The role of termite mounds in vegetation transition to woody plants in grassy ecosystems in KwaZulu-Natal, South Africa

by

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ABSTRACT

Woody plants encroachment, the increase in woody plant cover and density in grassy ecosystems, poses a significant threat to biodiversity and ecosystem functioning across southern Africa and globally. While drivers such as elevated atmospheric CO_2, climate change, land use and land management practices contribute to this phenomenon, landscape-scale processes such as termite activity plays an important role. Termites, through mound-building and soil modification, create nutrient-rich and stable microhabitats that facilitate woody plant establishment and the formation of bush clumps. This study investigated the role of termite mounds in promoting bush clump development and driving woody plant community dynamics in Cumberland Nature Reserve and Uitkomst Conservation Area in KwaZulu-Natal, South Africa. Specifically, the study aimed: (1) to establish the growth rate and expansion of bush clumps facilitated by termite mounds; (2) to assess the influence of termite mounds on woody species richness, diversity, and composition, including the role of bird-mediated seed dispersal in amplifying woody plant establishment; (3) to explore changes in woody species richness, diversity, and composition in relation to termite mound size, and assess the relationship between spatial distribution of termite mounds and woody vegetation cover; and (4) to investigate the patterns and processes of woody plant succession associated with bush clump development on termite mounds.

Using a time series of aerial photographs (1964, 1983, 2003, and 2024), the development and expansion of bush clumps were studied in Uitkomst. Bush clumps were consistently found to initiate on termite mounds, with the earliest clumps present before 1964. Clumps recorded before 1964 were also the largest by 2024, suggesting that clump size reflects successional age. From 1964 to 2024, bush clump area increased significantly, tripling in size. Growth rates of bush clump area varied with land-use type: grassland clumps expanded at 4.7 m^2 $year^{-1}$ from 1964 to 2003, whereas in the cropland area, clumps grew at only 0.15 m^2 $year^{-1}$ during the same period. However, following cropland abandonment post-2003, clumps in these areas expanded rapidly (~17.51 m^2 $year^{-1}$), with a tenfold increase in area between 2003 and 2024.

Vegetation surveys on 62 termite mounds and 71 matrix plots across Cumberland and Uitkomst recorded 2432 plants representing 54 woody species. Termite mounds supported significantly greater woody plant density and diversity compared to the matrix: 72% of species were mound-exclusive, and mound plots exhibited higher sapling and mature tree densities, stem density,

species richness, and Shannon diversity index. Notably, matrix vegetation was dominated by *Vachellia sieberiana*, while termite mound assemblages were dominated by *Lantana camara*, *Rubus ulmifolium*, *Cussonia spicata*, and *Searsia pyroides*. *Lantana camara, C. spicata*, and *S. pyroides* were significant termite mound indicator species (indicator value < 60%), whereas none were identified for matrix assemblages. Bird-dispersed species with drupe-type fruits were more common on mounds, suggesting avian dispersal influences species composition.

To test whether the size and spatial distribution of termite mounds influenced the woody plant composition and distribution of bush clumps, woody vegetation assemblages on bush clumps occurring on termite mounds of varying sizes were studied. In addition, termite mound density, bush clump density, and the number of termite mound–facilitated clumps were quantified within 41 open-area plots at both Cumberland and Uitkomst to assess spatial relationships between mound occurrence and bush clump formation. Termite mound density ranged from 4.7 to 5.4 mounds ha^{-1}, with bare mound densities at between 1.2 and 2.4 mounds ha^{-1} and vegetated mounds at between 3 and 3.4 mounds ha^{-1}. Mound surface area varied from 1.46 m^2 to 111.12 m^2. Bush clump density was significantly and positively associated with termite mound density ($R^2 = 0.512$, $F_{(3, 37)} = 12.92$, $P < 0.0001$), indicating that greater mound densities correspond to greater woody clump densities. Species richness of woody plants increased with mound surface area ($R^2 = 0.362$, $F_{(3, 58)} = 10.96$, $P < 0.0001$), and the proportion of termite mound indicator species was significantly higher on large mounds than on medium and small mounds. Woody plant density and sapling density were ~3 times higher on large mounds, and mature tree density was ~2 times higher than on smaller mounds. Stem density was ~4 times higher on large mounds.

