *P. angustifolia*. The methodology used for scoring and assessing impacts can vary based on the assessment's focus (as detailed in Nentwig et al., 2016).

3.4 Results

3.4.1 Background information of the respondents

The age categories interviewed were evenly distributed, approximately 20% in each of four of the categories, with fewer respondents in the over 55 years old category (10%, n = 21, Table 3.1). More male respondents were interviewed (66%, n = 135) than females (34%, n = 71). The study mostly consisted of the African ethnic group (83%, n = 173) and, to a lesser extent, white (14%, n = 30) and coloured (2%, n = 5). The majority of the respondents were employed (60%, n = 114), but some were unemployed (14%, n = 26), self-employed (12%, n = 22), students (9%, n = 17) or pensioners (6%, n = 12). The period of stay (n = 208) differed among respondents. The period of stay referred to the time the respondent has lived in the area of the interview. Most respondents were permanent residents who had stayed in their area of interview for more than ten years (59%, n = 119), and some were permanent residents who had stayed in the area for 5 - 10 years (22%, n = 45) or stayed for less than 5 years (15%, n = 30) in the area. A minority of the respondents were visitors visiting the study area a few times a week (1.5%, n = 3), a few times a month (0.5%, n = 1) or a few times a year (2%, n = 4). Residential was the major land type the respondents were associated with (75%, n = 156), and some were also associated with conservation units (9%, n = 19), public works (5%, n = 10), animal and crop farms (3%, n = 6), animal farms only (3%, n = 7), business (2%, n = 4), holiday farms (1%, n = 3) or crop farms only (1%, n = 1).

3.4.2 Population status

Respondents were asked to estimate the number of individual *P. angustifolia* plants they have seen in the area. More than 50% (n = 72) of the respondents selected more than 30 individual *P. angustifolia* plants, followed by 1-5 plants (22%, n = 41), 5-15 plants (13%, n = 24), 15-30 plants (10%, n = 18) and no populations (2%, n = 4; Figure 3.2a). The population estimates included the estimated number of individuals in one's property, another person's property and any land in the town of interview. Some respondents (at least 5%) commented that there were hundreds of plants in their areas. Overall, the respondents indicated that the population numbers were increasing (52%, n = 97) in their respective areas (Figure 3.2b). Aliwal North (2%, n = 4) in the Eastern Cape Province, Bethlehem (1%, n = 2), Clarens (9%, n = 17), Clocolan (8%, n = 14), Ficksburg (8%, n = 14), Fouriesburg (%, n = 5), Hobhouse (%, n = 1), Wepener (0.5%, n = 5) and Zastron (9%, n = 17) in the Free State Province, and Magaliesburg (0.5%, n = 1), Melville (0.5%, n = 1) in the Gauteng Province had perceived increasing populations, while Bergville (0.5%, n = 1), Kokstad (%, n = 16) in the KwaZulu-Natal Province, and Stellenbosch in the Western Cape Province (1%, n = 2) were the same. Thaba Nchu (1%, n = 2) in the Free State Province was perceived to have no populations at all, while the population status in Ladybrand in the Free State Province was not known (4%, n = 7) as the respondents were not sure. Several respondents mentioned that peach trees (*Prunus persica*) are increasing in distribution near Fouriesburg town in the Free State Province.

Table 3.1: Sample composition and demographic information of the respondents gathered from questionnaire surveys on uses, population status and management of the invasive alien plant, *Pyracantha angustifolia*, in South Africa.

Category (N = 208)	**Selections**	**No. of responses**	**Percentage of responses (%)**
Age	18-25 years	43	21
	26-35 years	55	26
	36-45 years	44	21
	46-55 years	45	22
	>55 years	21	10
	Total	**208**	**100**
Gender	Male	135	66
	Female	71	34
	Total	**206**	**100**
Ethnic group	African	173	83
	Coloured	5	2
	White	30	14
	Total	**208**	**100**
Occupation	Employed	114	60
	Pensioner	12	6
	Self-employed	22	12
	Student	17	9
	Unemployed	26	14
	Total	**191**	**100**
Period of stay	Permanent (> 10 years)	119	59
	Permanent (5 - 10 years)	45	22
	Permanent (< 5 years)	30	15
	Visitor (Few times a month)	1	0.5
	Visitor (Few times a week)	3	1.5
	Visitor (Few times a year)	4	2
	Total	**202**	**100**
Land type	Animal and crop farm	6	3
	Animal farm	7	3
	Business	4	2
	Conservation unit	19	9
	Crop farm	1	1
	Holiday farm	3	1
	Public works	10	5
	Residential	156	75
	Other	2	1
	Total	**208**	**100**


a.
South Africa
Magaliesburg
Melville
Bethlehem
Clarens
Fouriesburg
Phuthaditjhaba
Bergville
Clocolan
Ficksburg
Thaba Nchu
Tweespruit
Ladybrand
Hobhouse
Wepener
Pietermaritzburg
Zastron
Kokstad
Aliwal North
Stellenbosch
75 0 75 150 225 300 km
Legend
Population estimates per town
>30 plants
15-30 plants
5-15 plants
1-5 plants
No plants
South African Provinces

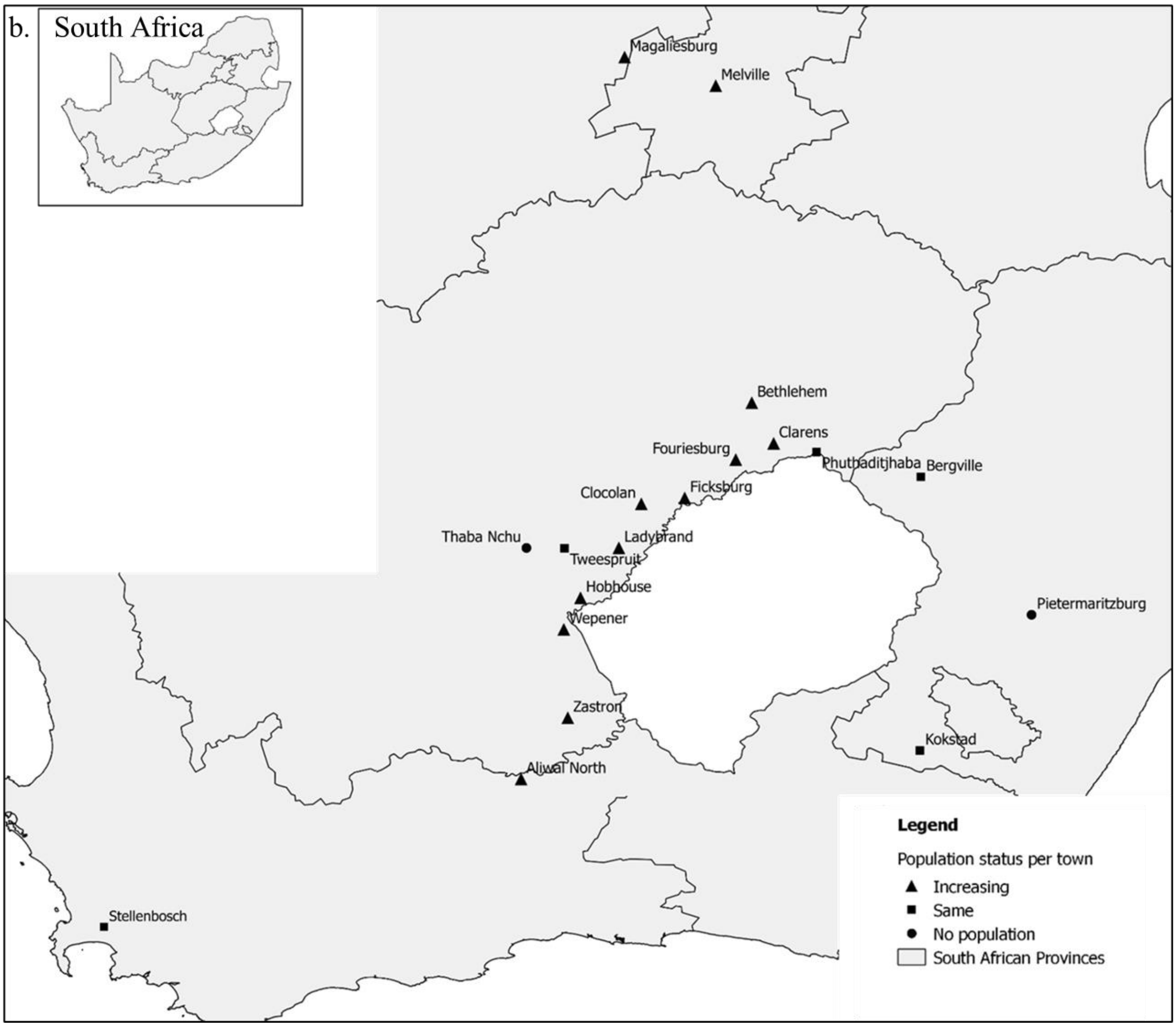

Figure 3.2: Maps showing *Pyracantha angustifolia* a) population estimates per town in South Africa and b) their status over time recorded by the respondents. There was no decrease in population numbers reported by the respondents.

3.4.3 Local people's perceptions and uses

All respondents could confidently identify the species. Ethnic group ($p \leq 0.05$) and land type ($p > 0.05$) were significant predictors in the model for predicting local people's perceptions. Most respondents (80%) associated with the residential (75%, n = 156) land type did not regard the plant as a problem in their area. In contrast, those associated with conservation units and farms regarded the plant as a problem.

Although roots, leaves, whole plants, and stems were harvested, fruits were the most harvested plant parts by the communities (Figure 3.3a). The plant was harvested, to a lesser extent, for feedstock enhancement because of high nutrient provision for domestic chicken (*Gallus domesticus*), cattle (*Bos taurus*) and other livestock, medicine for livestock and humans, for selling, propagation and wood, although the wood is not easy to handle because of sharp thorns. Consumption was the most frequent reason for harvesting (Figure 3.3a). Most respondents who reported consumption indicated that they had seen children eating the fruits for fun or had eaten them before themselves. Fruits could also be boiled to make juice or cooked to make jam. Of interest, one respondent commented, "Norwood Coaker, a British pharmacist from England, made medicine out of its fruits in Ladybrand around 1908. The fruits are high in vitamin C. He made a lot of money selling juice made from the fruits. Most of the old stone buildings in Ladybrand were built by him, including a factory where he produced medicines using fruits from this plant."

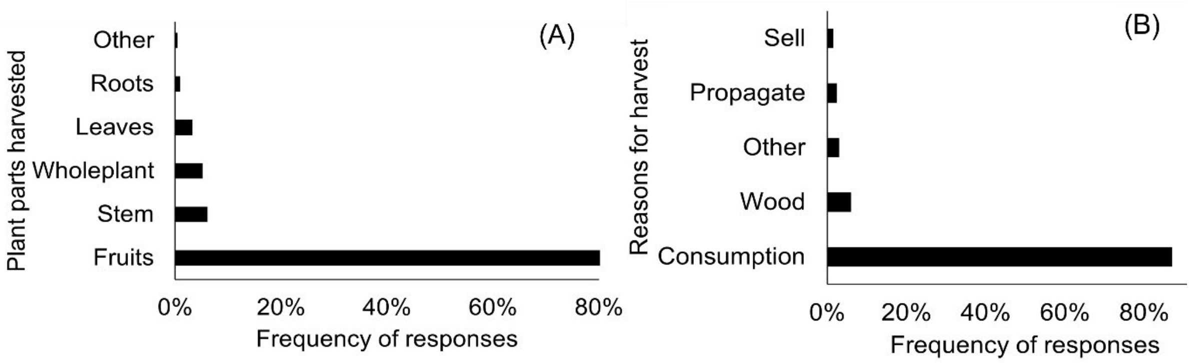

Figure 3.3: Frequency of responses on plant parts harvested and the reasons for harvesting *Pyracantha angustifolia* by the communities. (Note: 180 respondents harvested plant material, and 28 respondents did not harvest the plant).

3.4.4 Potential seed or propagule dispersal

Some of the respondents who mentioned the consumption of fruits indicated that they swallow (31%, n = 20) the seeds, while some crush (30%, n = 19) or throw them away (39%, n = 25) (Figure 3.4). Seeds thrown away were regarded as potential seed dispersal events (39%, n = 25) and crushed and swallowed as potential seed predation (61%, n = 39). Thus, humans act both as potential seed dispersal agents and predators. Respondents also made comments on possible causes of spread (n = 40) under the comment sections on the questionnaire. Frugivorous birds, ostriches (*Struthio*), Boer goats (*Capra hircus*), chacma baboons (*Papio ursinus*), cattle (*Bos taurus*), sheep (*Ovis aries*), elephants (*Loxodonta africana*), and mongooses (Herpestidae) were animals seen feeding on *P. angustifolia* fruits. Birds (30%, n = 12), goats (28%, n = 11), and baboons (20%, n = 8) were the most frequent animals reported feeding on fruits.

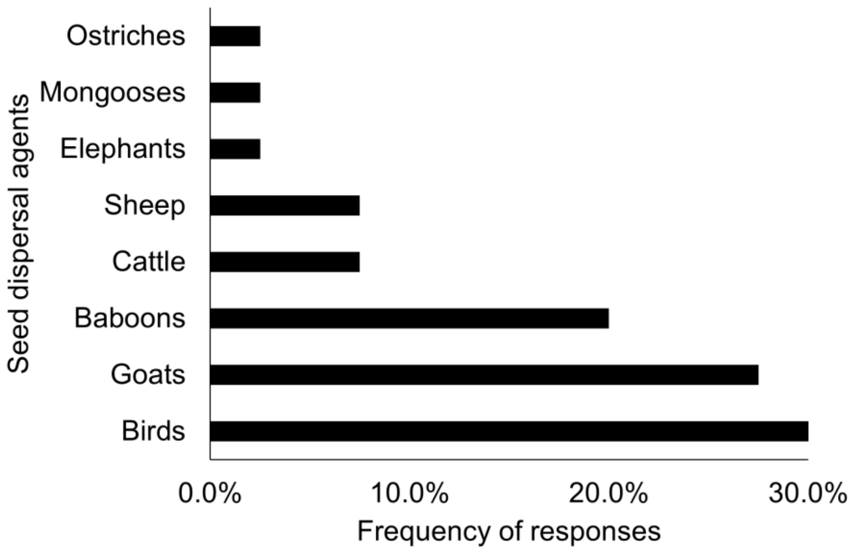

Figure 3.4: Frequency of responses identifying potential seed dispersal agents of *Pyracantha angustifolia* from the community respondents. (Seed dispersal agents refer to animals observed by the community feeding on fruits).

3.4.5 Socio-economic and environmental impacts

Environmental impacts (n = 29) reported by the communities were threatening freshwater bodies (10%, n = 3), taking over grasslands (62%, n = 18), and competing with native vegetation (28%, n = 8) (Table 3.2). Restriction of access (33%, n = 7), reduction of grazing capacity (33%, n = 7), damaging of property (10%, n = 2), blockage of roadsides (10%, n = 2) and alteration of recreational use such as restriction or blockage of hiking and mountain biking trials (14%, n = 3) were the main socio-economic impacts (n = 21) reported.

Table 3.2: Socio-economic and environmental impacts of *Pyracantha angustifolia* reported by the communities in South African grasslands through questionnaires.

Environmental impacts reported	**No. of responses**	**Percentage responses (%)**
Environmental (n = 29)		
Threaten freshwater bodies	3	10
Take over grasslands	18	62
Compete with native vegetation	8	28
Socio-economic (n = 21)		
Restrict access	7	33
Reduce grazing capacity	7	33
Damages property	2	10
Block roadside	2	10
Alter recreational use	3	14

3.4.6 Attempted control methods and their effectiveness

In an attempt to control *P. angustifolia* invasion, the communities have used biological control (1%, n = 2), fire (23%, n = 11), mechanical (32%, n = 15) and chemical control (43%, n = 20) (Figure 3.5), with mechanical and chemical being the most frequent control methods. Although there were responses on fire, the respondents explained that the fire was used for rotational burning of the grasslands and ended up burning *P. angustifolia* plants.

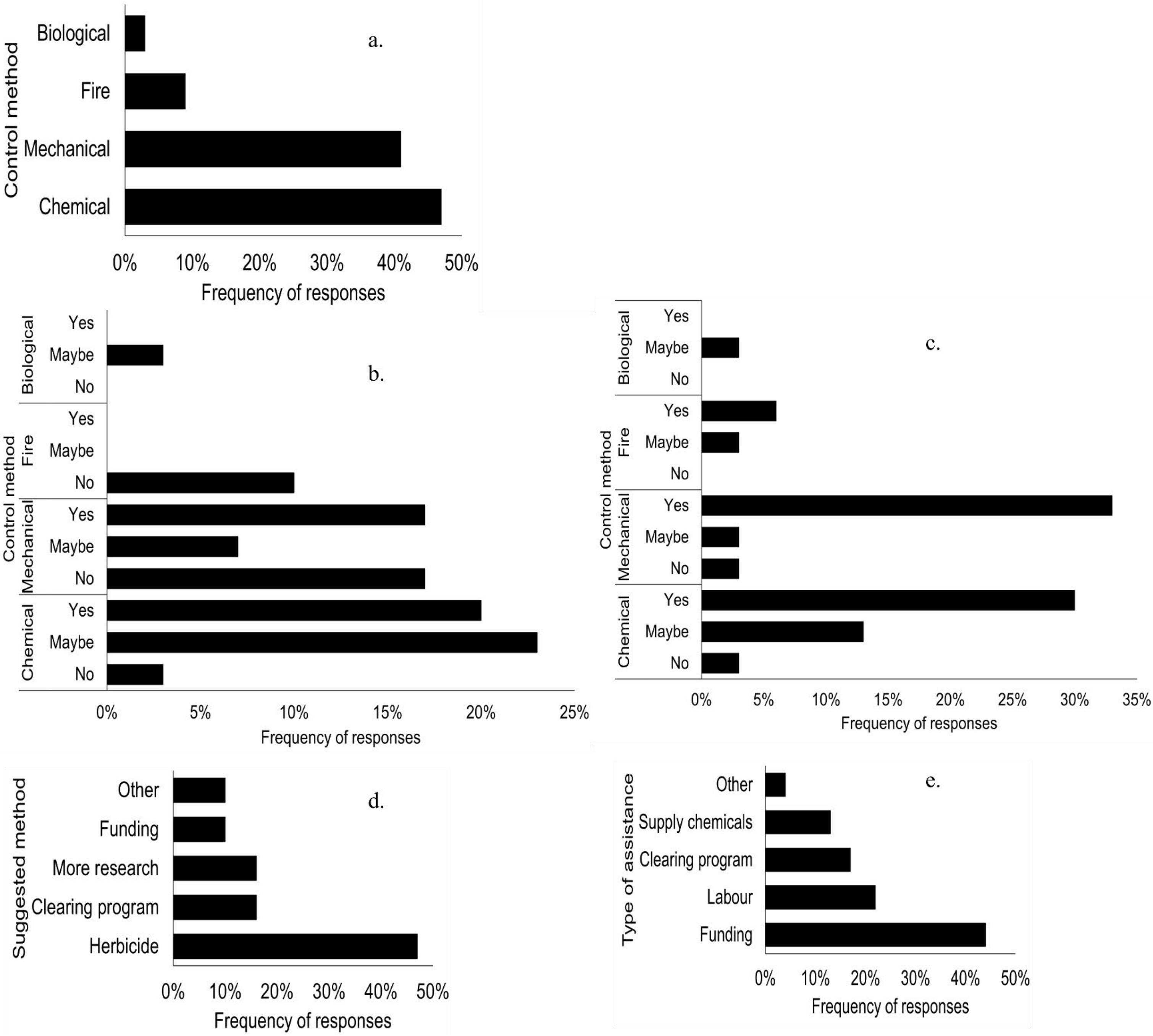

Figure 3.5: Frequency of responses from the communities on (a) types of control methods attempted to control *Pyracantha angustifolia* in their land and (b) control method effectiveness. Respondents indicated if the method (c) could be improved, and (d) suggested methods which could be used to improve their attempted control methods' effectiveness. Respondents also indicated if they would like to get any assistance from the government and specified the (e) type of assistance if yes.

The community was unsure if biological control was an effective treatment method to control the species, while fire was reported to be the least effective of all control measures attempted (Figure 3.5b). Mechanical and chemical control had higher rates of success than fire and biological control. Most of the respondents believed that the methods of controlling the species could be improved (Figure 3.5c). Herbicide (47%, n = 9) was the most frequent suggestion to improve the control effectiveness, followed by the introduction of a clearing program (16%, n = 3), more research (16%, n = 3) to understand the control dynamics, funding for clearing labour (10%, n = 2), and other suggestions (10%, n = 2) (Figure 3.5d). Most respondents (76%, n = 16) would like to receive assistance from the government. In comparison, some were sceptical about receiving assistance from the government and responded with "maybe" on the questionnaire (14%, n = 3), and others did not want any assistance from the government (10%, n = 2). Funding, provision of labour, clearing programs and supply of chemicals were the main types of assistance the communities would like to get from the government (Figure 3.5e). Several respondents indicated that there used to be a clearing programme led by Randwater that used to assist them in clearing invasive alien plants on their land by spraying them with a herbicide.

3.5 Discussion

3.5.1 Community perceptions of the species

Land type and ethnicity were the better predictors of perceptions of invasions by *P. angustifolia*, and age, gender, occupation, and town were not the best predictors of perception. Africans were more likely to be the most dominant respondents in numbers because of population dynamics; 81% of the South African population consists of Black Africans, including the study sites (Statistics South Africa, 2022). Moreover, Africans are mostly associated with residential land types, and most of the commercial farming area in South

Africa is owned by white farmers. According to a land audit, Whites own 26 663 144 ha or 72% of the total 37 031 283 ha of commercial farms and agricultural holdings (Rural Development and Land Reform 2017). This was probably why ethnicity and land type were the best predictors of the model. Farmers are likely to be more aware of invasive alien plants as they have experienced their negative impacts first-hand or have heard about them from other farmers. On the other hand, residents are at the other end of the spectrum as they are benefiting from the species.

3.5.2 Benefits and possible conflicts

Pyracantha Roem species have highly expected conflicts of interest because of their nutritional, medicinal and horticultural benefits (Keser, 2014; Doello et al., 2022). This is because species from this genus must be eradicated in South Africa. Fruits of *Pyracantha* species contain important nutrients such as amino acids, soluble sugars, fatty acids, mineral elements, proteins, starches, pectin and dietary fibre, vitamins, and other nutrients (Yuan et al., 2010; Zhao et al., 2015; Doello et al., 2022). The fruits can be cooked to make jams, jellies, sauces, and marmalade (Keser, 2014). *Pyracantha* roots, leaves and fruits have medicinal value, which can help improve immunity, anti-oxidation, digestion, and spleen nourishment (Sharifi-Rad et al., 2020). In South Africa, *P. angustifolia* roots have been harvested in Limpopo Province to cure body pains (Semenya et al., 2012).

Using a published scoring system used to identify conflict-generating species on the list of alien species (Zengeya et al., 2017), *P. angustifolia* was found to have low (1 to 3) economic benefits because it is harvested or traded by local communities on a small scale and does not produce employment or any income dependence. The results showed that although the communities eat *P. angustifolia* fruits, it was not for a subsistence role, thus, fewer conflicts should be expected.

3.5.3 Potential seed or propagule dispersal

Species with many introduction pathways tend to have a high likelihood of spreading and become difficult to manage (Kumschick et al., 2020; Turbelin et al., 2022). With *P. angustifolia,* respondents mentioned many potential seed dispersal agents, including birds and mammals. Birds have been confirmed as potential seed dispersal agents of *P. angustifolia* as they excrete viable seeds post-ingestion, and germination is enhanced when the fruit pulp is removed through physical removal and/ or ingestion (Adams et al., 2022). Humans also contribute to seed dispersal by throwing seeds away when consuming the fruits (Chapter 3). Mammals also excrete viable seeds and/or enhance germination through ingestion (Chapter 6). Results showed that although selling and planting of the species has been prohibited legally according to National Environmental Management: Biodiversity Act 963 (NEMBA, Act 10 of 2004) Alien and Invasive Species Regulations (Department of Environmental Affairs, 2014), some community members still traded the species and planted it as well; thus, further spread is likely to occur. Furthermore, seed fate after consumption also increases the risk of spread as some seeds are thrown away and might germinate and establish new populations. Humans thus contribute to seed predation and fruit consumption, which may significantly impact the demography and population abundance of *P. angustifolia* (Chari et al., 2020).

3.5.4 Socio-economic and environmental impacts

The most apparent environmental impact of *P. angustifolia* invasion was the change of vegetation structure, as most respondents indicated that the plant becomes dominant in the landscape. In South Africa, the species is believed to reduce eco-tourism revenue because of biodiversity loss and high visual impact in conservation areas and places of scenic beauty

(Henderson, 2020). This threatens grasslands as they are already threatened by land use change and other factors. *Pyracantha angustifolia* also has a moderate socio-economic impact (Bacher et al., 2017) because its negative effects lead to changes in the extent of an activity; thus, fewer people participate in an activity, although the activity is still carried out. Respondents commented that livestock grazing, hiking and mountain biking were the main examples where the species reduced the activity size where it has invaded. Although the impacts are moderate, their magnitude might increase as the species has a high potential to increase its spread.

3.5.6 Attempted control methods used and their effectiveness

Chemical and mechanical methods were the most widely used by the communities to control *P. angustifolia*. This has also been observed in places such as Australia and Hawaii (Chari et al., 2020). Although the names of chemicals used by the communities were not collected in this study, glyphosate, hexazinone, imazapyr, picloram, tebuthiuron, and triclopyr are several chemicals known to be used to control *Pyracantha* species (DiTomaso et al., 2013). Cut stump treatments with glyphosate or triclopyr oils are generally more effective than spraying stems or canopies (Chari et al., 2020). Further investigation of the control methods of this species needs to examine specific chemicals used by the communities, and thorough details should be acquired from other attempted control methods as well. Fire was the least effective method reported in the study. In Australia, moderate success has been achieved through prescribed burning, and where bare ground is replanted after fire. Rather than a control method, seasonal burning of the grasslands acts as a driver of invasion as it clears ground where *P. angustifolia* might invade the burned patches. Although a few respondents indicated that they use biological control to control the species, no biocontrol has been released to control *P.*

angustifolia globally. However, the species is a candidate for biological control in South Africa (Martin, 2021).

2.5.6 Required assistance from the communities

From the results, it is evident that the communities have tried to control the *Pyracantha* species, but the progress was not satisfactory. The majority of the respondents believed that the attempted control methods could be improved. The assistance mostly identified as needed by the communities to improve the control of the invasions included funding and the introduction of a clearing program.

3.6 Conclusions

There was less conflict between the government and communities than expected in terms of the subsistence role, like *P. angustifolia* as a food source. This is because communities do not depend on P. angustifolia and its congener species for sustenance.”Unaided introduction to new sites was highly expected because of the high diversity of seed dispersal agents. Moreover, humans are contributing to the spread of the species. *Pyracantha angustifolia* has high socio-economic and environmental impacts that need further investigation. Mixed methods seem to work better to control the invasion, according to the community. Funding and government initiatives could drastically improve species control, and more research should be done on other control methods, such as biocontrol. The data provided by the community can be used to improve the management of *P. angustifolia*.

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3.9 Supplementary Information

Supplementary information Survey 3.1 A sample of the electronic questionnaire survey that was used online and in-person to collate data on community perceptions of the fleshy-fruited invasive alien plant *Pyracantha angustifolia* in South African grassland communities.

Fleshy-fruited invasive alien plants in grasslands

We are investigating the uses, public perceptions, and management of fleshy-fruited invasive alien plants in the grasslands. This questionnaire is for information purposes only, and we would highly appreciate it if you could contribute to our study based on your observations. This research forms part of a PhD study on fleshy-fruited invasive alien plants in the grasslands, which is presently being undertaken in the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg campus by Lehlohonolo Adams (PhD candidate) under the supervision of Prof CT Downs. If you have any queries about the questionnaire, please contact Lehlohonolo Adams at 0658019833 or email adams20165@gmail.com or Downs@ukzn.ac.za.

* Indicates required question

1. Are you 18 or above? *

   Mark only one oval.

   ◯ Yes

   ◯ No

2. I understand the purpose and procedures of the study. I declare that my participation in this study is * entirely voluntary and that I may withdraw at any time without affecting any of the benefits that I usually am entitled to.

   Mark only one oval.

   ◯ Yes

   ◯ No

Background information

3. Town

   ____

4. Age

   Mark only one oval.

   ◯ 18-25 years

   ◯ 26-35 years

   ◯ 36-45 years

   ◯ 46-55 years

   ◯ >55 years

5. Gender

   Mark only one oval.

- Male
- Female

6. Ethnic group
Mark only one oval.
- African
- White
- Coloured
- Indian
- Other: ______

7. Current occupation?
Check all that apply.
- [ ] Student
- [ ] Employed
- [ ] Unemployed
- [ ] Pensioner
- [ ] Self employed
- [ ] Other: ______

8. Level of education? *Mark only one oval.*
- No education
- Primary
- Secondary
- Undergraduate
- Masters
- PhD
- Other: ______

9. Do you stay here permanently?
Mark only one oval.
- No
- Yes (Less than 5 years)
- Yes (5 - 10 years)
- Yes (> 10 years)
- Other: ______

10. If no, how often do you visit the place?
Mark only one oval.
- Ever years
- Few times a year
- Few times a month
- Few times a week
- Other: ______

Plant population growth

For plants that are not in anyone's garden or cultivation. Please choose one plant that you know. If you know both, please kindly submit two questionnaires at your convenience

11. Do you know this plant?

Mark only one oval.

- Yes
- No
- Maybe

12. Pyracantha. Have you ever eaten or saw someone feeding on this fruits?

Mark only one oval.

- Yes
- No
- Maybe

13. Pyracantha. If yes, did they swallow the seeds inside or throw them away?

Check all that apply.

- Swallow them
- Throw them away
- Crush them

14. Do you know of any populations nearby your town?

Mark only one oval.

- Yes
- No (Go to section 4)

15. If yes, how big is the population?

Mark only one oval.

- 1-5 plants
- 5-15 plants
- 15-30 plants
- >30 plants Other:

16. How has the number of plants been for the past years?

Mark only one oval.

- ⬭ Increasing
- ⬭ Same
- ⬭ Decreasing
- ⬭ Not sure
- ⬭ Other: ____________

17. Comment

____

Plant uses

18. Have you or anyone that you know used/harvested this plants before

Mark only one oval.

- ⬭ Yes
- ⬭ No
- ⬭ Maybe

19. If yes, which part(s) of the plant were used?

Check all that apply.

- ☐ Whole plant
- ☐ Roots
- ☐ Stem
- ☐ Leaves
- ☐ Fruits
- ☐ Other: ____________

20. What were the collected part(s) used for?

Check all that apply.

- ☐ Wood
- ☐ To consume
- ☐ Sell
- ☐ Plant
- ☐ Other: ____________

21. Comment

____

Management and impacts

For those who have these plants in the land they are associated with (e.g farm, conservation unit, estate....)

22. What type of land do you own or are you associated with?
Check all that apply.

- ☐ Animal farm
- ☐ Crop farm
- ☐ Conservation unit
- ☐ Holiday Farm
- ☐ Other:

23. If other, specify:

24. Is this plant a problem in your area?
Mark only one oval.

- ⬭ Yes
- ⬭ No
- ⬭ Maybe

25. If yes, explain impacts:

26. What methods do you use to control invasive alien plants
Check all that apply.

- ☐ Mechanical
- ☐ Chemical
- ☐ Biological
- ☐ Other:

27. If other, specify

28. How do you track control progress?

29. Is the control mechanism effective?
Mark only one oval.

- ⬭ Yes
- ⬭ No
- ⬭ Maybe

30. Do you think the control mechanism can be improved?
Mark only one oval.

- ⬭ Yes
- ⬭ No
- ⬭ Do not know

31. If yes, how?

32. Is the government assisting in any way in the control of the invasive plant species?
Mark only one oval.

- ⬭ Yes
- ⬭ No

33. If yes, how?

34. If no, would you like any assistance from the government?
Mark only one oval.

Yes
No
Maybe

35. If yes, what kind of assistance?

36. Comment

End of study

37. Would you like to contribute further to the study

Mark only one oval.

Yes
No
Maybe

38. If yes, please write your name and email address or phone number

39. Thank you for your contribution! If you would like to contribute further to the study. Please include your email or contact numbers. Regards, Lehlohonolo Donald Adams,Ph.D. Candidate, South African National Biodiversity Institute& Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, P/Bag X01, Scottsville, Pietermaritzburg, South Africa, 3209.

CHAPTER 4

Fleshy-fruited plant change over time along roadsides of South African grasslands

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Running header: Change detection of woody fleshy-fruited invasive aliens in grasslands

4.1 Abstract

Invasive alien plants, particularly fleshy-fruited shrubs and trees, are rapidly spreading in South African grasslands. This escalating problem is transforming the grassland ecosystem and negatively impacting both the environment and human well-being. To effectively address this issue, it is crucial to identify the factors driving the spread of these invasive plants and monitor species abundance change over time. Various factors, including elevation, land use patterns, and perching structures, influence the recruitment dynamics of fleshy-fruited invasive alien plants. Our study investigated the drivers of invasion and species composition along elevation gradients (650-1900 m a.s.l). We also investigated species abundance changes over 12 years. We used Google Street View (GSV) imagery to monitor plant abundance in South African grasslands. Species composition varied along the survey route, with certain invasive plants exhibiting broader distributions and some having higher occurrence records at higher elevations. Species abundance assessments over time revealed increases in several species, while successful management strategies, particularly biological control measures, led to decreases in others. Challenges associated with GSV sampling, including limited coverage, temporal limitations, and resolution of image issues, were identified, but the method showed promise in monitoring species abundance changes cost-effectively over time. Despite challenges, GSV analyses provided valuable insights into invasion dynamics, facilitating an understanding of facilitation processes, native-alien interactions, and ecological impacts. This study has shown the importance of considering topographic factors, land use patterns, and perching structures in managing biological invasions and highlights the potential of GSV for long-term monitoring of plant species abundance in anthropogenic landscapes.

Keywords: change detection, fruit-producing woody plants, Grassland Biome, plant invasions, street view imagery.

4.2 Introduction

Invasive alien plant invasions in grasslands pose significant challenges, with the number of invasive alien plants (both in species abundance and richness) predicted to increase in the future (Seebens et al., 2021). This trend will exacerbate the already severe impacts on the environment and human well-being (Vilà and Hulme, 2017). In the grasslands of South Africa, invasive alien shrubs and trees continue to be troublesome invaders. Recently, invasive alien fleshy-fruited shrubs and trees have increased in numbers and are changing the vegetation structure of the grassland ecosystem (Carbutt et al., 2011; Chari et al., 2020; Martin, 2021; Masole et al., 2022; Adams et al., 2023). There has been a significant increase in the number of woody plants in grasslands worldwide, a process known as bush encroachment (Skowno et al., 2019). This trend is particularly evident in southern African grasslands, savannas, and mixed grass-shrub ecosystems. Fleshy-fruited invasive alien shrubs are also responsible for woody thickening in South African grasslands. The drivers of the spread of these fleshy-fruited invasive alien plants need to be determined to understand the invasion better and improve present invasion management strategies. In this study, we assessed drivers of invasion and species abundance change over time. Species abundance is the number of individuals of a given species in a region (Levin, 2013).

Documenting and understanding changes in vegetation over time is crucial in the field of vegetation ecology, especially amidst ongoing industrialization, land-use change and agricultural intensification (Pickard, 2002; Depauwet al., 2022). One of the methods by which this has been done in invasion biology is with the use of repeat photography (Hoffman and O'Connor, 1999). This method has been used to assess vegetation change over a century and has been instrumental in capturing snapshots of landscapes and evaluating landscape changes in various disciplines, including geology, botany and geography (Robert et al., 2010; Pickard, 2002; Rohde and Hoffman, 2012; Masubelele et al., 2015). Repeat photography is the practice of locating the site of a historical photograph, reoccupying the position of the camera that took the historical photograph and taking a recent photograph (Robert et al., 2010; Rohde and Hoffman, 2012).

One of the major challenges in repeat photography is finding historical photographs; thus, most of the studies include relatively few photographs. For example, one study re-photographed 65 historical landscape photographs to measure long-term changes in the cover of grasses, dwarf shrubs, tall shrubs and alien plants (Masubelele et al., 2015). Moreover, the emergence of iEcology, a research approach using data from digital sources collected for other purposes, offers promising opportunities to quantify patterns and processes in the natural world (Jarić et al., 2020). This approach, facilitated by technologies backed up in public archives such as Google Street View, can provide new insights into species occurrences, traits, phenology, and environmental features (Jarić et al., 2020). The use of Google Street View as a data source has revolutionised urban analytics and geospatial data collection, offering extensive coverage and insights into environments, with approximately half of the world's surfaced roads now covered by street view imagery (Goel et al., 2018; Biljecki and Ito, 2021). Its widespread availability has facilitated applications across various domains, including real estate valuation, demographic studies, and infrastructure mapping (Gebru et al., 2017; Law et al., 2019).

Furthermore, Google Street View has been employed in ecological research to assess the distribution of species, providing valuable data for understanding ecological patterns (Rousselet et al., 2013; Nesse and Airt, 2017). Indeed, street view imagery has been likened to a counterpart of remote sensing imagery, providing complementary insights into urban landscapes (Zhang et al., 2019). This accessibility and unique viewpoint make street view imagery an indispensable tool for studying vegetation and landscape change. In vegetation ecology, the integration of Google Street View holds the potential for monitoring invasive alien plants along roadsides (Deus et al., 2016; Barone et al., 2021; Kotowska et al., 2021), including what is facilitating their invasion. Understanding the processes driving plant invasions across spatial and temporal scales is essential for effective management (Müllerová et al., 2023). Despite its advantages, research gaps remain, including the lack of temporal manipulation in studies and challenges in collecting large-scale vegetation data (Schaffland and Heidemann, 2022).

To address this lack of sufficient photographs for analyses in repeat photography, we used Google Street View to access historical photographs of roadside invasions. In this study, we assessed vegetation change in grasslands because of invasion by fleshy-fruited invasive alien shrubs and trees over time using Google Street View and determined the drivers of invasion. The main objectives of our study were (1) to assess the frequency and abundance of fleshy-fruited invasive alien plants species abundance size adjacent to the road, (2) to assess the factors influencing their species abundance size, and (3) to assess the potential of Google Street View in determining species composition over time.

4.3 Methods

4.3.1 Study area

The Grassland Biome is one of nine biomes in southern Africa and accounts for approximately 28% of the region's terrestrial surface area, making it the second largest biome after the Savanna Biome (Mucina and Rutherford, 2006; Carbutt et al., 2011). Topographically, the landscape of the Grassland Biome varies from flat or undulating terrain with hills and valleys to rugged mountain escarpments, with elevations ranging from 300 to 3482 m a.s.l. Winters are characterised by cold and dry conditions, often accompanied by frequent frosts and snowfalls in higher elevations. Rainfall across the biome varies spatially from 400 mm to

2500 mm per annum, with a strong seasonal pattern predominantly during summer. The growing season typically spans approximately half the year (Mucina and Rutherford, 2006).

Predominantly located on the cooler, high-lying central plateau of South Africa, the montane portion of the Grassland Biome exhibits high levels of plant endemism (Skowno et al., 2019). The Grassland Biome, second only to the Fynbos biome, hosts the highest number of threatened ecosystem types (Carbutt et al., 2011). Agriculture, primarily driven by industries such as dairy, wool, beef, maize, sorghum, wheat, and sunflower cultivation, is a major driver of transformation in the Grassland Biome (Carbutt et al., 2011; Carbutt, 2012). Additionally, approximately 65% of the Grassland Biome is used for livestock and game grazing (Grasslands Programme, undated). This biome is also affected by dam construction, coal mining, and gold mining activities, which pose threats such as overgrazing, cultivation, acid mine drainage, urban sprawl, and alien plant invasion (Mucina and Rutherford, 2006; Skowno et al., 2019). Over the past century, there has been a significant increase in the density and spread of woody species globally, known as bush encroachment or woody thickening (Skowno et al., 2019). This trend is prevalent in southern African grasslands, open savannas, and mixed grass/shrub ecosystems (Skowno et al., 2019).

The Grassland Biome is characterised by four distinct bioregions: Drakensberg Grassland, Sub-escarpment Grassland, Dry Highveld Grassland, and Mesic Highveld Grassland and comprises 72 different vegetation types or units (Mucina and Rutherford, 2006). A bioregion is a distinct spatial terrestrial unit characterised by shared biotic and physical attributes and processes at the regional scale (Mucina and Rutherford, 2006). These regions are delineated based on similarities of living organisms (biotic) and the natural environment (physical). They are primarily focused on plant diversity. The study area included the following bioregions: the Dry Highveld Grassland and Mesic Highveld Grassland in the Free State Province, Drakensberg Grassland and Sub-Escarpment Grassland in Eastern Cape Province and Sub-Escarpment Grassland in KwaZulu-Natal Province (Mucina and Rutherford, 2006).

South Africa has the longest total road network across the African continent and ranks 10th for the longest road network globally. Additionally, it ranks as having the 18th longest paved road network worldwide (Jones et al., 2003). The South African transport network is a cornerstone of the country's economy and societal well-being, encompassing road, rail, air, and sea transport systems (South African National Treasury, 2021). The robustness of this network is pivotal for South Africa's economic growth, competitiveness, and the enhancement of quality of life. The South African road network spans approximately 754,600 km, categorised according to the responsible sphere of government and road type. Among these, surfaced national toll and non-toll roads cover 15,600 km (2.1%), surfaced provincial roads extend over 348,100 km (46.1%), unproclaimed rural roads span 222,900 km (29.5%), and Metropolitan, Municipal, and other roads total 168,000 km (22.3%).