A space-for-time substitution approach was employed to investigate the developmental processes of bush clumps. Sixty-two bush clumps representing different successional stages were sampled to identify potential founder species and to examine changes in species composition as bush clumps matured and increased in size. Bush clump area ranged from 4 to 450 m^2 (mean ± SE = 102.14 ± 10.67 m^2). Each clump contained between 5 and 128 woody plants, averaging 28 ± 3 individuals. Species richness ranged from 2 to 20 species per clump (5.6 ± 0.41), and Shannon diversity index averaged 1.27 ± 0.07. Dominant species included *L. camara, R. ulmifolius, Lippia javanica, C. spicata*, and *S. pyroides*. Evidence indicated that bush clumps in both Cumberland and Uitkomst were simultaneously initiated by multiple species, with *S. pyroides* and *V. sieberiana* identified as the founder species in approximately 50% of the bush clumps. Species composition differed significantly between small and large

bush clumps (PERMANOVA $R^2 = 0.19$, $P = 0.001$), and compositional similarity (Morisita-Horn index = 0.76 ± 0.03) between saplings and mature trees supports a deterministic successional trajectory. A lognormal regression revealed that tree species richness, abundance, Shannon diversity, woody basal area, and stem diameter all increased significantly with clump size, indicating that bush clump expansion is accompanied by increased species richness, diversity, and structural complexity, consistent with successional development driven by founder establishment and ongoing recruitment. The proportion of representatives of founder species declined with clump size, while the proportion of alien woody species increased. However, community-weighted means for forest specialisation and species habitat breadth did not vary significantly with clump size.

PREFACE

The research contained in this thesis was completed by the candidate while based in the discipline of Ecological Sciences, School of Life Sciences of the Collage of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, South Africa. The research was financially supported by the National Research Foundation (NRF).

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

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Signed: Prof. Z. Tsvuura

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STUDENT DECLARATION

COLLEGE OF AGRICULTURE, ENGINEERING AND SCIENCE

DECLARATION 1 – PLAGIARISM

I, Vukani Ngcobo, student number: 217014734 declare that.

1. The research presented in this thesis, except where otherwise indicated, is my original research.

2. This thesis has not been submitted for any degree or examination at any other university.

3. This thesis does not contain other persons’ data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

a. Their words have been re-written, but the general information attributed to them has been referenced.

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Signed: Vukani Ngcobo

Date: 06/02/2025

DEDICATIONS

I would like to dedicate this thesis to my late mother Mrs Nonkululeko Nokuthula "KaMakhaye" Ngcobo (1976 – 2021). *Ma*, your unconditional love and support shaped the person I am today. You stood by us during the most challenging times, teaching us the importance of discipline and perseverance to achieve major goals. Your belief in my potential inspired me to dream beyond limits. Though you did not live to see me graduating with my Honours, embark on this Master's journey, and bringing it to completion, I feel your presence in every step of this accomplishment. Thank you, *Ma*.

To my father, Mr Nkosinathi Ngcobo, *Ngiyabonga kakhulu Fuze elihle* for all the support and motivation. Thank you for always being there for us, loving and protecting us even when *Ma* was no longer with us. Your words of encouragement and how you view life as whole always fuels me to do better and be a better person.

To my younger siblings, Siyabonga, Aphiwe, and Minenhle Ngcobo, and my son Esamisipho (*Sirius A. – the brightest star in the night sky*), you guys are my everyday motivation and source of strength.

I would like to also dedicate this thesis to the Khumalo family, my sister Mrs Silindile Khumalo and my brother-in-law Mr Khumalo, I thank you for all your continuous support and encouragement.

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Firstly, I would like to thank God the Almighty for helping me through this degree of Master of Science. Through His grace and favour, I made it through.

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A special thanks to my good friend Mr Philani Shabangu for helping with field from the first day until the very end – *Ngiyabonga bhuti*.