For our study, data collection focused exclusively on surfaced national and provincial roads because of their coverage by Google Street View (GSV) panoramas. Google Street View has extensive sampling on South African surfaced roads, leading to different bioregions being well sampled and represented in GSV data collection. This strategic selection allows for comprehensive data collection and landscape analyses over time. The roads we sampled cut through all four bioregions of the Grassland Biome (Mucina and Rutherford, 2006).

4.3.2 Field data collection

Data were collected on 711 km segments of regional and main roads in three South African Provinces in the grassland-dominated areas (Figure 4.1). The roads included the N6, R56 and R58, spanning a total distance of 379 km (53% of the total distance sampled), passing through towns Matatiele, Kokstad, Lady Grey and Aliwal North, to mention a few in the Eastern Cape

Province. (Note: R on the name of the road indicates that it is a regional road and N for national roads). In the Free State Province, roads sampled were R26, R711 and R726, with a total distance of 163 km (23%) passing through towns such as Zastron, Walaza, Wepener, Clarens, and Fouriesburg. In KwaZulu-Natal Province, the R56 was sampled with a total distance of 169 km (24%), passing through the towns of Ixopo and Kokstad.

Figure 4.1: Google Map of a section of South Africa and Lesotho with the thick blue line showing where repeat photograph data were collected using Google Street View along South African Roads and thin blue lines showing roads where historical Google Street View images were available.

Roads that were under construction and maintenance were not sampled. Target plant species abundance were identified by driving in a vehicle around 35-40 km/h. The data collection team consisted of the driver and two observers from May until June 2022. This season was selected for data collection for easy detectability of species as they were fruiting.

One observer looked for the abundance of target plant species on the right side of the road, and the other observer looked at the left side of the road. Although indigenous fleshy-fruited plants were not the target species for the study, they were included for comparison with the invasive fleshy-fruited plants. The car was stopped when the abundance of target plant species was identified. The geographical location was recorded with a handheld global positioning system unit (GPS coordinates, Garmin, USA), elevation was noted, and 4-8 panoramic pictures were taken at each point using a 13 megapixel smartphone camera (Huawei Y7 Android 8.1 EMUI 8.2, Shenzhen China) with GPS location on for easy identification of the location on Google maps and a 20.1 megapixel digital camera for backup (SONY DSC-W800, China). The images were backed up on Google Photographs until image processing.

4.3.3 Image processing

For each image, we identified target species to genus or species level, and we noted plant species abundance, habitat and within-site bird perching structures. The species abundance of each observed alien species was recorded as the total number of individuals of the same species in the image. The type of habitat the focal species was recorded in was recorded. The perching structure was recorded as the number of individual plants under a specific perching structure. Types of habitats included livestock and or game farms, crop farms, roadsides, settlements, abandoned buildings and unoccupied land, and perching structures included roadside barriers, fencelines, power lines or poles, and shrubs or trees. Unoccupied land referred to open land that had no demarcations like fences.

To assess change in alien species communities in an area, we looked at panoramic images on Google Street View. We found the image's location using Google Maps, and then we looked at the panoramic view of that spot on Google Street View. The historical panorama was accessed on Google Street View by clicking ‘see more dates’, and all historical panoramas were found for 2010, giving us 12-year temporal difference to assess the alien species species abundance change over time. On each point/panorama, we noted plant species' abundance, size, habitat, and perching structure. Recent images taken using a digital camera were used to compare with old GSV images. It is worth noting that new GSV images were uploaded to the GSV archives at the end of the field trip in 2022; therefore, recent GSV images were also used to supplement the recent digital camera images.

4.3.4 Data analyses

We used generalised linear models (GLMs) to analyse factors affecting species abundance. Plant species abundance was recorded as count data, and GLMs are appropriate for modelling such data (Gurka and Edwards, 2011). For the calculation of species abundance change over time, the number of individual plants per point from the recent sampling was subtracted from the number of individual plants from the historical images. Negative values indicated a decrease in abundance, while zero and positive indicated the same and increasing abundance, respectively. Initial modelling focused on overall plant species abundance, where the dependent variable was plant count for all fleshy-fruited plant species. The second modelling focused on species-specific plant species abundance, where analyses were run per plant species. Predictor variables for all models were 1) habitat types: livestock and game farms, crop farms, roadside, settlement, abandoned buildings, unoccupied land), 2) elevation and 3) bird perching structures: roadside barriers, fencelines, power lines or poles, and shrub or tree. Poisson regressions were used when the data assumed Poisson distribution, and negative binomial regressions were used for data with overdispersion. We used McFadden's pseudo R-square as a descriptive approach to assess model fit. Data were analysed using the IBM Statistical Package for Social Sciences v. 20 (SPSS, Tulsa, OK, USA).

4.4 Results

4.4.1 Drivers of invasion - perching structures and land use

The goodness of fit of the model showed that the Pearson Chi-Square value (0.85) was closer to 1, which showed the model dealt with the overdispersion of the data. Akaike's Information Criterion (AIC) and/or Bayesian Information Criterion (BIC) of the full model (Negative binomial regression) values were also compared with that of the competing model (Poisson regression). Negative binomial (AIC = 2894.278, BIC = 2953.236) was preferred over Poisson (AIC = 4238.965, BIC = 4293.388) because of lower AIC and BIC values. McFadden's pseudo R-square value of 0.22 computed using Microsoft® Excel® for Microsoft 365 showed that 22% reflects the proportion of the total variation (Supplementary information Table. S4.1).

Elevation, habitats (livestock farms, roadsides, crop farms), and perching structures (roadside barriers, fencelines, and power lines or poles) were significant predictors ($P \leq 0.05$) of woody alien plant species abundance (Table 4.1). Human settlements, abandoned farmhouses, unoccupied land, and shrub/tree as perching structures were not significant predictors ($P > 0.05$) of plant species abundance. Elevation was a significant predictor of plant species abundance. Plant species abundance was expected to increase by a factor of one by the model with an increase in elevation. Livestock farms, crop farms, and roadsides had a positive predictor relationship with plant species abundance, which is expected to increase by 1.1 per observation in those three habitats. This showed that livestock farms, crop farms and road sites are expected to be equally invaded by fleshy-fruited alien plants. Bird perching structures such as roadside barriers, fencelines, power lines and poles were significant positive predictors of plant species abundance. The count observation of plants is expected to increase by a factor of 1.1. 1.0 and 1.0 for roadside barriers, fencelines, power lines and poles, respectively.

Table 4.1: Parameter estimates for negative binomial regression model on fleshy-fruited invasive alien plants species abundance (Chi d.f. = 1.

Parameter	B	Std. Error	95% Wald Confidence Interval		95% Wald Confidence Interval for Exp(B)			
			Lower	Upper	Wald Chi-Square	Sig.	Lower	Upper
Livestock_farm	0.095	0.0043	0.087	0.104	486.320	0.000	1.091	1.110
Crop_farm	0.104	0.0097	0.084	0.123	113.353	0.000	1.088	1.130
Roadside	0.128	0.0115	0.106	0.151	124.878	0.000	1.111	1.163
Settlement	0.205	0.1105	-0.012	0.421	3.435	0.064	.988	1.524
Abandoned_farmhouse	0.033	0.0320	-0.030	0.096	1.044	0.307	.970	1.100
Unoccupied_land	0.143	0.1093	-0.071	0.357	1.710	0.191	.931	1.429
Under roadside_barrier	0.134	0.0386	0.059	0.210	12.080	0.001	1.060	1.234
Under_fence	0.072	0.0209	0.031	0.113	11.900	0.001	1.032	1.120
Under power line/pole	0.080	0.0382	0.005	0.155	4.373	0.037	1.005	1.167
Under shrub_tree	-0.180	0.1383	-0.451	0.091	1.700	0.192	0.637	1.095
(Negative binomial)	0.255	0.0218	0.215	0.301				

4.4.2 Species composition

A total of 123 points were sampled. Fleshy-fruited plant species (n = number of species abundance) recorded were *Cotoneaster pannosus* Franch. (Rosaceae) (n = 15), *Lantana camara* L. (Verbanaceae) (n = 1), *Ligustrum lucidium* W.T.Aiton (Oleaceae) (n = 1), *Melia azedarach* L. (Meliaceae) (n = 6), *Opuntia ficus-indica* (L.) Mill. (Cactaceae) (n = 35), *Prunus persica* L. (Rosaceae) (n = 18), *Pyracantha angustifolia* (Franch.) C.K.Schneid. (Rosaceae) (n = 74), *Pyracantha crenulata* (D.Don) M.Roem. (Rosaceae) (n = 3), *Rosa rubiginosa* L. (Rosaceae) (n = 28), *Schinus molle* L. (Anacardiaceae) (n = 2), *Searsia* spp. F.A.Barkley (Anacardiaceae) (n = 14) and *Solanum mauritianum* Scop. (Solanaceae) (n = 9). The data suggests that certain species may prefer certain elevation bands, but there were differences in species composition over elevation; thus, species population size changed with elevation (Table 4.1). Species that occurred at the lowest elevation were *M. azedarach* at 700 to 800 m and *S. mauritianum* (700 to 1400 m asl) (Figure 4.2). *Searsia* spp. and *C. pannosus* occurred and were abundant (1300 to 1700 m asl) and *P. angustifolia* and *R. rubiginosa* at (1400 to 1800 m asl). *Opuntia ficus-indica* was recorded at the broader elevation range (700 to 1900 m asl) but most abundant in the mid-elevation (1300 to 1400 m asl), with *P. persica* being distributed equally at 1400 to 1900 m asl elevation range. *Ligustrum lucidium* and *L. camara* were recorded at 750 m and 700-900 m asl elevation ranges, respectively.

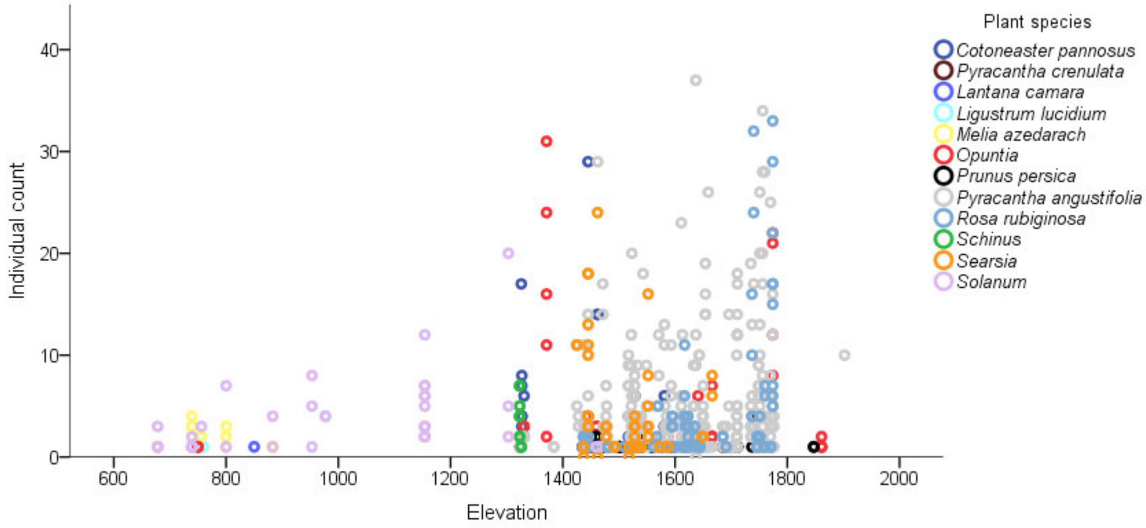

Figure 4.2: Species composition counted as individual plant count of fleshy-fruited invasive alien plant over elevation (m) in South African grasslands. (*Searsia* spp. is not an invasive alien plant but was included for comparison as it is a fleshy-fruited native shrub).

4.4.3 Species abundance changes over time

Species abundance changes over time were recorded as the difference between the number of individuals of the same species recorded in 2010 and 2022 (Mean ± SE species abundance). Negative showed a decrease in species abundance size, while a positive showed an increase. The majority of species' species abundance richness had increased over time (Figure 4.3). Species' richness that increased over 12 years were *P. angustifolia* (9.0 ± 2.0), *Searsia* spp. (6.0 ± 2.6), *S. mauritianum* (4.0 ± 2.9), *P. crenulata* (4.0 ± 2.3), *M. azedarach* (2.0 ± 0.9) and *C. pannosus* (2.0 ± 0.7), and *R. rubiginosa* (2.0 ± 0.7). *Prunus persica* (0.3 ± 0.2) and *S. molle* (0) stayed the same, while *O. ficus-indica* (-6.0 ± 5.9) decreased in numbers. *L. camara* (-1) and *L. lucidium* (0) were only observed at one point each; thus, population growth over time was inconclusive for *L. camara* and *L. lucidium*. Important invasion processes were also noted (Figure 4.4).

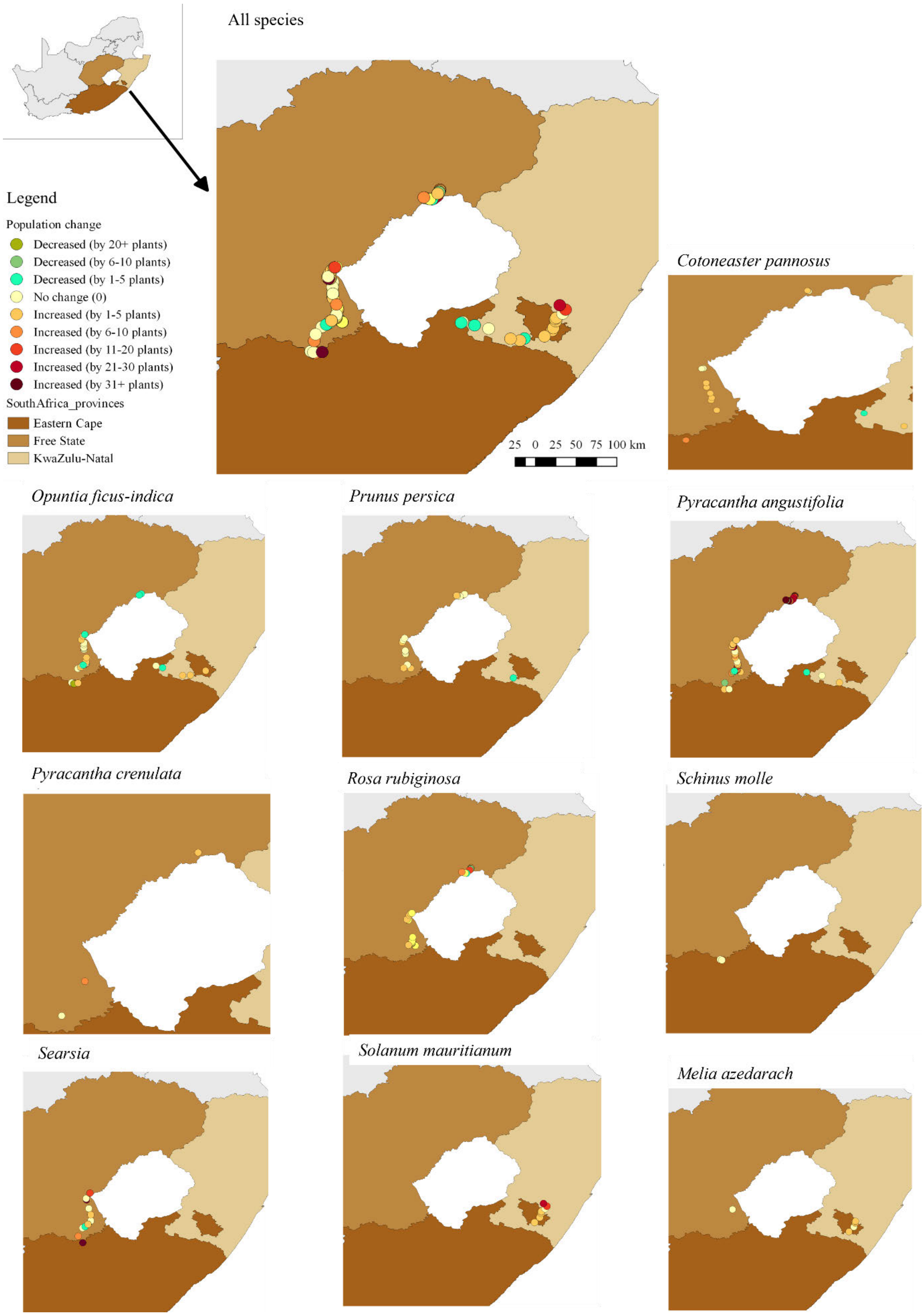

Figure 4.3: Map of repeat photographs showing the change in fleshy-fruited plant species abundance over 12 years in South African grasslands.

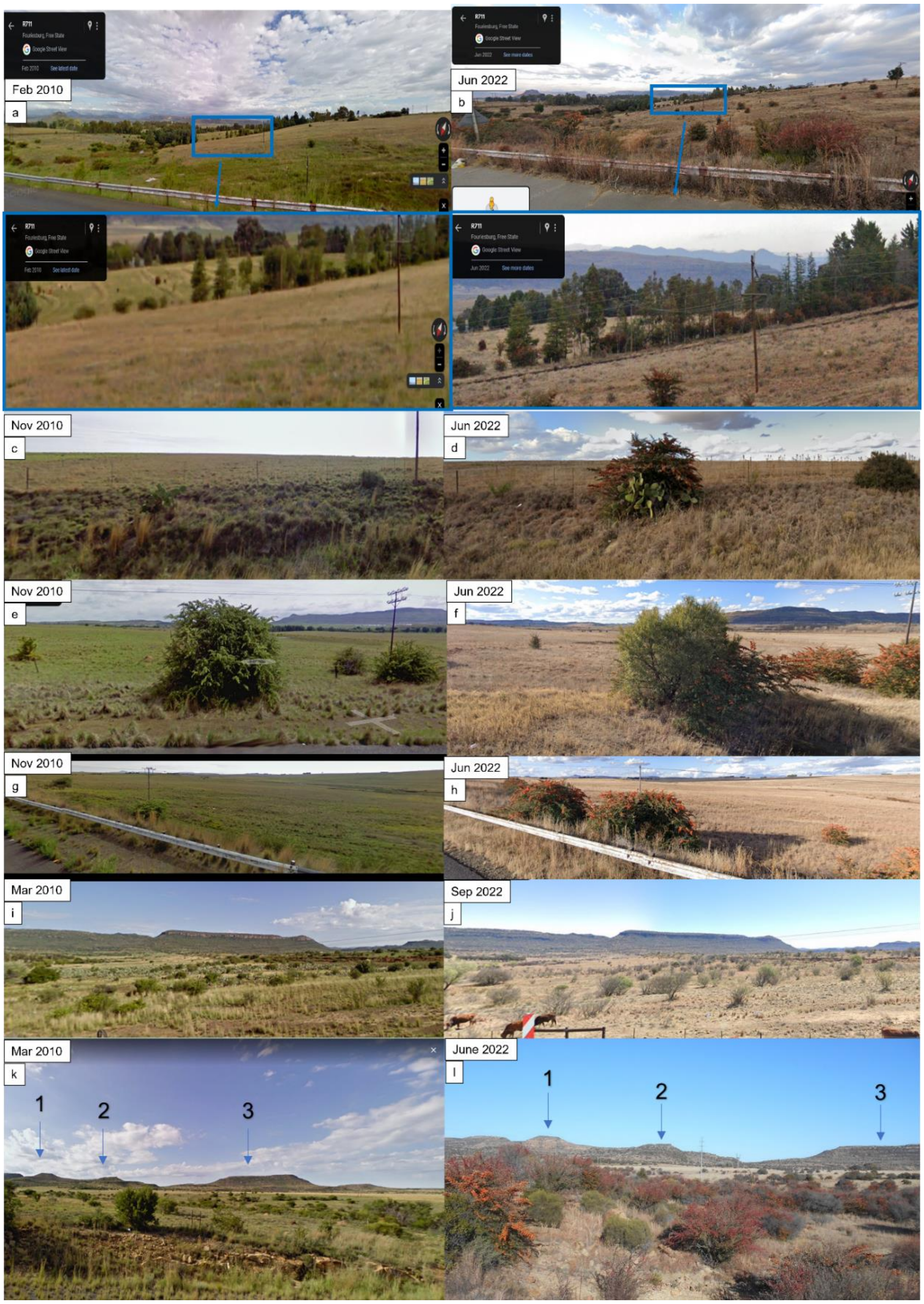

Figure 4.4: Repeat photographs of fleshy-fruited plant species invasions along roadsides in South African grasslands. The collage of repeat photographs shows the increase in image quality (a. and b.) of Google Street View over time, allowing better detection of *Pyracantha angustifolia*, potential facilitation where alien plant *Opuntia ficus-indica* modifies the

environment in ways that favour the recruitment of another alien plant *P. angutifolia*(c. and d.), alien plant *P. angustifolia* used by a native plant *Searsia* spp. for species abundance (e. and f.), and the potential to record phenology, *P. angustifolia* flowering (e.) and fruiting (f.), power lines and poles as recruitment infrastructure used by birds for perching (g. and h.), reduction of *Opuntia ficus-indica* (i. and j.), change in vegetation structure and increase woody biomass in the grassland (k. and l.). Numbers 1, 2 and 3 show landmarks that were used to locate the direction of the image.

4.5 Discussion

4.5.1 Drivers of invasion - perching structures and land use

Roadsides were identified as significant predictors, indicating that the proximity to roads influences plant recruitment, possibly because of the availability of open spaces and disturbed habitats. Perching structures were important predictors of fleshy-fruited invasive plant species abundance, as found in other studies (Gosper et al., 2005; Guidetti et al., 2016; Guidetti et al., 2022). Specifically, roadside barriers, fencelines, and power lines or poles showed significant associations with plant recruitment, as in other studies (Milton et al., 2007; Dylewski et al., 2017). These structures serve as perches for birds and other dispersal agents, facilitating the spread of fleshy-fruited plant species into adjacent areas (Gosper et al., 2005; McCay et al., 2009; Spotswood et al., 2012). In contrast, habitats associated with settlements, abandoned farmhouses, unoccupied land, and shrub/tree perching structures did not show significant associations with plant species abundance. This suggests that certain land use types like settlements, abandoned farmhouses, and perching structures may have limited influence on recruitment, as found in other studies (Pándi et al., 2014).

Overall, these results highlight the important interplay between land use patterns, and perching structures in shaping the recruitment dynamics of fleshy-fruited invasive alien plants

(Milton et al., 2007). Understanding these factors is crucial for effective conservation and management strategies aimed at controlling biological invasions in anthropogenic landscapes.

4.5.2 Species composition

The environmental changes associated with elevation drive changes in bird assemblages and fruit consumption by seed dispersers, which are associated with disperser abundance and elevation (Juncosa-Polzella et al., 2023). Although the data suggests that certain species may prefer certain elevation bands, it is inconclusive because of the low sample size comparison.

Species composition along elevation gradients in our study is consistent with findings from a study aimed at identifying and analysing invasion patterns at multiple scales in South African mountain ecosystems (Canavan et al., 2021). Similar to our study, *O. ficus-indica* exhibited a broad distribution along the elevation gradient compared with other fleshy-fruited invasive alien plants. Additionally, *S. molle* was recorded at 1469 m and lower elevations, overlapping with the 1300 - 1400 m asl elevation range in our study. *Solanum mauritianum* was also recorded at a similar range of 1528 - 1651 m asl, lower than the 700 - 1400 m asl range observed in our study. Although we only recorded *L. camara* at 750 - 850 m asl, it was also observed at around 1651 m asl, indicating its occurrence at lower elevations, as in other studies (Cavana et al., 2021).

Different alien plant assemblages invaded the highest elevation areas in both studies than lower adjacent areas. Surveys have found specific species becoming more abundant or even restricted to higher elevation areas, such as *C. pannosus* and *P. angustifolia* at about 1651 m asl (Canavan et al., 2021; Juncosa-Polzella et al., 2023), which was consistent with the trends observed in our results. However, contrasting patterns were also observed with *M. azedarach* found at different elevations (1355 - 1528 m asl and lower) and as the most abundant alien plant in both lower and high-elevation areas (Canavan et al., 2021).

4.5.3 Species abundance changes over time

Google Street View was effective in recording different invasion processes and drivers of invasion (Figure 4.4). Repeat photographs of fleshy-fruited plant species roadside invasion in South African grasslands showed an increase in Google Street View image quality over time, allowing better detection of species.

The analysis of species abundance over 12 years provides valuable insights into the dynamics of fleshy-fruited plant species in the study area. Most species populations demonstrated an increase in numbers, reflecting potential shifts in species abundance and distribution over time. The detection of seedlings also might be a challenge. For example, a seedling will be difficult to detect from Google Street View, but 12 years later, the mature shrub that has developed would be much more detectable.

Among the species showing species abundance increases, *P. angustifolia*, *Searsia* spp., and *S. mauritianum* displayed the highest average growth, followed by *P. crenulata, M. azedarach*, *C. pannosus,* and. *R. rubiginosa*. These findings suggest favourable conditions or ecological factors that have influenced population expansion for these species over the study period (Canavan et al., 2021). This expansion may result in outcompeting native grassland vegetation, leading to changes in species composition and ecosystem structure.

Opuntia ficus-indica have shown a decrease in numbers, highlighting potential management successes that have suppressed species abundance growth. This could be because of the successful establishment of biocontrol agents (Annecke and Moran, 1978; Zimmermann and Moran, 1991). Biological control agents, such as the cactus moth *Cactoblastis cactorum* Berg (Pyralidae) and different cochineal insects from the *Dactylopius* genus, have effectively decreased large-scale populations in numerous countries, including South Africa (Humphries et al., 2022). On a smaller scale, the use of herbicides through injection or spraying directly onto the cladodes also offers efficient control (Humphries et al., 2022). However, ongoing monitoring and management efforts are necessary to prevent a resurgence and ensure effective control of this invasive species (Humphries et al., 2022).

4.5.4 Challenges of sampling with Google Street View

Using Google Street View in research to assess plant populations along roadsides presents several challenges. There is limited coverage as Google Street View may not cover all roads or areas of interest, particularly in remote or less populated regions (Nesse and Airt, 2017). For example, the N8 road from Ladybrand to Lesotho border gates did not have historical photographs. This limited coverage can result in gaps in data and incomplete assessments of plant species abundance along roads. There were also temporal limitations associated with this type of data collection. Google Street View imagery may be uploaded on less desired dates, leading to a lack of desired historical dates, such as 100 years ago (He et al., 2020). The oldest historical photographs were uploaded in 2010, giving us only a 12-year temporal difference to assess change. Changes in vegetation composition and structure over time may not be accurately captured, affecting the reliability of the data for longitudinal studies or monitoring programs.

The resolution and image quality of Google Street View imagery may vary, impacting the ability to identify and differentiate plant species, especially smaller or less conspicuous species (Nesse and Airt, 2017). This can introduce errors and inaccuracies in plant assessments. In our study, images accessed in 2022 had a higher quality than those dating back to 2010. Google Street View imagery may capture scenes during specific seasons, potentially biasing plant population assessments towards certain times of the year (Biljecki and Ito, 2021). Seasonal variability in vegetation phenology and growth patterns may not be adequately represented, affecting the accuracy of plant species abundance estimates (Nesse and Airt, 2017; He et al., 2020).

Google Street View provides a relatively low level of detail and scale compared to on-the-ground surveys or higher-resolution remote sensing methods. Fine-scale variations in vegetation composition, density, and distribution of plant species may not be discernible, limiting the precision of plant species abundance assessments. For example, large infestations of *C. pannosus* could not be identified solely through Google Street View compared with on-the-ground surveys. This is because Google Street View has low resolution and cannot identify plant species from a distance. Assessing plant species abundance solely based on Google Street View imagery may lack validation or ground-truthing data. Ground-truthing efforts, such as field surveys or remote sensing validation, are essential for validating and calibrating the accuracy of plant assessments derived from Google Street View imagery. Another limitation is that with Google Street View imagery you can only sample close to roads, so not truly capture the effect of the road.

4.5.5 Use of Google Street View to monitor change over time

Despite the aforementioned challenges, the potential to use Google Street View to assess species abundance change over time by analysing archived images taken at the same location offers several advantages. This method has been demonstrated to be effective in tracking changes in fleshy-fruited woody plant composition and distribution over time in the grasslands of South Africa. The method is expected to improve with time and will allow long-term data analysis for longer-term trends in vegetation dynamics. The temporal analysis of plant populations can be cost-effective compared with conducting repeated field surveys or acquiring high-resolution satellite imagery. Researchers can access archived imagery at no cost and analyse vegetation changes without extensive fieldwork (Deus et al., 2016; Barone et al., 2021). Google Street View images also offer a unique spatial context by providing views of the surrounding environment, including roadways, buildings, and landscape features. In our study, we managed to assess plant species abundance over 12 years. The method could further be used in the management of biological invasions to assess the effectiveness of the control methods. Important invasion processes like facilitation of invasion by other plants, native-alien species interactions, phenology, and environmental impact on vegetation structure were shown to be effectively detected. These are important context-dependent processes that allow better understanding of biological invasions of woody fleshy-fruited plants (Milton et al., 2007; Lediuk et al., 2014; Ferreras et al., 2023; Vega-Polanco et al., 2023). The indirect increase of native tree seed dispersal by fleshy-fruited invasive shrubs should be further investigated to assess the extent of benefits provided by the aliens to the natives (Vergara-Tabares et al., 2022).

4.6 Conclusions

Using Google Street View archives to assess species abundance changes over time offers a valuable and cost-effective approach to studying vegetation dynamics and ecosystem responses to environmental change. By harnessing the temporal dimension of Google Street View imagery, we can better understand the long-term vegetation ecological trends and inform conservation and management strategies, including invasion status. Such data can be used to assess the effectiveness of control methods in biological invasions over time. The method works best in combination with others, like in-person field surveys and remote sensing, as each has its own strengths and weaknesses that could complement the other (Deus et al., 2016; Barone et al., 2021; Kotowska et al., 2021). This study contributes a new method of assessing change over time compared with traditional repeat photography and remote sensing. This will allow for cost-effective status of invasion assessment for plant species that are easily recognised through Google Street View. Our study also showed that fleshy-fruited invasive alien plants are increasing in abundance in the grasslands and need immediate interventions, with *O. ficus-indica* as an exception, but they still need further monitoring.

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4.9 Supplementary Information

Supplementary information Table. S4.1. McFadden's pseudo R-square value calculations based on the log likelihood of intercept and full model.

Model	Log likelihood (LL)	(-2LL)	McFadden's
Intercept-only	-1835,91	3671,82	
Full model	-1435,139	2870,278	0,22

CHAPTER 5

Fruit selection of birds for selected fleshy-fruited invasive alien plants

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Running header: Invasive fruit selection by frugivorous birds

5.1 Abstract

Invasive alien plant species with fleshy fruits pose a significant threat to various ecosystems, particularly in South Africa, where fleshy-fruited shrubs like *Cotoneaster* spp., *Pyracantha* spp., *Rosa* spp., and others are invading grasslands. This invasion is facilitated by frugivorous birds, creating a need to understand the ecological interactions driving these invasions. Despite extensive research in forest ecosystems, the mechanisms of invasion and the role of fruit selection in predicting invasion success remain understudied in grasslands. To address this gap, we conducted feeding experiments with four frugivorous bird species: black-collared barbet (*Lybius torquatus*), dark-capped bulbuls (*Pycnonotus tricolor*), red-winged starlings (*Onychognathus morio*), and rose-ringed parakeets (*Psittacula krameri*) in captivity at the University of KwaZulu-Natal animal house, Pietermaritzburg, South Africa. We examined their fruit selection among fleshy-fruited invasive alien plant species including *Cotoneaster franchetii* (silver-leaf cotoneaster), *Duranta erecta* (forget-me-not tree), *Eriobotrya japonica* (loquat), *Ligustrum lucidum* (glossy pivet), *Pyracantha angustifolia* (yellow firethorn), *Schinus terebinthifolia* (Brazillian pepper tree), and *Solanum mauritianum* (bugweed). Fruits of *C. franchetii* and *S. terebinthifolia* were positively selected, while *D. erecta*, *E. japonica*, *P. angustifolia*, and *S. mauritianum* were less preferred. These preferences could be driven by various fruit traits such as colour, size, nutrient composition and quantity, pulp proportions, presence of toxins, or even shape, and future experimentation should aim to tease out these preferences, perhaps with artificial fruits. These findings contribute to understanding avian foraging behaviours and suggest that fruit selection will have an impact on the seed dispersal of fleshy-fruited invasive alien plants when fruiting seasons overlap among fruiting plants.

Keywords: invasive alien plants; frugivorous birds; fruit selection; functional traits; grassland ecosystems; invasion mechanisms

5.2 Introduction

Invasive alien plants (IAPs) are a significant threat to ecosystems and agriculture, causing devastating impacts on ecosystem services (Pyšek et al., 2020; Bhatta et al., 2023; Gioria et al., 2023; Rai et al., 2023). In South Africa, the annual loss of ecosystem services because of IAPs is estimated at ~6.5 billion South African Rand (de Lange and van Wilgen, 2010; van Wilgen et al., 2022). The introduction of new species into novel ranges is increasing, with each new introduction potentially becoming invasive (Seebens et al., 2017; Pyšek et al., 2019; Gioria et al., 2023). South Africa currently records approximately 2033 alien plant species outside of cultivation, of which 759 are considered naturalised or invasive (Richardson et al., 2020). Understanding invasion processes is crucial for better management of these species (Pyšek et al., 2020; Seebens et al., 2017; Richardson et al., 2020).

Fleshy-fruited invasive plants are increasingly abundant globally, particularly in forest systems where they are predominantly bird-dispersed (Henderson, 2007; Thabethe et al., 2015; Henderson, 2020; Mora and Smith-Ramírez, 2016; Bitani and Downs, 2020; Juncosa-Polzella et al., 2023). In South Africa, fleshy-fruited plants invade various ecosystems, including grasslands (Carbutt, 2012; Masole et al., 2022; Adams et al., 2023). These plants, such as those from the Rosaceae genera *Cotoneaster* spp., *Pyracantha* spp., and *Rosa* spp., exploit frugivorous birds to proliferate and invade unoccupied environmental niches in grasslands (Adams et al., 2022, 2023). While interactions between frugivorous birds and fleshy-fruited plants are well-studied in forest ecosystems (Thabethe et al., 2015; Mora and Smith-Ramírez, 2016; Bitani and Downs, 2020), research in montane grassland ecosystems is lacking.

Understanding the mechanisms of alien invasive species' invasion into new habitats is crucial (Cordeiro et al., 2004; Henderson, 2007; Wilson and Downs, 2012). In South Africa, invasive species are typically managed after widespread distribution, emphasising the need for an approach based on functional traits to identify potential interactions and aid in early invasion stage management and predicting future invasions (Wilson et al., 2013; da Silveria Pontes et al., 2015; Balaguru et al., 2016; Bitani and Downs, 2020). A predictive approach is essential for conservation planning, prioritising invasion management, and reducing uncertainty in management strategies (da Silveria Pontes et al., 2015; Balaguru et al., 2016; Bitani and Downs, 2020).

Birds play a crucial role as dispersal agents for many invasive plant species, involving both mutualistic and non-mutualistic relationships (Dean and Milton, 2000; Richardson et al., 2000; Palacio and Montalti, 2023; Juncosa-Polzella et al., 2023). Crucial frugivore traits for plant invasions include their ability to disperse seeds and the seed shadows they create (Gosper, 2005; Palacio and Montalti, 2023). These traits encompass fruit handling techniques, gut passage rates, movement patterns, and dietary composition, which may vary within the same bird species depending on the fruits they consume (Avery et al., 1993; Rey and Alcántara, 2000; Palacio and Montalti, 2023). The way birds handle fruits influences seed dispersal and plant invasions significantly, and they are categorised as seed gulpers, seed discarders, or seed predators (Avery et al., 1993; Rey and Alcántara, 2000). Dietary composition, particularly the proportion of fruit in their diet and fruit preferences, can help identify functionally similar frugivores, aiding in predicting potential dispersers and associated dispersal patterns of invasive species (Sato, 2022).

We conducted feeding experiments in captivity to address the intricate hierarchy of frugivore decisions observed in the field. These experiments involved four frugivore species making paired comparisons of different fruit species, leading to the identification of species-specific fruit choices (Blendinger et al., 2016).

5.3 Methods

5.3.1 Bird species and ethical note

We investigated the fruit choice of frugivorous birds on fleshy-fruited invasive alien plants. Bird species included three native species, dark-capped bulbul (*Pycnonotus tricolor*) (n = 9), red-winged starling (*Onychognathus morio*) (n = 5), and black-collared barbet (*Lybius torquatus*) (n = 1), and one invasive species, the rose-ringed parakeet (*Psittacula krameri*) (n = 5). The native species were selected because they are widely distributed in the study area and have a high chance of encountering plant species under study. The birds were also selected according to body size, fruit handling behaviour (i.e. fruit gulpers or chewers), diet and availability. Birds were caught (ethical clearance number: 020/15/Animal) in walk-in traps in July 2021, placed in outdoor flight cages and provided with food and water *ad libitum*. Parakeets and starlings were already in captivity in the flight cages at the animal house. This was not expected to influence any comparisons in the study as all birds were acclimatized before the experiment. The walk-in trap used was manual to ensure that birds did not get trapped in the traps for too long.

The maintenance diet included bananas, apples, pears, oranges and commercial pellets. Birds were later transferred into indoor experimental cages for seven days of acclimatisation once enough birds were caught to start the experiment. They were provided with the same maintenance diet until the experiments started in August 2021. Experimental fruits were incorporated into the maintenance diet to ensure that birds were familiar with the experimental fruits to prevent possible neophobic reactions to novel food items (Greenberg, 1984). We also fed birds using the Petri dishes a day before the experiment so that they identified Petri dishes as food containers. Fruit preference experiments took four days. Before being released at their capture site after the study, the birds were banded with SAFRING numbered metal identification rings (SAFRING, University of Cape Town, Cape Town) to avoid using them again for subsequent studies.

Birds were observed for unusual behaviour every morning and afternoon and episodically while feeding them. Individuals who showed inactivity during the acclimatisation were released.

5.3.2 Fruit sampling

We collected ripe fruits (July 2021) from different fleshy-fruited invasive alien plants in KwaZulu-Natal Province around Pietermaritzburg. Fruits were collected from at least five individual plants per species, depending on the availability of plants fruiting in the field. Upon collection, we stored fruiting branches in sealed plastic bags inside a refrigerator on the same day of collection, and they were used within, at most, five days of collection. The fruits were rinsed with distilled water, and we used a digital calliper to measure the length (mm) of the first 50 fruits per plant species (Table 5.1). Fruit size was measured as fruit diameter by taking the measurement of the widest part of the fruit. Number of seeds per fruit was also noted. Plant species from which the fruits were collected were silver-leaf cotoneaster *Cotoneaster franchetii Bois* (Rosaceae), forget-me-not tree *Duranta erecta* L. (Verbenaceae), loquat *Eriobotrya japonica* (Thunb.) Lindl. (Rosaceae), glossy pivet *Ligustrum lucidum* W.T.Aiton (Oleaceae), yellow firethorn *Pyracantha angustifolia* (Franch.) C.K.Schneid. (Rosaceae), Brazillian pepper tree *Schinus terebinthifolia* Raddi (Anacardiaceae), and bugweed *Solanum mauritianum* (Solanaceae) (Table 5.1). The plant species used in this study were all invasive alien plants in South Africa (Henderson, 2020).

5.3.3 Feeding trials

In each trial, we offered birds a pair of fruits, each in a separate Petri dish. Birds were given five fruits per plant species, and the location of the two petri dishes in the cage (e.g., from left or right) was changed between trials (Whelan and Willson, 1994). The fruit pair was changed after two to five choice trials; therefore, each bird took part in at least two trials for each fruit pair. If the bird did not eat anything, the fruit pair was changed. Each trial took a maximum of 15 min. We recorded the number and types of fruits eaten by each bird. All the feeding trials were done between 08h00 and 14h00. We removed maintenance food at 18h00 the evening before feeding trial fruits, which were the first food the birds offered on an experiment day.

Birds were observed from when they were fed. The presence of humans appeared not to have affected their feeding behaviour as they mostly ate immediately after being offered the fruits. A trial was considered completed when the subject ate half of the available fruit, or 15 min had elapsed from the beginning of the trial. In each trial, we recorded the number of each plant species' fruits consumed by each bird and their feeding behaviour. We regarded a plant as the "preferred" choice if (1) a higher number of fruits were eaten, (2) fleshy pulp was eaten, and/or (3) when half of its fruit was eaten before or at the end of the trial. Preference was not observed if the bird ate nothing until time elapsed. Nineteen different pairs of fruits were derived from seven different fruits to ensure that each fruit was tested against all other fruits.

5.3.4 Data analyses

Generalised linear models (GLMs) were used to analyse data using the IBM Statistical Package for Social Sciences v. 20 (SPSS, Tulsa, OK, USA). Our data resulted in binary win or loss outcomes as the dependent variable with categorical independent variables, such as colour of fruit and numerical independent variables, such as size of fruit, number of seeds, and size of seeds. Binomial logistic regressions were used to model the probability of a discrete binary fruit choice outcome (selected or not selected fruit) (Edgar and Manz, 2017). We used the Wald Chi-square test for independence to assess the relationship between the categorical independent variables and the dependent variable. Before conducting any statistical test, we assessed the data for assumptions and ensured that the data met the requirements of the chosen test. We used a linear regression test to test for collinearity between the predictor variables before the binomial logistic regression models were run.