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CHAPTER 1

General introduction

Background

Globally, grassy ecosystems are threatened by the expansion of woody vegetation (also known as bush encroachment or woody plant encroachment) (Stevens et al., 2016), with Africa experiencing the highest rate of encroachment (Stevens et al., 2016). Woody plant encroachment alters the structure and function of open grassy ecosystems, leading to a decline in their productivity and have negative implications for biodiversity conservation (Ward, 2005; Skowno et al., 2017). Woody plant encroachment is driven by a combination of factors, including but not limited to climate change and land-use, land management changes (Kgosikoma and Mogotsi, 2013; O'Connor et al., 2014). At landscape scales, termite mounds may be one of the important factors influencing woody vegetation assemblages (Seymour et al., 2014). For example, through their mound-building and foraging activities, termites improve soil fertility and soil water holding capacity thereby creating patches of high-quality resources in nutrient poor landscapes (Sileshi et al., 2010; Seymour et al., 2014; Muvengwi et al., 2017).

Elevated nutrient concentrations and improved soil moisture may be beneficial to woody plant establishment and growth (Joseph et al., 2013a), which may ultimately lead to a dense concentration of woody plants on termite mounds, called bush clumps. These bush clamps can expand as they mature and merge with other nearby bush clumps in areas with high termite mound density, leading to a formation of woodlands or closed canopy forests. However, the underlying mechanisms and feedback loops influencing woody vegetation on termite mounds remain poorly understood. As a result, understanding the role of termite mounds in grassland transition to woody plants is crucial for effective rangeland management in grassy ecosystems of southern Africa. Studying the specific mechanisms by which termite mounds facilitate woody vegetation establishment, thereby contributing to an increasing woody vegetation cover and density in a landscape can help mitigate the impacts of woody plant encroachment by informing management strategies.

Problem statement

While drivers such as elevated atmospheric CO_2, climate change, overgrazing, and suppression of fire are frequently implicated in woody plant encroachment (Kgosikoma and Mogotsi, 2013; O'Connor et al., 2014), emerging literature highlights the potential role of local biotic agents, particularly termites, in shaping vegetation dynamics (Sileshi et al., 2010; Seymour et al., 2014; Muvengwi et al., 2017). Termite activities significantly suppress herbaceous vegetation while facilitating the growth of woody species (Muvengwi et al., 2017). This could facilitate widespread woody plant encroachment due to reduced competition from grass and high nutrient availability in impacted landscapes. However, it is not clear how termite activities directly impact the tree and grass ratio. Some studies argue that termites increase soil fertility by concentrating clay or providing nutrient subsidies to mound soils thereby facilitating regeneration of woody plants, and the formation of bush clumps by increasing seed germination success (Blösch, 2008; Seymour et al., 2014; Muvengwi et al., 2017). Other studies highlight the importance of termite interaction with fire, arguing that termite mounds act as protective barrier for woody plants against wildfires that would kill young recruits (Joseph et al., 2013). Moreover, some studies suggest that birds use termite mounds for perching in grasslands and may act as focal points of seed deposition (Yamashina and Hara, 2019). When the deposited seeds germinate, they may lead to the establishment of clumps of woody recruits that provide more perching sites for bird seed dispersal thereby continuing the trajectory of seed deposition and tree seedling establishment.

Woody plant encroachment has already affected approximately 10 to 20 million ha of rangeland in South Africa (Kgosikoma and Mogotsi, 2013). Woody plant encroachment has also reduced the land carrying capacity for grazing to approximately 50%, which left 1.1 million ha of South African savanna rangeland unusable, and further threatening another ~27 million hectares (Symeonakis and Higginbottom, 2014). Moreover, woody plant encroachment often results in reduced species richness and domination of species with poor nutrition and low palatability for livestock and wild herbivores (Inman et al., 2020). Therefore, woody plant encroachment is a major concern for land users, particularly beef and sheep farmers such that it presents enormous negative economic consequences to them since grazer livestock represents their main source of income (Ward, 2005). Reduced agricultural productivity as a result of woody plant encroachment is likely to have serious implications on food security, ultimately threatening the livelihoods of millions of people specifically in rural areas.