Birds were grouped per secondary diet, fruit handling and species in the analyses. The secondary diet referred to the type of food the birds fed on in the field except for fruits, as they were all frugivorous birds (Chittenden et al., 2007). Granivorous birds were those that ate grain as the secondary diet, and insectivorous birds were those that ate insects. Insectivorous birds were dark-capped bulbuls and red-winged starlings, and rose-ringed parakeets were the granivorous birds in our study. Species categorised as "gulpers," were those which swallowed the entire fruit, and were restricted by the size of their bill gape size, limiting their ability to ingest fruits larger than these. Conversely, species categorised as "chewers" which chew fruits in their beaks or mouths, may avoid consuming fruits with large, hard seeds and minimal pulp (Rojas et al., 2021). Black-collared barbet, dark-capped bulbuls and red-winged starlings were gulpers, and rose-ringed parakeets were the chewers in our study.

5.4 Results

5.4.1. Feeding trials

Fruit colour, fruit diameter and number of seeds produced per fruit of fleshy-fruited invasive plant species used for the feeding fruit choice trials differed (Supplementary Table S5.1). We recorded 1607 fruit selections and non-selection interactions between four bird species and seven plant species, and all bird species responded to all plant fruits provided in the study except for black-collared barbet provided with *Duranta erecta* (Table 5.1).

Table 5.1: Number of sampling periods in which fruit species were consumed (C) and selected (S) by aviary frugivorous bird in choice test feeding trials run in the animal house at the University of KwaZulu-Natal, Pietermaritzburg, South Africa. Consumed is the number of times the fruit was consumed in each trial. We regarded a plant as the selected choice if (1) a higher number of fruits were eaten, (2) fleshy pulp was eaten, and seeds fell out of the fruit, and/or (3) when half of its fruit was eaten before or at the end of the trial.

Animal species	**Dark-capped bulbul (*Pycnonotus tricolor*)**					**Red-winged starling (*Onychognathus morio*)**					**Rose-ringed parakeet (*Psittacula krameri*)**					**Black-collared barbet (*Lybius torquatus*)**				
Plant species	N	C	%C	S	%S	N	C	%C	S	%S	N	C	%C	S	%S	N	C	%C	S	%S
Cotoneaster franchetii	112	90	80	75	83	100	80	80	74	93	63	62	98	58	94	7	5	71	3	60
Duranta erecta	116	16	14	11	69	82	7	9	3	43	49	12	24	9	75	5	0	0	0	0
Eriobotrya japonica	53	12	23	12	100	66	15	23	15	100	22	3	14	2	67	0	0	0	0	0
Ligustrum lucidum	114	83	73	77	93	103	65	63	58	89	48	9	19	1	11	7	7	100	7	100
Pyracantha angustifolia	103	80	78	57	71	98	76	78	57	75	58	58	100	49	84	5	3	60	3	100
Schinus terebinthifolia	112	86	77	84	98	92	79	86	72	91	59	40	68	28	70	6	6	100	6	100
Solanum mauritianum	102	28	27	10	36	125	54	43	15	28	58	7	12	2	29	0	0	0	0	0

N = number of times the fruit was included in the trials

5.4.2 Overall predictors

The data passed collinearity tests for the independent variables of bird species, fruit size, fruit colour, number of seeds per fruit, and bird diet. The variance inflation factor was lower than 5 (1.0-1.5), indicating that there was no multicollinearity. Fruit handling behaviour was excluded from the analyses as it did not meet the logistic regression assumptions because collinearity was detected. Fruit handling had the same values as the diet; thus, it was removed from the analyses. The significant predictors of the fruit selection were fruit colour (Walds Chi-square value (χ^2 (df, n) (χ^2 (3, n = 1607) = 395.453, P < 0.05), fruit size (χ^2 (1, n = 1607) = 5.224, P < 0.05), plant species (χ^2 (6, n = 1607) = 386.216, P < 0.05) and bird diet (χ^2 (1, n = 1607) = 8.600, P < 0.05) (Table 5.2).

Table 5.2: Regression analysis result summary of fruit selection binary outcome by aviary frugivorous birds based on number of fruits eaten.

Model focus	Predictor	N	df	Wald χ^2	Sig.	Exp(B)	95%C.I.for EXP(B)	
							Lower C.I.	Upper C.I.
Overall (all predictors)	Colour	1607	3	395.45	P < 0.05	-	-	-
	Diet	-	1	8.60	P < 0.05	0.68	0.53	0.88
	Size		1	5.22	P < 0.05	0.70	0.52	0.95
	Plant species		6	386.22	P < 0.05	-	-	-
	Bird		3	15.29	P < 0.05	-	-	-
Bird specific predictions								
Black-collared barbet	Colour	30	3	0.33	P > 0.05	-	-	-
	Size		1	5.15	P < 0.05	0.59	0.38	0.93
	Plant species		4	0.43	P > 0.05	-	-	-
Dark-capped bulbuls	Colour	656	3	148.49	P < 0.05	-	-	-
	Size		1	56.86	P < 0.05	0.85	0.82	0.89
	Plant species		6	144.99	P < 0.05	-	-	-

Rose-ringed parakeet	Colour	294	3	105.99	P < 0.05	-	-	-
	Size		1	28.60	P < 0.05	0.81	0.76	0.88
	Plant species		6	73.73	P < 0.05	-	-	-
Red-winged starling	Colour	627	3	176.32	P < 0.05	-	-	-
	Size		1	68.46	P < 0.05	0.83	-	-
	Plant species		6	163.97	P < 0.05	-	-	-
Diet-specific predictions								
Frugivore granivore	Colour	294	3	105.99	P < 0.05	-	-	-
	Size		1	28.60	P < 0.05	0.81	0.76	0.88
	Plant species		6	73.73	P < 0.05	-	-	-
Frugivore insectivore	Colour	1313	3	327.62	P < 0.05	-	-	-
	Size		1	129.47	P < 0.05	0.84	0.82	0.87
	Plant species		6	314.78	P < 0.05	-	-	-

5.4.3 Plant species

Plant species played a role in fruit selection, but no significant differences ($P < 0.05$) were observed in fruit selection among black-collared barbets and rose-ringed parakeets. Specific plants such as *D. erecta*, *E. japonica*, *P. angustifolia*, and *S. mauritianum* were selected against, while *C. franchetii* and *S. terebinthifolia* had a higher selection on fruit selection. Fruit selection of *D. erecta*, *E. japonica*, *P. angustifolia*, and *S. mauritianum* was expected to decrease by factors of 0.5, 0.1, 0.5 and 0.1, respectively, for dark-capped bulbuls, while fruit selection by dark-capped bulbuls was expected to increase by factors of 1.7 and 2.7, respectively, for *C. franchetii* and *S. terebinthifolia*. *Duranta erecta*, *E. japonica*, *P. angustifolia*, and *S. mauritianum* fruit selections were less expected to be selected by the red-winged starlings by factors of 0.1, 0.1, 0.2 and 0.7, respectively. Fruits of *S. terebinthifolia* and *C. franchetii* were expected to be selected by a factor of 2.1 and 3.0, respectively, for red-winged starlings. *Ligustrum lucidum* fruit selection did not differ significantly among dark-capped bulbuls and red-winged starlings.

Duranta erecta, *E. japonica*, *P. angustifolia* and *S. mauritianum* were negative significant predictors of fruit selection in insectivorous birds, while *S. terebinthifolia* and *C. franchetii* were positive significant predictors of fruit selection for these bird species. *Ligustrum lucidum* was not a significant predictor of fruit selection. However, we did not observe significant differences among plant species in granivorous birds.

5.4.4 Fruit colour

Fruit colour exhibited varied effects. Orange and yellow fruits were negative predictors for dark-capped bulbuls and red-winged starlings, while red and black fruits were positive predictors. Fruit selection for orange and yellow fruits was expected to decrease by factors 0.5 and 0.1, respectively, in dark-capped bulbuls. In contrast, for red and black fruits, the fruit selection was expected to increase by factors of 1.3 and 2.8, respectively. In red-winged starlings, orange and yellow fruits were less likely to be selected by factors of 0.2 and 0.1, respectively, while black and red fruits were expected to be selected by factors of 2.4 and 1.7. In rose-ringed parakeets, orange and red fruits were positive predictors, while yellow and black were negative predictors. Orange and red fruits were expected to increase in selection by factors of 15.7 and 25.6, respectively, while yellow and black fruits were expected to decrease in selection by factors of 0.7 and 0.3, respectively. Orange and yellow fruits were consistently negative predictors, and black and red fruits were positive predictors for frugivorous bird species that ate grains and insects as their secondary diet.

Orange and yellow fruits were less likely to be selected by factors of 0.2 and 0.1, respectively, by secondary granivorous birds, while black and red fruits were expected to be selected by a factor of 2.4 and 1.7, respectively. Orange and yellow fruits were expected to be less selected by insectivorous birds by factors of 0.37 and 0.1, respectively, while red and black fruits were expected to increase in fruit selection by insectivorous birds by factors of 1.5 and 2.5, respectively.

5.5 Discussion

Prior research has shown a positive correlation between fruit size and the number of seeds dispersed by birds (Cazetta et al., 2008; Gosper et al., 2005; Galetti et al., 2011). However, large fruits are only favoured if their size falls within the bird's gape width (Herrera, 1984), and even then, this preference is not always consistent. For instance, Wotton and Ladley (2008) found that the New Zealand pigeon (*Hemiphaga novaeseelandiae*) exhibited no particular preference for larger fruits in New Zealand. Additionally, some seeds are too large to be effectively dispersed by the most common bird frugivores in New Zealand (Kelly et al., 2010).

Fruit size was a consistent negative predictor across all bird species in our study, this means that when the model predicts less selection with increase in fruit size. This observation is consistent with many studies (Green, 1993; Rey and Alcántara, 2000; Kitamura et al., 2002; Sebastián-González, 2017). The relationships between the sizes of fruits relative to the frugivores can impact how quickly fruits are removed (Brodie, 2017). Birds with large bills typically favour larger fruits without restriction because of beak gape size (Pegman et al., 2017). Bill dimensions can constrain the size of fruits that birds can ingest, thereby limiting the availability of potential food sources (González-Castro et al., 2015; Hazell et al., 2023). Consequently, smaller fruits may be more accessible to a broader range of frugivorous species than larger fruits (Kitamura et al., 2002; Sebastián-González, 2017).

Certain large fruits may possess a richer nutrient profile and numerous seeds, thereby elevating the likelihood of their dispersal by frugivorous birds (Moles and Westoby, 2006; Velázquez-Rosa et al., 2017). Species with large fruit, except those with abundant tiny seeds, attract few bird dispersers in both native (Green, 1993; Rey and Alcántara, 2000) and invasive communities of bird-dispersed plants. However, large fruits are only favoured if their size falls within the bird's gape width (Herrera, 1985). Furthermore, birds may also exhibit a preference for non-native fruits resembling native ones (Aslan and Rejmanek, 2012). Fruit crop size, representing the number of ripe fruits presented by plants, strongly predicted bird fruit consumption in one of the studies (Palacio and Ordano, 2018).

Consequently, invasive alien plants with large crop sizes could experience significant consumption by frugivorous species, thereby enhancing their invasive potential (Palacio and Ordano 2018). Through a combination of field observations and manipulative experiments, Sallabanks (1993) demonstrated that American robins (*Turdus migratorius*) foraging on hawthorn (*Crataegus monogyna*) exhibited a hierarchy of decision-making. Their use of individual shrubs correlated with crop size, fruit diameter, and pulp-to-seed ratio. Within a shrub, birds preferred larger fruits (Sallabanks, 1993; Balasa et al., 2023).

We predicted that red and black would be selected more than other fruit colours (Duan et al., 2014). This means our prediction is partially correct because fruit colour exhibited varied effects, as it applied only for dark-capped bulbuls and red-winged starlings and incorrectly for the rose-ringed parakeets. In our study, the orange and yellow fruits served as negative predictors for dark-capped bulbuls and red-winged starlings and thus were less selected, while red and black fruits were positive predictors, being more selected than other colours. However, in rose-ringed parakeets, orange and red fruits were positive predictors, while yellow and black were negative predictors. Orange and yellow fruits were consistently negative predictors, and less selected, and black and red fruits were positive predictors for both frugivorous birds that eat grains and insects as their secondary diet. Other studies have shown fruit selection by birds to be influenced by fruit colour, with brightly coloured fruits attracting avian frugivores (Siitari et al., 1999; Teichmann et al., 2020; Lim and Burns, 2021; Tedore et al., 2022; Hazell et al., 2023).

Advanced visual cues have been noted in invasive plant species, potentially enhancing fruit removal rates (Knight, 1986; Galetti, 2002). While birds commonly prefer darker fruits like red and black because of their rich lipid content (Schaefer et al., 2013), their colour preferences may vary based on factors such as age and previous experiences (Teichmann et al., 2020). In a study involving artificial fruits, birds preferred red and brown colours (Arruda et al., 2008). However, at the community scale, birds did not selectively choose artificial fruits matching the prevalent real fruit colours (Hazell et al., 2023). Additionally, birds may not select fruits based on detailed reflectance properties but rather on their overall colouration, which aids their detection (Fadzly et al., 2013). Overall, selection pressure may favour fruit pigments that protect against environmental conditions rather than those appealing to dispersers (Traveset and Willson, 1998; Burns, 2015; Lim and Burns, 2021).

Previous research has associated fruit removal rates with various factors, particularly their nutrient composition. For instance, migratory birds exhibit a preference for fruits rich in lipids over those with different nutrient profiles (Rumeu et al., 2019). Fruits containing secondary metabolites that deter fruit predators and pathogens are often less appealing to legitimate frugivores (Schaefer et al., 2003).

The timing of fruiting, known as fruiting phenology, can also impact fruit consumption by local frugivores. Invasive alien plants that fruit asynchronously with native plants may be perceived as attractive resources during times of scarcity (Vergara-Tabares et al., 2018). Previous studies have revealed that invasive species often exhibit longer fruiting durations and/or fruit when native fruits are scarce, thus limiting feeding options for frugivorous dispersers (Chimera and Drake, 2010; Lediuk et al., 2014; Bitani et al., 2020).). In one study, longer fruiting duration and smaller seed size were identified as significant predictors for avian frugivore consumption, while fruit colour did not significantly influence fruit choice (Sperry et al., 2021).

Frugivorous birds can adjust their nutritional preferences based on seasonal requirements such as migration or reproduction (Lepczyk et al., 2000; Albrecht et al., 2018). Furthermore, at finer temporal scales, the internal state of the bird can impact its selectivity. Hungry birds or those facing food scarcity may be less selective about their food choices once they find it (Schaefer and Schaefer, 2006; Morán-López et al., 2020). The temporal dynamics of fruit choices can be incorporated by modelling the internal state of frugivores. For instance, animals may alter their foraging preferences based on their current nutritional needs and the nutrient content of fruits (Morán-López et al., 2018). This modelling approach could be expanded to include the accumulation of secondary metabolites within animals and their influence on foraging choices. The experimental setup was the limiting factor, as the driving choice of birds might have been other cues that were not tested here. This includes bird experience, toxins, shape, taste, smell and others.

5.6 Conclusions

Our study showed that plant species generally play a significant role in fruit selection. Although results show colour and size to be significant predictors, fruiting season, as shown by other studies, is the final determining factor of seed dispersal. We recommend further experimentation to test the preferences of birds for different colours and sizes, including dyed fruits of various species or artificial fruits of different colours and sizes. Understanding the factors influencing fruit selection and consumption by frugivorous birds is crucial for predicting the dispersal patterns of fleshy-fruited invasive alien plants. This research sheds light on the ecological mechanisms driving the spread of invasive species. It underscores the importance of considering bird-mediated dispersal in the management and control strategies of invasive plants. By identifying the traits that make certain fruits more attractive to birds, conservationists and land managers can develop targeted interventions to mitigate the spread of invasive plants. Overall, the study provides valuable insights into the complex interactions between birds and fruit-bearing plants, offering implications for ecological research and practical conservation management strategies. These findings contribute to understanding avian foraging behaviours and the ecological dynamics of fruit selection among different bird species. This impacts the seed dispersal of fleshy-fruited invasive alien plants when there is an overlap in the fruiting season among fruiting plants.

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5.9 Supplementary information

Supplementary Table S5.1. Information on fruit traits and plant information of fleshy-fruited invasive plant species used for the feeding fruit choice trials (Henderson, 2020; Plants of the World Online, 2024).

Plant species	Fruit colour	Fruit diameter (mm)	#Seeds per fruit	Origin	Areas invaded in South Africa
Cotoneaster franchetii	Red	7.2 ± 0.05	2	China	Grassland, forest margins, kloofs, riverbanks, rocky outcrops.
Duranta erecta	Yellow	9.2 ± 0.07	4	Tropical America.	Savanna, forest edges, riverbanks, other moist sites, ravines.
Eriobotrya japonica	Yellow	25.5 ± 0.26	2	China, Japan.	Forest, watercourses, roadsides.
Ligustrum lucidum	Black	6.4 ± 0.08	2	China, Korea.	Forest, woodland, watercourses.
Pyracantha angustifolia	Orange	9.9 ± 0.08	5	SW China.	High altitude grassland, forest and bush clumps, erosion channels, rocky ridges, watercourses.

Schinus terebinthifolia	Red	3.9 ± 0.05	1	S America.	Forest margins, savanna, coastal grassland, watercourses, wetlands.
Solanum mauritianum	Yellow	14.0 ± 0.16	100+	S America.	Forest margins, plantations, savanna, watercourses, urban areas.

CHAPTER 6

Role of local medium to large mammalian species in seed dispersal of fleshy-fruited invasive alien plants in the montane Grassland Biome of South Africa

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Running header: Seed dispersal by selected terrestrial mammals

6.1 Abstract

Fleshy-fruited invasive alien shrubs are an increasing problem in the grasslands of South Africa, where they impact vegetation structure and threaten biodiversity. These species are predominantly bird-dispersed in forest systems, but their spread in grassland ecosystems remains understudied, including their dispersal by mammals. Mammals facilitate seed movement and promote seedling emergence and establishment, all contributing to the increase in invasion. This study aimed to determine the role of various terrestrial mammals in the seed dispersal of fleshy-fruited invasive alien plants present in montane grasslands. The faeces of eland (*Taurotragus oryx*), chacma baboon (*Papio ursinus*), domestic goat (*Capra hircus*), and black-backed jackal (*Lupulella mesomelas*) were collected in the grasslands of the eastern Free State, South Africa. Seeds were removed from the faeces, identified to species level, and planted in a greenhouse. Seeds of the invasive fleshy-fruited species silver-leaf cotoneaster *Cotoneaster pannosus*, yellow firethorn *Pyracantha angustifolia* and eglantine *Rosa rubiginosa* (all Rosaceae) were identified from the faeces together with the seeds of the indigenous star-apple *Diospyros austro-africana*. Seed composition of faeces samples differed significantly between animal species. Seedling emergence experiments showed no differences in seedling emergence between ingested *P. angustifolia* seed and manually de-pulped controls, while there were significant differences in *C. pannosus* seedling emergence compared with manually de-pulped controls. Overall seedling emergence of *R. rubiginosa* seeds from faeces was very low (<2%), similar to controls. *Diospyros austro-africana* had the highest seedling emergence percentage for seeds from jackal and eland faeces. The locally found medium to large terrestrial mammals were shown to be significant dispersers of invasive fleshy fruiting plants in the grasslands of eastern Free State Province, facilitating the spread of these alien plant species.

Keywords: seedling emergence; biological invasions; mammalian scats; seed viability.

6.2 Introduction

Seed dispersal is the transportation of plant seeds, which may result in the establishment of new populations (Corlett, 2017; Rogers et al., 2021a). This process is important as it is one of the major drivers of vegetation composition because it allows the plants to colonise new areas, maintain genetic diversity and has implications on regeneration, succession and conservation (Janzen, 1973; Wang and Smith, 2002; Corlett, 2017; Jordano, 2017; Wandrag et al., 2017; Rogers et al., 2021a; Estrada-Villegas et al., 2022). Transportation of seeds may occur through abiotic processes, which involve wind, gravity and water as vectors, and biotic processes, which include various animal agents such as fish, reptiles, birds and mammals (Schowalter, 2011; Rogers et al., 2021b). In this study, we focus on potential seed dispersal by various terrestrial mammals as information on the seedling emergence of fleshy-fruited plant species after ingestion by such mammals is lacking for Afromontane regions.

Although seed dispersal by mammals occurs in many terrestrial ecosystems, it is most prevalent in tropical forests with a high abundance of fleshy-fruited woody plants that are adapted for animal consumption (Fleming and Kress, 2013; Fuzessy et al., 2016; Corlett, 2017). Conversely, landscapes not dominated by trees, such as shrublands or grasslands, have lower levels of native fleshy fruiting fruit and, therefore, dispersal by animals, but are also less studied (Donoso et al., 2022). However, many grasslands are now becoming encroached by fleshy-fruited woody invasive alien plant species, altering the availability of food resources for mammalian frugivores. This study focussed on grasslands where fleshy-fruited woody plants are naturally not common, but invasive representatives are becoming abundant (see Canavan et al., 2021).

Endozoochory, rather than epizoochory (with seeds trapped in fur/hair), is known to be the dispersal mode by mammals consuming fleshy fruits. However, for ruminants, endozoochorous dispersal includes not only defecation of faeces after movement through the digestive tract, but also "spitting" of seeds while chewing fruit in the cud, as observed for members of the Bovidae and other families (see Delibes et al., 2019), including species such as goats *Capra hircus* and wildebeest *Connochaetes gnou*. For this study, we focused on endozoochory involving passage through the digestive tract, as fleshy-fruited plants are rarely involved in epizoochory.

The efficiency of endozoochory is influenced by several important functional traits in mammals, such as animal body size, feeding regime, digestive physiology (ruminant or not) and gut retention time (Baltzinger et al., 2020; Karimi et al., 2020). Large herbivores are effective seed dispersal agents. This is because their bigger bodies allow them to eat more seeds with less damage during chewing. However, the seeds might spend more time inside these larger animals, potentially harming some seeds if retained past the optimal duration to break dormancy and are at higher risk of mortality because of acidic conditions killing the seed embryo (Jaganathan et al., 2016). The longer a seed stays inside the animal (retention time), the further it can potentially travel before being defecated – which can take anywhere from less than a day to several days for large grazers (Abraham et al., 2021). Primates are important seed dispersal agents because of their food choice, as their diet can sometimes primarily be fruits, depending on season when their most preferred diet is not in abundance (Slater and du Toit, 2002; Bravo, 2021; Chen et al., 2023) Carnivorous mammals (Order Carnivora) also contribute to seed dispersal as they are known to eat fruits opportunistically and can also occupy larger home ranges in different types of habitats, giving them the ability to disperse seeds over longer distances (Draper et al., 2021; Rubalcava-Castillo et al., 2021).

Most studies on seed dispersal by mammals have been more opportunistic, intending to study the mammal’s diet rather than seed dispersal (Goldenberg et al., 2010; Klare et al., 2010; Brassine and Parker, 2012; Steenkamp, 2018), except for forests, as the focus might have been on the mammalian diet and feeding ecology rather than on the seed dispersal process itself (Genovesi et al., 1996). For example, some studies investigating the general diet of a focal mammalian species would note seeds as part of the study mammal's diet. Thus, seed composition in mammalian faeces has been included in literature more often than the effect of ingestion on the seedling emergence of the seeds found in mammalian faeces and possible settlement and spread within high altitude grassland biome. A handful of studies, however, have tested the viability of seeds extracted from medium to large mammalian species faeces (e.g. Williams et al., 2000; Slater and du Toit, 2002; Bobadilla et al., 2020). Various factors, such as seed dormancy, determine seedling emergence upon ingestion by mammals (Young and Kelly, 2018). Among these factors, the effects of ingesting fruits and seeds on seedling emergence have received extensive experimental attention (Samuels and Levey, 2005; Torres et al., 2020).

Animal-mediated seed dispersal represents a crucial subset of plant-animal interactions that can significantly contribute to the spread and establishment of plants (Richardson et al., 2000; Moore and Dittel, 2020). However, there has been limited focus on the role of mammals as seed dispersers of invasive alien plants (Davis et al., 2010; Abbas et al., 2018, 2020; Baltzinger et al., 2020). Mammal endozoochory has the potential to facilitate invasions by alien plant species (Williams et al., 2000; Bourgeois et al., 2005; Barrios-Garcia and Simberloff, 2013; Baltzinger et al., 2020). This mechanism serves as a long-distance dispersal method, accelerating plant invasions (Myers et al., 2004; Trakhtenbrot et al., 2005; Baltzinger et al., 2020). The increased propagule supply resulting from endozoochory can enhance the probability of recruitment at the invasion front and promote the invasion of new sites, especially when dispersal is directed to locations that favour seedling establishment and survival (Briggs et al., 2009; Baltzinger et al., 2019).

Understanding the extent of seed dispersal following endozoochory is imperative for effectively managing invasive alien plants (Constible et al., 2005; Baltzinger et al., 2020). In the montane grasslands of South Africa, several medium to large terrestrial mammalian species were observed feeding on invasive alien fleshy-fruited plants (G Martin, pers. obs.). These fleshy-fruited invasive alien shrubs are an increasing problem in the grasslands of South Africa, where they impact vegetation structure and threaten biodiversity (Chari et al., 2020; Canavan et al., 2021; Bitani and Downs, 2022; Masole et al., 2022). Therefore, our study aimed to investigate the contribution of locally occurring medium to large terrestrial mammalian species to the seed dispersal of fleshy-fruited invasive alien plants in the grasslands of South Africa. We predicted that the invasive alien plants would have better seed dispersal advantages than the indigenous plants in terms of 1) more seed found in the selected mammalian species' faeces and 2) higher seedling emergence percentages.

6.3 Materials and methods

6.3.1 Study area

We collected multiple faecal samples from locally occurring medium to large terrestrial mammalian species from grasslands encroached by fleshy-fruited alien plants near the town of Clarens in the eastern Free State Province, South Africa (Figure 6.1). Clarens is situated in the Maloti Mountain foothills, which fall under the Rooiberg Mountain range and form part of the Drakensberg (Wessels and Wessels, 1991). The area comprises part of the Drakensberg Grassland bioregion under the Grassland Biome (Mucina and Rutherford, 2006). This bioregion is in some of the highest-elevation regions in southern Africa, with relatively large temperature variations (Mucina and Rutherford, 2006). The dominant vegetation in the area is the Eastern Free State Sandy Grassland (Gm 4), which is part of the Mesic Highveld (Mucina and Rutherford, 2006). About 77 invasive alien plants have been recorded in the area, with genera *Acacia* Mill., *Eucalyptus* L'Hér., *Populus* L. and *Salix* L. being the dominant woody invaders (Baard et al., 2017). Recently, woody fleshy-fruited invasive alien plants have increased invaded this area, including yellow firethorn *Pyracantha angustifolia* (Franch.), C.K.Schneid, silver-leaf cotoneaster *Cotoneaster pannosus* Franch., eglantine *Rosa rubiginosa* L., *Rubus* L. spp., (all Rosaceae), and glossy privet *Ligustrum lucidum* W.T.Aiton (Oleaceae).

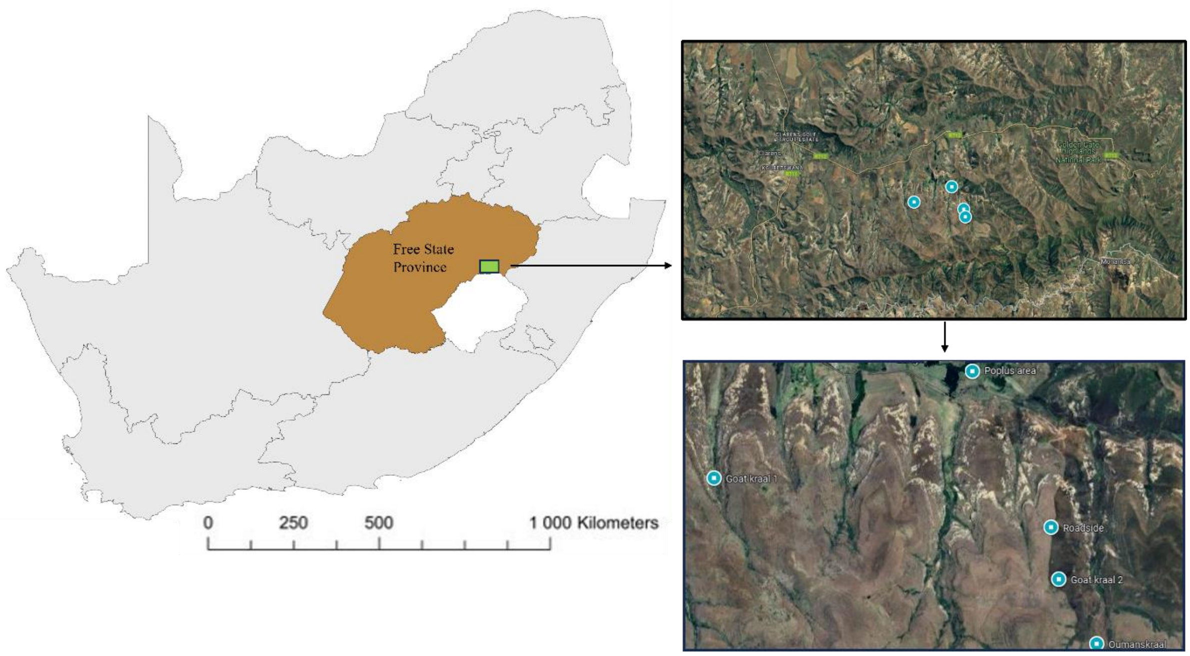

Figure 6.1: Study sites where animal faeces were collected in the Free State Province, South Africa. These are shown by blue dots. Arrows show the direction of magnification of areas. (Note: Inserted 3D map sourced from Google Maps)

Mean annual rainfall in the study area ranges between 1800 and 2000 mm during the rainfall season from September to April (Daemane et al., 2010). Summers can be hot with episodic thunderstorms, while winters are cold and have occasional snow. The Eastern Free State Sandy Grassland is an endangered vegetation type and needs conservation action (Van Wyk and Smith, 2001; Mucina and Rutherford, 2006; Carbutt et al., 2011). Although part of this vegetation type forms part of the Golden Gate Highlands National Park, this vegetation type is poorly protected and needs high conservation priority (Mucina and Rutherford, 2006).

The area is dominated by grasses (family Poaceae), with at least 55 genera, followed by forbs from the Asteraceae family, with more than 51 genera. Grasslands in the area are chiefly on the high central plateau , with undulating terrain and rivers and streams dominated by *Eragrostis* Wolf. grass species, *Tristachya leucothrix* Trin. ex Nees and *Themeda triandra* Forssk. Scrubland and grass-dominated deep valleys separate plateaus and high mountain ridges (Daemane et al., 2010). Target species, fleshy-fruited invasive alien plants, are abundant in the landscape and openly accessible to mammals as propagule sources for dispersal. Native fleshy fruited shrubs, like the poison star-apple *Diospyros austro-africana* (Gand.) De Winter, also occur in the study area (Moffett, 2018).

Over 58 large and 52 small mammalian species have been recorded in the area (see Rautenbach, 1976; SANParks, 2020). The study sites share mammalian species with the nearby Golden Gate Highlands National Park. These include small to medium-sized herbivores such as the mountain reedbuck *Redunca fulvorufula*, grey Rhebuck *Pelea capreolus*, blesbok *Damaliscus pygargus*, springbok *Antidorcas marsupialis*, common eland *Tragelaphus oryx*, black wildebeest *Connochaetes gnou*, the plains zebra *Equus burchelli* and oribi *Ourebia ourebi*. Furthermore, 12 rodent and 12 carnivore species, including the caracal *Caracal caracal*, black-backed jackal *Lupulella mesomelas* and Cape fox *Vulpes chama*, have been documented as present in the Park (SANParks, 2020). These mammalian species are regarded as free-ranging because there are no fences between the park and the surrounding foothills.

6.3.2 Faecal sample collection and storage

We collected faecal samples during or after the fruiting season of focal plant species from September to November 2022. The fruiting season for *P. angustifolia* is from April to November, August to January for *C. pannosus*, and June to July for *R. rubiginosa* (Adams et al., 2023; Invasives South Africa, 2024). We searched for locally occurring medium to large terrestrial mammalian species' faeces/ faeces piles in the field by walking on animal tracks and from livestock kraals on nearby farms (see Supplementary information Table S6.1 for geographical location of study sites). Once a faecal sample was located, we assessed it for any insect activity and seed predation traces. If the faecal sample was clear of insect perforations, we recorded the geographical location using a geographical position system (GPS, Garmin, United States of America (USA)), then placed the faecal sample in a zip-lock plastic bag, weighed it and labelled the bag. All faecal samples (n = 308) collected were relatively dry but varied in texture and moisture content. A field expert confirmed and identified all faecal samples collected for the specific mammalian species.

6.3.3 Faecal sample processing and seed extraction

The faecal samples were placed in large heavy-duty bags and stored in a freezer (-17^{o}C) for up to 30 days to preserve them and avoid decay until they were processed. In winter, the foothills, meadows, valleys and adjacent slopes of the study sites experience mild to cold winters, which preserve the seeds' dormancy, and they germinate during the next spring, assuming that rodents had not eaten them. The seeds were preserved in the freezer; thus, their viability should not have been significantly diminished. The main aim of cold treatment was the preservation of dung samples. However, control fruits also underwent the same stratification before removing seeds. We did this to ensure consistency in stratification. Faecal samples were soaked in water overnight before the seeds were removed from them. Soaked faecal samples were pressed with fingers under running tap water to separate seeds on a mesh sieve (0.085 mm). Seeds remained on the sieve, along with other large objects from the faeces that could not pass through the mesh. We collected the seeds left on the sieve mesh and discarded the remaining faecal sample. Seeds removed from faecal samples were placed on a paper towel until dry, then placed in small open plastic bags to be stored at room temperature in a well-ventilated room until planted. Fruits of fleshy-fruited woody plants in the study area were collected, and we manually removed seeds by hand (depulped). The seeds removed from fruits were used to identify seeds extracted from the mammalian faecal samples collected.

6.3.4 Potential seedling emergence

We planted seeds from three different treatments individually in seedling trays (265 × 180 × 75 mm; 3 577.5 cm^3) filled with potting soil. Each seed or whole fruit was planted ~ 0.7 cm deep beneath the soil surface in the soil tray (Molefe et al., 2020). These trays were then placed in a greenhouse at the University of KwaZulu-Natal, Pietermaritzburg. The light regimen of the greenhouse depended on Pietermaritzburg sunrise and sunset times in spring and summer. In spring, sunrise ranged between 04:50 and 06:13 SAST, and sunset between 17:43 and 18:43 SAST. Sunrise times ranged between 04:50 and 05:00 SAST, and sunset times between 18:44 and 19:00 SAST in summer.

Treatments included (1) seeds from mammals (baboon, eland, goat or jackal), (2) seeds planted in whole fruits, and (3) seeds from the depulped whole fruits. Seeds found in faecal samples belonged to the alien species *P. angustifolia*, *C. pannosus, R. rubiginosa*, and the indigenous *D. austro-africana*. These seeds were planted in trays placed in the seedling trays and kept in a greenhouse at 26 ˚C maximum temperature (Jordaan et al., 2011). For comparison, whole fruits were collected from the mature shrubs of two alien fleshy-fruited woody plant species in the study sites during the fruiting season. A total of 1000 fruits each for both *C. pannosus* and *P. angustifolia* were collected from at least ten individuals of the same species. Whole fruit and depulped seed treatments were used for *P. angustifolia* and *C. pannosus* planting trials, whereas only seeds collected from faecal samples were planted for *R. rubiginosa* and *D. austro-africana*.

Seeds in seedling trays were assessed daily and watered when topsoil was dry, and any seedling emergence was recorded every 2 or 3 days for 150 days in spring and summer between September 2022 and February 2023. A total of 136 seedling trays were planted. The number of seeds per tray differed for each tray as the number of seeds planted depended on the number of seeds recovered from the faeces (see Supplementary information Table S6.2 and Table S6.3 for faecal sample information summary and tray information, respectively).

6.3.5 Data analyses

We compared the mean number of seeds per plant species (seed composition) found in faecal samples between the mammalian species using a Kruskal Wallis test followed by Dunn's multiple comparisons *post hoc* tests. We calculated seed composition as the mean number of seeds per faecal sample for each animal species. We determined seedling emergence success as the total cumulative percentage of germinated seeds. The seedling emergence rate was calculated as the time in days taken for each seed to germinate since it was planted in the greenhouse, and seedling emergence was presented using survival analysis curves. All data were analysed using GraphPad Prism 8 software (GraphPad Software, San Diego, CA, USA).

6.4 Results

6.4.1 Seed composition

During the field survey, we collected 308 dry faecal samples from locally occurring medium to large terrestrial mammalian species, totalling 18 kg from eland, chacma baboon, domestic goat, and jackal. Most of these faecal samples had seeds of *P. angustifolia*, *C. pannosus*, *R. rubiginosa* and *D. austro-africana*. A total of 23,103 seeds of fleshy-fruited woody plant species were recovered from the faecal samples. The majority of faecal samples collected (86-100%) contained fleshy-fruited plant seeds (Figure 6.2). Baboon (30% of all faecal samples) and eland (21%) faecal samples containing seeds were the most common, while jackal was the least common (4%). Goat faeces (45%) were also the most common because they were collected from kraals (fenced enclosures).

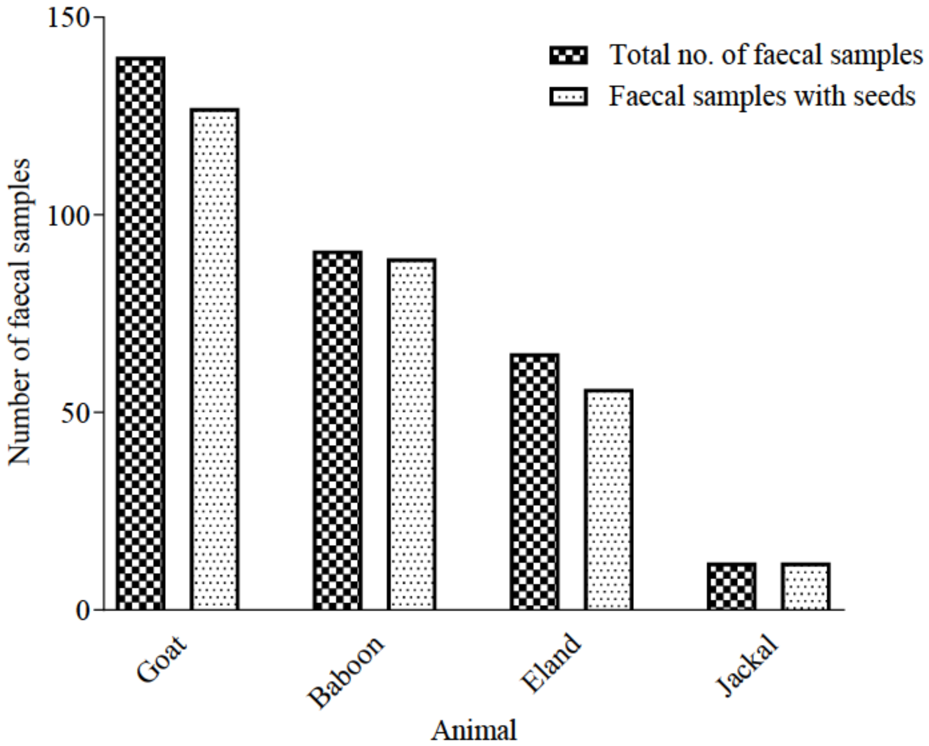

Figure 6.2: Total number of faecal samples collected and the total number of these that contained the seeds of fleshy-fruited woody plant species.

The number of seeds of *C. pannosus* was significantly higher (H-value = 32.26, $P < 0.05$, df = 3) in eland faeces and less common in baboon and goat faeces while none were found in jackal faeces (Figure 6.3). There were significant differences in *R. rubiginosa* seed numbers recovered from locally occurring medium to large terrestrial mammalian species' faeces (H-value = 32.37, $P < 0.05$, df = 3). From the baboon faeces, eglantine seed dominated , while they were less common in eland faeces, and none were found in goat and jackal faeces. Significant differences in *P. angustifolia* seed numbers were found in locally occurring medium to large terrestrial mammalian species' faeces (H-value = 42.37, $P < 0.05$, df = 3). *Pyracantha angustifolia* was mostly abundant in baboon faeces, less common in eland and goat faeces, and was not found in jackal faeces. Significant differences in *D. austro-africana* seed numbers found in locally occurring medium to large terrestrial mammalian species' faeces were also observed (H-value = 129.4, $P < 0.05$, df = 3). High numbers of *D. austro-africana* seeds were found in eland and jackal faeces and were less common in baboon faeces, while none were found in goat faeces.

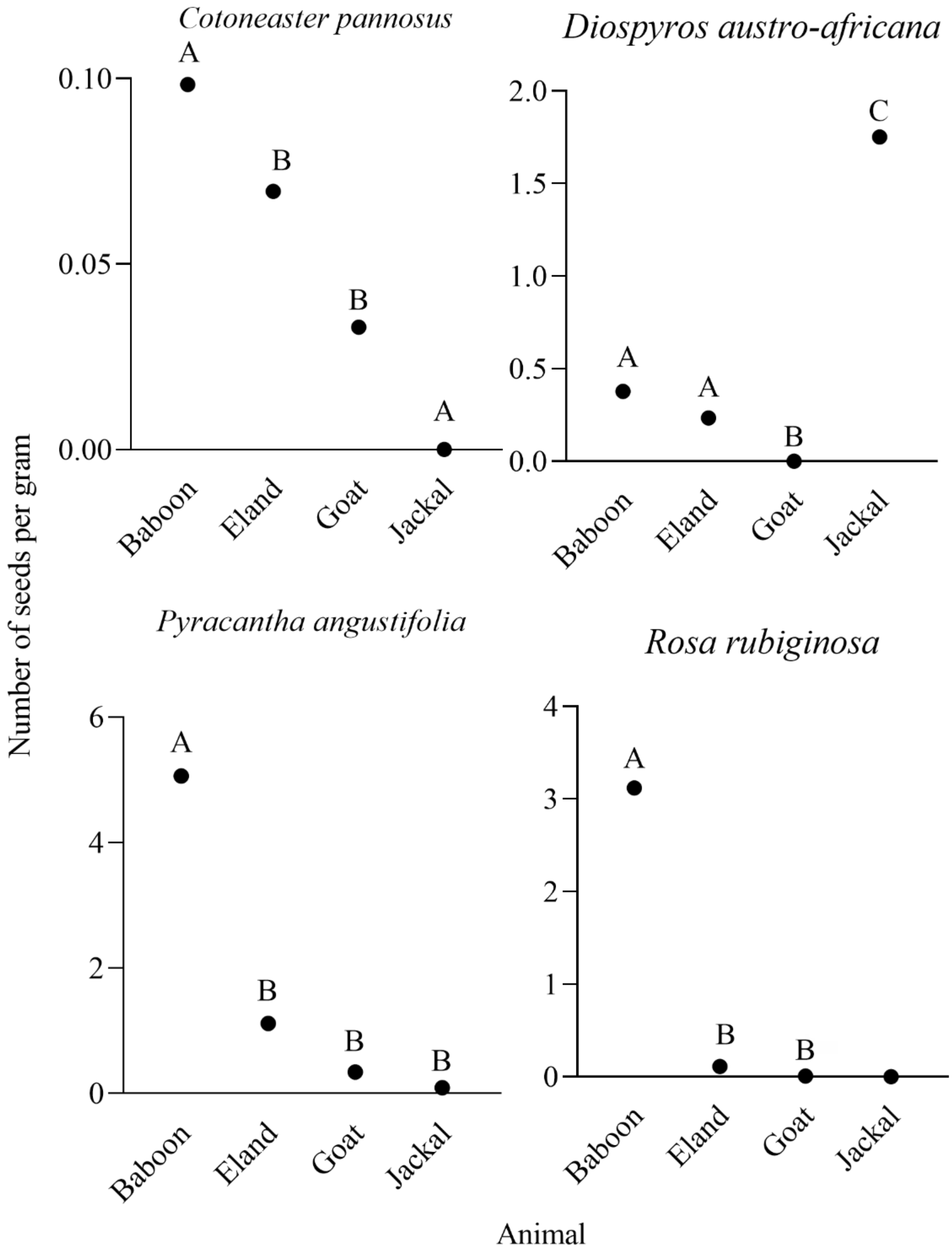

Figure 6.3: Mean number of seeds per gram per faecal sample of different mammalian species for silver-leaf cotoneaster *Cotoneaster pannosus*, eglantine *Rosa rubiginosa*, firethorn *Pyracantha angustifolia* and poison star-apple *Diospyros austro-africana*. (Note: Different letters above bars indicate a statistically significant difference ($P < 0.05$)).

6.4.2 Seedling emergence

On average, seeds planted in the greenhouse took a maximum of 60 days to germinate (Figure 6.4). For the invasive alien *C. pannosus*, seeds from whole fruits (1%) and seeds that were manually depulped by hand had lower rates of seedling emergence success (2%). Seeds from eland faeces had the highest seedling emergence success (34%) followed by baboon (13%) and goat (7%). Similar to *C. pannosus*, the highest seedling emergence success rate in *P. angustifolia* was reached from seeds collected from eland faeces (51%), followed by seeds from goat faeces (42%), then those from manually depulped fruit (40%), and then seeds from baboon faeces (27%). The lowest seedling emergence success rate was observed in seeds planted from whole fruits (14%) in *P. angustifolia*. *Rosa rubiginosa* had the lowest seedling emergence success of all the plant species (less than 1%) for seeds found in baboon (0.4%) and eland (1%) faeces. The most successful seedling emergence percentages recorded were for *D. austro-africana* seeds from eland (58%) and jackal (63%) faeces, followed by seeds from baboon faeces (42%). Although seeds were followed up to 150 days, survival curves reached stability by the 80th day as all seedling emergence ceased.

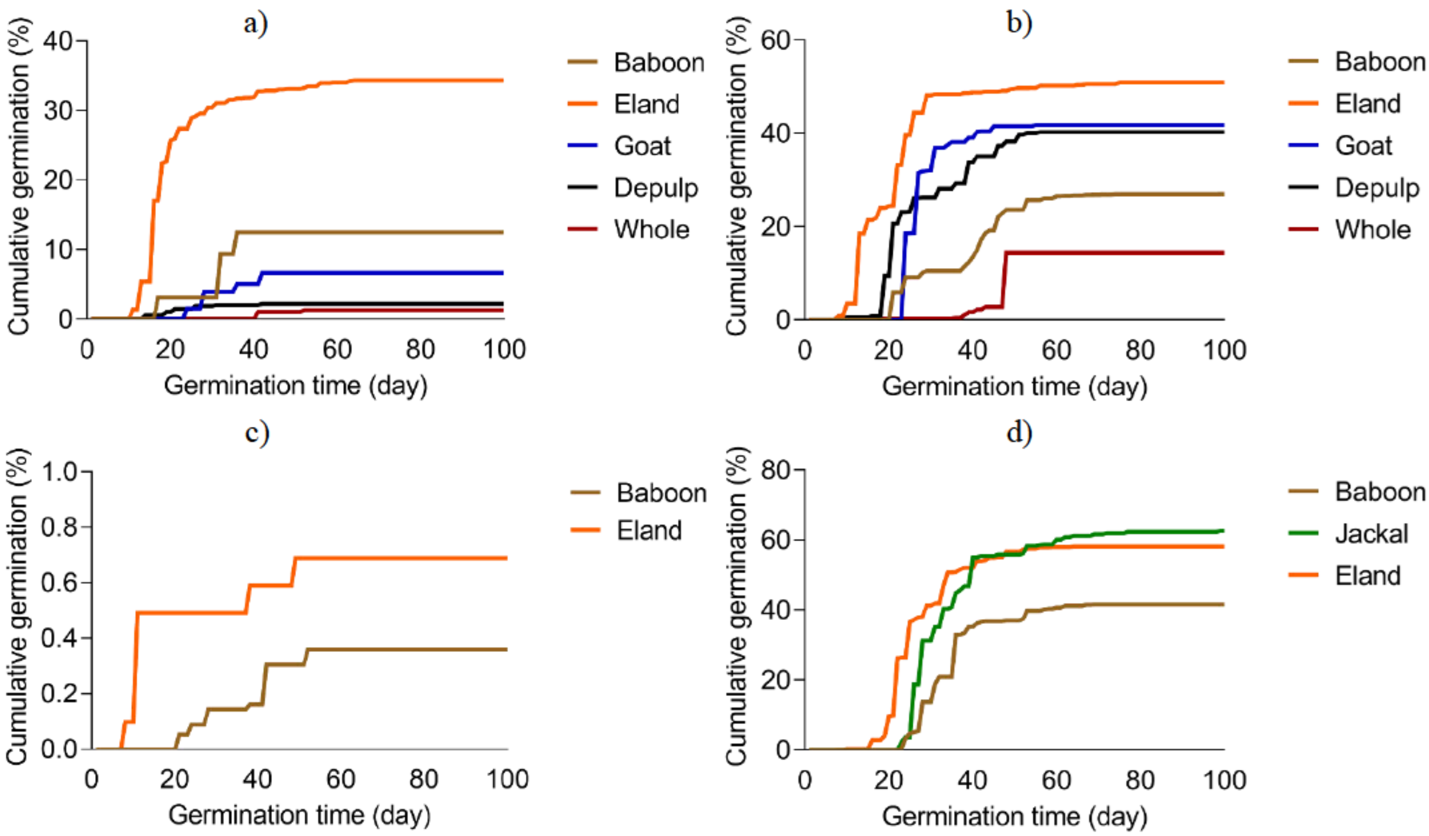

Figure 6.4: Cumulative seedling emergence percentages against the number of days after planting for seeds from whole fruits, depulped and defecated seeds from the respective mammalian species where a. silver-leaf cotoneaster *Cotoneaster pannosus*, b. firethorn *Pyracantha angustifolia*, c. eglantine *Rosa rubiginosa* and d. star-apple *Diospyros austro-africana*. Although seeds were followed up to 150 days, seedling emergence curve reached stability within 80 days.

6.5 Discussion

Our study showed the role of mammalian carnivores, particularly black-backed jackals, in seed dispersal with a focus on the presence of *D. austro-africana* seeds in their faeces (Kok and Nel, 2002; Walton and Joly, 2003). Although regarded carnivores, black-backed jackals exhibit a varied diet, including fruits, invertebrates, scavenged meat, and killed prey (Rowe-Rowe, 1982; Brassine and Parker, 2012; Drouilly et al., 2017; Steenkamp, 2018; Wilkins, 2021). Their adaptability to seasonal fluctuations influences fruit occurrence in faeces (Klare et al., 2010; Temu et al., 2022), making them effective seed dispersers impacting plant species distribution (Herrera et al., 1989; Shikesho et al., 2024). Of particular interest is the observation indicated by this study that black-backed jackals appear to feed only on indigenous fleshy fruits. Our study observed the germination of native *D. austro-africana* seeds post-ingestion, highlighting their ecological role (Favaretto, 2020). Carnivores such as the side-striped jackals *Canis adustus* in Ethiopia and various jackal species in Zimbabwe, shows the interconnected relationship between mesopredators and plant species, necessitating comprehensive studies on seed dispersal dynamics (Atkinson et al., 2002; Takele and Raju, 2011; Kamler et al., 2020).

Similar to carnivores, some herbivores may accidentally ingest fruit. The common eland, known for its browsing behaviour, has been observed feeding on star-apple shoots and has been considered an effective intermediate feeder that can also sustain on grass diets (Watson, 1999; Goheen et al., 2010; Hejcmanová et al., 2020). Our study found evidence of eland dispersing seeds of fleshy-fruited plants, including *C. pannosus* and *D. austro-africana*. Although a previous study indicated low germination rates for a *Cotoneaster* spp. seeds from eland faeces, our study demonstrated a higher seedling emergence rate (~34%) for *C. pannosus* seeds extracted from eland faeces, suggesting eland as effective seed dispersers (Slater and du Toit, 2002). Eland in the study region have extensive ranges, often covering the lowland lying areas to the high altitudes, thus potentially moving seeds into a much higher altitude area, which is of much conservation concern. Domestic goats are recognised as significant seed dispersers because of their versatile foraging behaviours and ability to cover long distances (Mitchell et al., 1987; Mancilla-Leytón et al., 2011; Muñoz-Gallego et al., 2019, 2023). While goat farming is not prevalent in the study region, their role in spreading invasive plant seeds should be acknowledged. While *D. austro-africana* seeds were not found in goat faeces, related studies have noted browsing behaviour on similar species bluebush *Diospyros lycioides* Desf. (Maroyi, 2017).

In various habitats, chacma baboons consume a variety of fruits, including Fynbos star-apple *Diospyros glabra* (L.) De Winter, dune guarri *Euclea racemose* L., Hottentot's cherry *Maurocenia frangula* Mill., tortoise berry *Muraltia spinosa* (L.) F.Forest & J.C.Manning, black ironwood *Olea capensis* L., dune currant *Allophylus natalensis* (Sond.) De Winter, Peruvian pepper tree *Schinus mole* L., nana-berry *Searsia dentata* (Thunb.) F.A. Barkley, small-leaved guarri *Euclea undulata* Thunb., *D. austro-africana*, Karoo crossberry *Grewia robusta* Burch., bee-sting bush *Azima tetracantha* Lam., *Lycium* spp., sycamore fig *Ficus sycomorus* L., and Namaqua rock fig *Ficus cordata* Thunb (Davidge, 1978; Hamilton et al., 1978; Lieberman et al., 1979; Slater and du Toit, 2002; Tew et al., 2018). Viability testing was not conducted for seeds recovered in some studies (Tew et al., 2018). In India and Nepal, the Kashmir grey langur *Semnopithecus ajax* also contributes to seed dispersal by consuming leaves and ripe fruits of specific plant species (Sayers and Norconk, 2008; Singh and Thakur, 2017). This and other studies show how important omnivores are as seed dispersal agents. Of note from the present study was where the seeds of the invasive fleshy fruited species consumed by baboons were often deposited on high rock faces in difficult-to-reach terrain. This also results in populations of fleshy fruiting species building up on cliff edges and rocky outcrops where management is particularly difficult (Adams et al., 2023). Mammals, including various species such as Pallas's squirrel (*Callosciurus erythraeus*), European fox (*Vulpes vulpes*), coyote (*Canis latrans*), black rats (*Rattus rattus*), brushtail possums (*Trichosurus vulpecular*), domestic animals including horses (*Equus ferus*), goats, cattle (*Bos taurus*), baboons, and eland, have been identified as important vectors for the dispersal of *P. angustifolia* (Williams et al., 2000; Bobadilla et al., 2016; Chari et al., 2020; Adams, 2020). Our study confirmed the potential of goats, baboons, and eland as seed dispersers for *P. angustifolia*. In addition to *P. angustifolia*, other fleshy-fruited plants like *Cotoneaster granatensis* Boiss. and *R. rubiginosa* are dispersed by various animals, including birds and horses (Herrera et al., 1989; Hatton, 1989; Zimmermann et al., 2011, 2012). Intact seeds of glaucous cotoneaster *Cotoneaster glaucophyllus* Franch. and *R. rubiginosa* have been found in the faeces of brushtail possums and hedgehogs *Erinaceus europaeus*, respectively, while European rabbits *Lepus cuniculus* and horses have also been recorded dispersing viable seeds (Hutton, 1989; Williams et al., 2000; Jones and Norbury, 2011; Wotton and McAlpine, 2015; Bobadilla et al., 2020).

Both birds and mammals are drivers of woody plant invasions in the eastern Free State grassland biome, facilitating invasion through seed dispersal. Birds have previously been confirmed to be potential seed dispersal agents of these fleshy-fruited invasive alien plants (Adams et al., 2022). The present study confirmed locally occurring medium to large terrestrial mammalian species as potential seed dispersal agents. These findings contribute to understanding the species' invasion dynamics and allow well-informed decisions regarding the control of such species. This facilitation makes it difficult to manage the invasion by these fleshy-fruited woody invaders as these mammals have access to neighbouring areas, including protected areas such as the Golden Gate Highlands National Park. Compared with birds, these mammalian species deposit large quantities of seeds within a single defecation event and travel long distances (Dudenhoeffer and Hodge, 2018).

6.6 Conclusions

Our study confirmed the contribution of terrestrial mammals to the establishment (dispersal) of fleshy-fruited invasive alien plants via faecal deposits in the grasslands of the eastern Free

State. Mammals are potential seed dispersal agents of the plant species studied, and invasion by alien fleshy-fruited plants is expected to increase in distribution. The results showed that the seeds of invasive species, found in faecal samples and therefore able to facilitate dispersion, were able to survive and successfully emerge in greenhouse trays, suggesting a role of mammals in the establishment of fleshy-fruited invasive alien plants.

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6.9 Supplementary information

Supplementary information Table S6.1 Actual geographical coordinates of the study sites where the faecal samples were collected

Study site name	No. of faecal samples collected	GPS coordinates	
Goat Kraal 1	28	S28˚32.762'	E 28˚30.477'
Goat Kraal 2	112	S28˚33.28'	E 28˚32.49'
Roadside	31	S 28˚32.217'	E 28˚31.987'
Poplus area	7	S 28˚33.013'	E 28˚32.445'
Oumanskraal	115	S28˚33.609'	E 28˚32.710'
Total	**293**		

Supplementary information Table S6.2 Summary of faecal samples and fleshy-fruited plant seeds found in the study sites in the present study.

Species	Total faecal samples	Samples with seed	Total dry faeces mass (g)	Average number of seeds per faecal sample				Mass (g) per faecal sample Mean ± SE
				Pyracantha angustifolia	***Cotoneaster pannosus***	***Rosa rubiginosa***	***Diospyros austro-africana***	
Goat	140	127 (91%)	5964.3	14	1	0	0	42.6 ± 1.23
Baboon	91	89 (98%)	1907.4	115	1	37	11	21.0 ± 1.13
Eland	65	56 (86%)	9805.8	26	15	3	23	150.9 ± 10.09
Jackal	12	12 (100%)	310.7	0	0	0	31	25. 9 ± 5.85
Total	308	284	17988.1	155	17	40	65	

Supplementary information Table S6.3. Tray information on seeds that were planted in the greenhouse after being collected from the animal faeces in the eastern Free State grasslands.

Plant	Yellow firethorn *Pyracantha angustifolia*					Silver-leaf cotoneaster *Cotoneaster pannosus*					Eglantine *Rosa rubiginosa*			Star-apple *Diospyros austro-afric*		
	Baboon	Depulp	Eland	Goat	Whole fruits	Baboon	Depulp	Eland	Goat	Whole fruits	Baboon	Eland	Goat	Baboon	Eland	Jac
	210	100	146	73	125	32	200	145	24	100	200	46	46	55	44	
	269	100	88	215	125		200	102	124	100	263	74		107	40	
	226	100	161	437	125		200	111	108	100	200	94		42	94	
	243	100	213	402	125		78	143			249	101		81	101	
	432	100	200	451				200			200	107		57	107	
	265	200	121	181				200			291	96		111	96	
	243	200	200	237				189			229	110		90	110	
	136		200								262	113		146	113	
	320		200								157	123		137	123	
	211		200								261	152		90	152	
	375		135								257				108	
	263										200				191	
	369										242				140	
	356										287					
	415										202					
	215															
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CHAPTER 7

General discussion, conclusions and recommendations

7.1 Background

The persistence of native species and ecological systems is threatened by various anthropogenic factors, including climate change, habitat loss, and the introduction of alien species (Carwardine et al., 2018; Prakash and Verma, 2022). Biological invasions have garnered increased attention globally because of their adverse effects on native species' abundance, diversity, genetic makeup, and ecosystem function, leading to immediate and long-term consequences (Nuñez et al., 2021; Pyšek et al., 2020; van Wilgen et al., 2022; Bhatta et al., 2023). These impacts, affecting nutrient cycles, habitat structure, and trophic networks, are expected to worsen in the future (Duffy et al., 2017; Hughes et al., 2020; Bhatta et al., 2023; Hao and Ma, 2023). In South Africa, renowned for its biodiversity hotspots, invasive species pose significant threats to ecosystems, water resources, and rural farming areas (van Wilgen et al., 2020; Slingsby et al., 2023). National programs aim to mitigate these impacts, requiring species-specific studies to enhance control efforts (van Wilgen and Wannenburgh, 2016; Wilson et al., 2018; Richardson et al., 2022). Numerous invasive terrestrial plants and invertebrates have been recorded in the country (van Wilgen et al., 2020). Woody alien invasive plants are prevalent in various regions because of horticultural activities, and they significantly impact grasslands and alter ecosystems' thermal landscapes and food resources (Richardson and Rejmánek, 2011; van Wilgen et al., 2022).

Species like *Cotoneaster pannosus* Franch. (Rosaceae), *Pyracantha angustifolia* (Franch.) C. K. Schneid (Rosaceae), and *Rosa rubiginosa* L. (Rosaceae) are prominent fleshy-fruited invasive species in South Africa and also invade other parts of the world (Henderson, 1991; Chari et al., 2020; Adams et al., 2022, 2023; Masole et al., 2022). These species are subject to restrictions under the Alien and Invasive Species Regulations, requiring eradication or control efforts by National Environmental Management: Biodiversity Act 963 (NEMBA, Act 10 of 2004) Alien and Invasive Species Regulations (Department of Environmental Affairs, 2014). Research on the ecology and spread of these species is crucial for effective management and conservation. Studies conducted in grasslands aim to understand the drivers of invasion, socio-economic and environmental impacts, animal seed dispersal, and population dynamics (Adams, 2020; Bitani et al., 2020; Bitani and Downs, 2022). Grasslands, despite their importance as biodiversity reservoirs and providers of ecosystem services, are increasingly degraded, emphasising the need for preservation (O'Mara, 2012; Gibbs and Salmon, 2015; Carbutt and Kirkman, 2022).

The study aimed to address knowledge gaps regarding the effects of fleshy-fruited invasive plants in montane grassland ecosystems, focusing on community perceptions, potential animal seed dispersal, and population change over time. Objectives included reviewing existing research, determining potential management conflicts and human impact through questionnaires, evaluating invasion effects on vegetation and landscape through repeat photography and surveys, assessing animal involvement in seed dispersal via mammal faecal sample analyses and field observations, and evaluating birds' role in seed dispersal through fruit choice trials with captive frugivorous birds. By determining the main drivers of invasion and assessing associated impacts and risks, the study contributes to informed decision-making and conservation practices for safeguarding montane grassland biodiversity and ecosystem integrity (Henderson, 2007; Bellis et al., 2020).

7.2 Research findings

This section provides the key findings of the study and how they fit into the unified framework of biological invasions (Blackburn et al., 2011). The proposed framework recognises that the invasion process can be divided into a series of stages, and that in each stage, there are barriers that need to be overcome for a species or population to pass on to the next stage. Study species, fleshy-fruited invasive alien plants, have been introduced in the grasslands for horticulture and have established in the grasslands. Chapter 4 shows that these plants have been established as they are increasing in numbers. Chapter 3, 5 and 6 showed that the spread of these plants is exacerbated by humans, birds and mammals respectively. According to the framework, the fleshy-fruited invasive alien plants in the grasslands are at the ‘Boom and Bust’ stage. This is a stage where the self-sustaining population is in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction (Chapter 4). These species are now fully invasive, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence. At this stage, eradication and containment are difficult, and prevention is impossible.

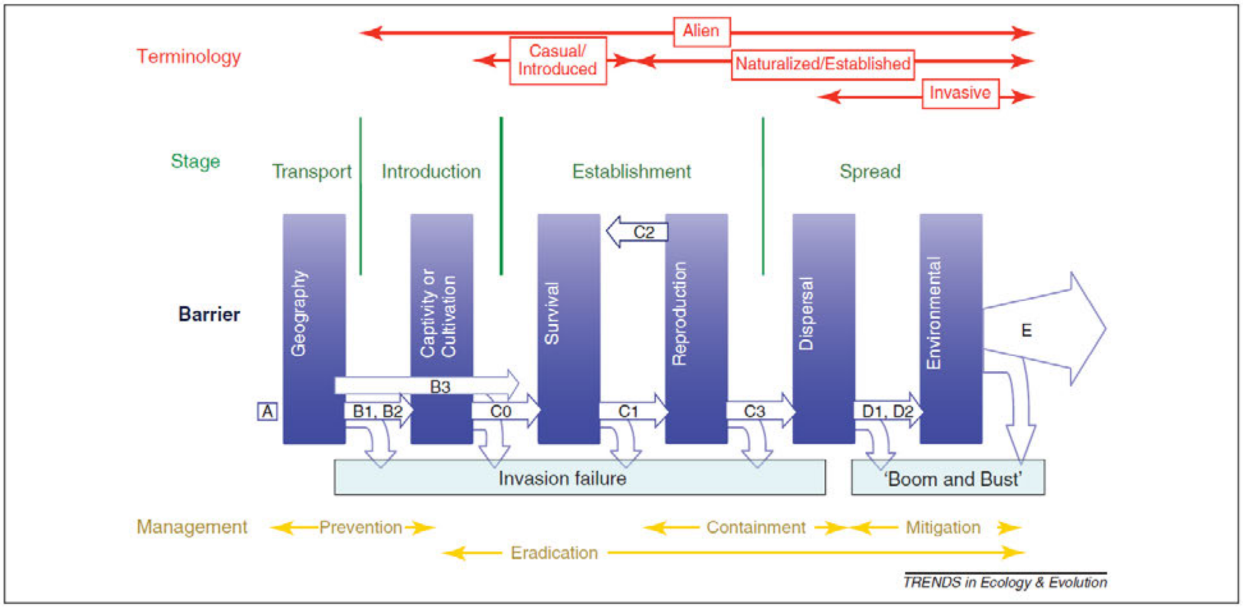

Figure 7.1: The proposed unified conceptual framework for biological invasions (Reproduced from Blackburn et al. (2011)).

In **Chapter 2**, 32 peer-reviewed publications from 1994 to 2023 were reviewed, and these showed an increasing trend in publication records starting from 2016 and peaking in 2022. Seed dispersal emerged as the most studied concept, with studies conducted in various countries, including Argentina, Belgium, Canada, China, Czech Republic, France, Hungary, India, Kenya, Sicily, South Africa, the United States of America, and Zimbabwe. Most studies were conducted in South Africa, followed by Argentina. *Lantana camara* L. (Verbenaceae), *Ligustrum lucidum* W.T.Aiton (Oleaceae), *Melia azedarach* L. (Meliaceae), *Morus alba* L. (Moraceae), and *P. angustifolia* were the most frequently studied invasive fleshy-fruited plant species, with Rosaceae and Solanaceae being the most frequently studied plant families. Bird-mediated seed dispersal was the most studied plant-animal interaction, followed by predation and seed dispersal by mammals. The increase in research publications aligns with trends observed in other fields, attributed to factors such as technological advancements, growing interest, funding availability, evolving methodologies, international collaborations, and improved research infrastructure (Zheng et al., 2015; Ahmad et al., 2021). This information was detailed in a study by Wilkinson et al. (2023) on global research concerning Hyaenidae, Cordier et al. (2022) focusing on camera trap research in Africa, and Mariani et al. (2023) exploring artificial intelligence in innovation research. This synthesis emphasises the need for ongoing research on fleshy-fruited invasive alien plants in grasslands and other treeless ecosystems to address their increasing threats, with broader implications for conservation, ecosystem management, and global biodiversity preservation. Further research is necessary on seed dispersal by agents other than birds, pollination, environmental and socioeconomic impacts, management and control strategies, rehabilitation efforts, and their cultural significance in diverse communities.

In **Chapter 3**, interviews across various demographic categories were conducted. The study revealed that socio-demographic variables such as age, gender, occupation, and town were not the best predictors of perception regarding the invasion of *Pyracantha angustifolia*, with land type and ethnicity emerging as the most influential factors. This finding can be attributed to the dominance of African respondents, who are primarily associated with residential land types, and the ownership of commercial farming areas by white farmers in South Africa (Rural Development and Land Reform, 2017).

Pyracantha angustifolia offers various nutritional, medicinal, and horticultural benefits, including the production of fruits rich in essential nutrients such as amino acids, vitamins, and dietary fibre (Keser, 2014; Doello et al., 2022). However, despite these benefits, the species is associated with conflicts of interest because of its invasive nature (Keser, 2014; Doello et al., 2022). The study also detailed the harvesting practices of the community, with fruits being the most harvested plant part, mainly for consumption. Respondents mentioned various animals feeding on the plant's fruits, with birds, goats, and baboons being the most frequent. The species exhibits characteristics that contribute to its potential spread, including multiple introduction pathways and effective seed dispersal agents such as birds and mammals (Adams et al., 2022). Although the selling and planting of *P. angustifolia* are prohibited by law, some communities continue to engage in these activities, increasing the risk of further spread (Department of Environmental Affairs, 2014).

The invasion of *P. angustifolia* was reported by the communities to have significant environmental impacts, particularly in changing vegetation structure and threatening grasslands, leading to biodiversity loss and reduced eco-tourism revenue (Henderson, 2020). Additionally, the species has moderate socio-economic impacts, affecting activities such as grazing livestock and recreational pursuits (Bacher et al., 2017). Communities have employed chemical and mechanical methods to control *P. angustifolia*, with glyphosate, hexazinone, and imazapyr being among the chemicals commonly used (DiTomaso et al., 2013). However, the efficacy of these control methods varies, with fire being reported as the least effective (Chari et al., 2020). Despite efforts to control the species, respondents expressed dissatisfaction with the progress and called for improved control measures, including funding and the introduction of clearing programs. The study estimated plant populations, with over 30 individual plants being the most common observation, and the majority of respondents reported an increase in population numbers while peach trees *Prunus persica* (L.) Batsch were noted to be spreading near Fouriesburg town. The study highlights the need for improved management strategies, including government assistance, funding, and further research into alternative control methods like biocontrol.

In **Chapter 4**, change in fleshy-fruited invasive alien plants' population size over time was assessed along roadsides in the grasslands. Elevation was found to be a crucial predictor, with different species occurring at different elevation gradients. Livestock farms, roadsides, and crop farms significantly impacted plant recruitment, indicating favourable conditions for population size in agricultural landscapes. Perching structures such as roadside barriers and power lines were important predictors, facilitating plant spread by providing perches for dispersal agents like birds. However, certain land use types like settlements and abandoned farmhouses showed limited influence on plant recruitment. The study stresses the complex interplay between land use patterns, elevation, and perching structures in shaping the recruitment dynamics of fleshy-fruited invasive plants. Understanding these factors is essential for effective conservation and management strategies to control biological invasions in anthropogenic landscapes.

Species composition across elevation gradients were assesed, revealing variations in species distribution consistent with previous findings. Fleshy-fruited invasive alien plant species recorded were *Cotoneaster pannosus* Franch., *Lantana camara* L., *Ligustrum lucidium* W.T.Aiton, *Melia azedarach* L., *Opuntia ficus-indica* (L.) Mill., *Prunus persica* L., *Pyracantha angustifolia* (Franch.) C.K.Schneid., *Pyracantha crenulata* (D.Don) M.Roem., *Rosa rubiginosa* L., *Schinus molle* L., and *Solanum mauritianum* Scop. and native fleshy-fruited plant *Searsia* F.A.Barkley spp.

Furthermore, population changes of fleshy-fruited invasive plants in montane grasslands over time using Google Street View archives were investigated. The analyses revealed an increase in plant populations over 12 years for most species, indicating potential shifts in abundance and distribution. However, *O. ficus-indica* populations showed a decrease, suggesting successful management efforts, possibly because of biocontrol measures. Despite challenges associated with using Google Street View, such as limited coverage and temporal constraints, the method offered a cost-effective approach to assess population changes over time. The study emphasised the importance of combining Google Street View data with other methods like field surveys and remote sensing for comprehensive vegetation dynamics assessment (Deus et al., 2016; Barone et al., 2021). New approaches are required to predict potential invasive species, probable invasion success, and consequent invader impacts under future terrestrial conditions that have where historical comparisons are lacking. The approach in this chapter is one of approaches with predictive power that can assist in predicting potential invasive plants.

This chapter highlights the effectiveness of Google Street View archives in studying vegetation dynamics and ecosystem responses to environmental change. The method provides valuable insights into long-term vegetation trends and informs conservation and management strategies for controlling biological invasions. By combining Google Street View data with other methodologies, researchers can better understand plant population dynamics and assess the effectiveness of management interventions over time.

In **Chapter 5**, differences in fruit selection among various frugivorous bird species were investigated, particularly focusing on selected invasive plant species. It was found that plant species played a crucial role, with specific plants having varying effects on fruit selection by different bird species. For instance, *Duranta erecta*, *E. japonica*, *P. angustifolia*, and *S. mauritianum* were negative significant predictors for some bird species, while *S. terebinthifolia* and *C. franchetii* were positive significant predictors as found in other studies (Gosper et al., 2005). Additionally, fruit size and colour were also noted to influence fruit selection patterns. Fruit size was consistently found to be a negative predictor across all bird species, impacting fruit accessibility based on bill dimensions and availability of food sources (Kitamura et al., 2002; Sebastián-González, 2017). However, fruit colour exhibited varied effects, with darker fruits generally preferred because of their lipid content, but preferences varied based on bird species and previous experiences, as found in other studies (Teichmann et al., 2020).

Findings from other research have shown fruit selection to be driven by factors other than colour and fruit size. For example, frugivorous birds in the South African Mediterranean climate region prefer invasive alien plants' abundant, sugar-rich fruits over native species (Mokotjomela et al., 2013). Their fruit removal rates are influenced by nutrient composition, with migratory birds favouring lipid-rich fruits (Rumeu et al., 2019). However, fruits containing deterrent secondary metabolites are less appealing. The timing of fruiting, or fruiting phenology, also affects fruit consumption, as invasive species often fruit asynchronously with natives, providing attractive resources during scarcity (Vergara-Tabares et al., 2018). Longer fruiting durations and smaller seed sizes predict avian frugivore consumption, while fruit colour does not significantly impact choice (Sperry et al., 2021).

Birds generally adjust their nutritional preferences based on seasonal needs, with hunger or food scarcity reducing selectivity (Schaefer and Schaefer, 2006; Morán-López et al., 2020). Models incorporating frugivore internal states and fruit nutrient content can help understand the temporal dynamics of foraging choices, considering secondary metabolite accumulation in animals (Morán-López et al., 2018). Overall, the study underscored the importance of considering plant species, fruiting phenology and secondary metabolites in understanding fruit selection patterns by frugivorous birds. These findings contribute to predicting the dispersal patterns of fleshy-fruited invasive alien plants and offer implications for ecological research and conservation management strategies.

In **Chapter 6**, field surveys were conducted and dry faecal samples from medium to large terrestrial mammalian species were collected in montane grasslands. Seeds of *P. angustifolia*, *C.*

pannosus, *R. rubiginosa*, and *D. austro-africana* were found in faecal samples of eland (*Taurotragus oryx*), chacma baboon (*Papio ursinus*), domestic goat (*Capra hircus*), and black-backed jackal (*Lupulella mesomelas*). The majority of samples contained fleshy-fruited plant seeds, with baboon and eland samples having the most. The number of seeds of *C. pannosus*, *R. rubiginosa*, *P. angustifolia*, and *D. austro-africana* differed significantly among faeces from different mammalian species. Seed germination rates varied, with eland faeces showing the highest rates for most species. Chacma baboons, eland, domestic goats, and jackals were identified as significant seed dispersers for various plant species, including invasive alien plants. Seed composition varied significantly among different mammalian species, with viable seeds present in all faecal samples. Germination success differed significantly among seeds from the different mammalian species.

This chapter highlighted the role of mammalian carnivores, particularly black-backed jackals, in seed dispersal, focusing on the presence of *D. austro-africana* seeds in their faeces. Despite being carnivores, black-backed jackals exhibit a varied diet that includes fruits, making the dispersers effective (Drouilly et al., 2017; Steenkamp, 2018; Wilkins, 2021). Additionally, herbivores like eland and domestic goats were observed dispersing seeds of fleshy-fruited plants, with eland demonstrating high germination rates for *C. pannosus* seeds (Hejcmanová et al., 2020; Slater and du Toit, 2002). Chacma baboons, known for their diverse diet, were also identified as significant seed dispersers (Davidge, 1978; Walton et al., 2021). Various mammals, including goats, baboons, and eland, were confirmed to be disperser effective for *P. angustifolia* (Williams et al., 2000; Bobadilla et al., 2016; Adams, 2020; Chari et al., 2020). Findings from this chapter contribute to understanding invasion dynamics and inform decision-making regarding the control of invasive species. Invasion by alien fleshy-fruited plants is expected to increase in distribution.

7.3 Recommendations

The substantial growth in peer-reviewed publications in **Chapter 2** reviewing studies on fleshy-fruited invasive alien plants within grasslands signifies a increasing global focus on understanding and addressing biological invasions as well as the importance of grasslands. Previously overlooked, the recent surge in research on invasive trees and shrubs highlights their considerable ecological impact on factors like soil quality, fire regimes, microbial communities, and overall biodiversity. As research on this topic advances, seed dispersal, predominantly facilitated by birds, is emerging as a key driver of the spread of fleshy-fruited invasive plants. This shows the necessity for a holistic understanding of the ecological processes at play. Future research directions should be on (1) expanding research on seed dispersal mechanisms beyond birds to include other potential vectors like mammals and wind, (2) investigating the role of pollination ecology in the population size and spread of these invasive plants, (3) assessment of environmental and socioeconomic impacts of these invaders, (4) evaluate and explore various management and control strategies, including rehabilitation techniques and (5) investigate the potential role of these plants within the cultural systems of different communities.

Contrary to expectations, there was little disagreement regarding the role *Pyracantha angustifolia* play in subsistence practices in **Chapter 3**. However, the high diversity of seed dispersal agents suggests a high likelihood of unassisted introduction to new areas. Furthermore, human activity is demonstrably contributing to the invasiveness of this species. Given the significant socio-economic and environmental impacts of *P. angustifolia*, further research is needed on species impacts. A combination of control methods has proven most effective in managing this invasion. Increased funding and government initiatives could significantly improve control efforts, and the exploration of alternative methods like biocontrol is recommended. The data provided by the community is believed to be reliable and can inform *P. angustifolia* management strategies; however, to strengthen its application, incorporating research and existing literature is essential. As requested by the communities, government assistance in terms of clearing resources is highly recommended for the improvement of the management of invasive alien plants in the area.

Chapter 4 investigated how plant communities change over time. This research shows that freely available Google Street View archives can be a cheap and valuable tool for this purpose. By looking at historical Street View images, researchers can track vegetation changes and understand how ecosystems respond to environmental pressures. This information can then be used to create better conservation and management plans, including how to fight invasive plants. The study also highlights a rise in invasive plants within grasslands, calling for urgent action. We recommend that the area sampled be increased to account for the larger spatial distribution of the species and record more invasive alien plant populations. This will ensure that the population's status of invasion is more robust and detailed.

In **Chapter 5**, we assessed the role of fruit selection on seed dispersal by birds in aviary experiments. The study confirms that the type of fruit plant plays a major role in what birds choose to eat, as there were significant differences in fruit choice of different plant species. We recommend further experiments to explore bird fruit selection for different fruit colours and sizes. This could involve dyeing real fruits or creating artificial ones. Further research should also take bird experience, toxins in the fruit, fruit shape, taste and smell, and plant’s fruiting seasons.

In **Chapter 6**, the study investigated how mammals contribute to the spread of fleshy-fruited invasive alien shrubs in the grasslands of eastern Free State Province in South Africa.

Mammals were found to disperse seeds of these invasive plants, making it difficult to control the invasion. The present study confirmed medium to large terrestrial mammalian species to be effective seed dispersal agents as viable seeds were found in their faeces. These findings contribute to the understanding of the invasion dynamics of the species and allow well-informed decisions regarding the control of such species. We encourage future research to effectively monitor the movements of these mammals through radiotracking and other methods to assess their daily movements. Seed retention times should also be assessed in mammals to estimate the potential seed dispersal distances accurately.

7.4 Concluding remarks and management implications

This synthesis of this research emphasises the urgency for further studies on fleshy-fruited invasive alien plants, shrubs and trees, in particular, in grasslands and other treeless ecosystems, to address their escalating threats with broader implications for conservation, ecosystem management, and global biodiversity preservation. Additional research is needed on seed dispersal by other agents, pollination, environmental and socioeconomic impacts, management strategies, rehabilitation, and cultural uses by different communities. Despite expectations, there was less conflict than anticipated regarding the subsistence role of these species, with unaided introductions to new sites expected because of diverse seed dispersal agents.

Human activities contribute to the invasiveness of species like *P. angustifolia*, which requires further investigation because of its significant socio-economic and environmental impacts. Prescribed mixed methods are more effective in controlling invasion, with potential improvements through funding and government initiatives, including research on alternative control methods like biocontrol. Community-provided data, while credible, requires support from research and literature to enhance *P. angustifolia* management. Using Google Street View archives for assessing population changes offers a cost-effective approach to studying vegetation dynamics and ecosystem responses to environmental change, complementing traditional methods like field surveys and remote sensing. This study introduces a novel method for assessing change over time, allowing for efficient status assessment of plant invasions over time. This is one of the few studies that have assessed the change in fleshy-fruited invasive alien plant population over time using Google Street View archives. Most studies only look at invasion status or species abundance (Deus et al., 2016; Barone et al., 2021; Kotowska et al., 2021). It highlights the increasing abundance of fleshy-fruited invasive alien plants in grasslands, emphasising the role of fruit colour and size in fruit selection and the importance of fruiting season in seed dispersal.

Understanding the factors influencing fruit selection by frugivorous birds is crucial for predicting the dispersal patterns of fleshy-fruited invasive alien plants, shedding light on the ecological mechanisms driving their spread. Bird-mediated dispersal should be considered in management and control strategies, with targeted interventions based on traits that make certain fruits more attractive to birds. These findings offer insights into avian foraging behaviours and the ecological dynamics of fruit selection, impacting the seed dispersal of invasive plants. Additionally, the study identifies locally occurring medium to large terrestrial mammalian species to be seed disperser effective of selected invasive fleshy-fruited plants in grasslands, highlighting the need for further research in this area. Despite more seeds of invasive plants being found in mammalian faeces, native fleshy-fruited shrubs exhibited higher germination percentages.

This research provides crucial insights into the ecological mechanisms driving the spread of invasive alien plants, particularly fleshy-fruited species, with implications for plant invasion management and research. By identifying key factors such as seed dispersal mechanisms mediated by birds and mammals, fruit selection preferences, and the role of fruiting seasons, managers can develop targeted intervention strategies for managing invasive plants more effectively. Firstly, the seed dispersal part of the study provides an opportunity to assess the rate of spread should the management intervention be introduced. A repeat of this study after specific control has been attempted could provide plant population status and a method to track how much seed the animals are spreading at a given time. Google Street View imagery could also be incorporated into monitoring programs to assess change over time on fleshy-fruited shrubs. Secondly, since human-mediated dispersal is involved in the spread of these species, communities should be made aware of their contribution to spreading fleshy-fruited invasive alien plants through their use and consumption.

Understanding these dynamics contributes to conservation efforts and biodiversity preservation, while cost-effective monitoring methods like Google Street View archives offer efficient approaches to assessing population changes and helps prioritise species that are spreading rapidly. This underscores the importance of adopting a holistic approach to invasive species management, considering various factors such as seed dispersal, fruit selection, and ecological impacts. Moreover, the research highlights the need for further studies and collaboration between botanists, ecologists, zoologists, land managers, community-based organizations and social scientists, to mention a few, to address the complex challenges posed by invasive plant species comprehensively.

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