Woody plant encroachment not only reduces grazing capacity, but it also reduces the functioning of impacted ecosystems, which affects biodiversity. For example, Cape vultures (*Gyps coprotheres*) which are endemic to the southern African region are no longer breeding in Namibia as result of reduced open areas due to woody plant encroachment (Graw et al., 2016). Moreover, in South Africa and Namibia, woody plant encroachment has restricted the cheetahs hunting ranges (Meik et al., 2002). Woody plant encroachment also has negative impacts on other ecosystem services such as soil water retention and protection from soil erosion (Pule, 2021). For example, Manjoro et al. (2012) reported a drastic increase of soil erosion simultaneously with increasing woody vegetation cover and density on hill slopes in the Ngwalana Catchment in the Eastern Cape, South Africa, and this was attributed to increased bare soil patches formed as trees outcompete the grass layer, which in turn resulted in an increased runoff connectivity and concentration of overland flow. As a result, increased soil erosion can ultimately result in nutrient poor soils and increased sediment load in neighbouring streams, hence threatening water resource availability and functioning of impacted aquatic ecosystems. Moreover, Huang et al. (2006) reported that woody plant encroachment affects the availability of water in arid and semi-arid environments by reducing streamflow and ground water recharge.

Monitoring woody plant encroachment has become increasingly important for several reasons. For example, Ward (2005) outlined that monitoring woody plant encroachment allows land users, particularly farmers, to assess the carrying capacity of land and to identify areas that may be affected by woody plant encroachment in the future. Policy makers and land managers also benefit from woody plant encroachment studies as they provide a useful tool for the development of effective land use policies and land management as well as land use planning strategies for sustainable management of natural resources and biodiversity conservation in affected areas. Many researchers identify woody plant encroachment as an indicator of land degradation (Inman et al., 2020). Therefore, given the spatial extent of the problem in South Africa (see Skowno et al., 2017), there is a need for inventories and monitoring at different spatial scales using consistent, repeatable and spatially explicit methods (Symeonakis and Higginbotton, 2014).

Aims

This study investigates the role of termite mounds in shaping woody vegetation patterns within grassy ecosystems, with a particular emphasis on how termite mounds facilitate the formation and expansion of bush clumps, ultimately contributing to woody plant encroachment.

Objectives

The objectives of the study are:

1. To establish the growth rate and expansion of bush clumps facilitated by termite mounds.

2. To evaluate the influence of termite mounds on species composition, relative abundance and diversity, and the role of bird-mediated seed dispersal on woody plant community establishment.

3. To establish woody species composition and diversity in relationship to termite mound size and spatial distribution.

4. To establish successional patterns of woody species on termite mounds.

Key research questions

The study seeks to answer the following questions:

1. What is the rate of bush clump growth and expansion on termite mounds over time, and how does it compare across different land-use histories?
2. How do termite mounds influence woody plant species richness, diversity, and composition, and what role does bird-mediated seed dispersal play in shaping these communities?

3. How does woody species richness, diversity, and composition vary with termite mound size, and what is the relationship between the spatial distribution of termite mounds and the distribution of woody vegetation (bush clumps)?

4. What are the patterns and processes of woody plant succession during bush clump development, and which species are most likely to initiate bush clumps on termite mounds?

Study sites

The study was conducted in Cumberland Nature Reserve and Uitkomst Conservation Area, which are located in the uMgungundlovu District Municipality and eThekwini Metropolitan Municipality boundaries, respectively, in the KwaZulu-Natal Province of South Africa. The sites were selected because of the occurrence of bush clumps on termitaria. Additionally, the vegetation of the study sites exhibits savanna and grassland elements, which are relevant for the study.

Cumberland Nature Reserve

Cumberland Nature Reserve is a 560-ha private property located in the Table Mountain area of uMgungundlovu District Municipality, 20 km northeast of Pietermaritzburg (29°30'42"S, 30°30'48"E). The mean annual rainfall at Cumberland is 695 mm, receiving the highest rainfall in December and January (Figure 1.1). The area receives the lowest average rainfall in June, and experience average temperatures of < 10 °C between May and August (Figure 1.1). Cumberland experiences a hot, wet season (October to April) with average temperatures ranging between 16 °C and 20 °C (Figure 1.1). Habitats found at Cumberland include mosaics of savannas and grasslands that range from scattered trees to thicket bush clumps, woodland, valley thickets, a wetland, and a substantial riverine habitat along the uMngeni River and its tributaries (Muller and Ward, 2013).

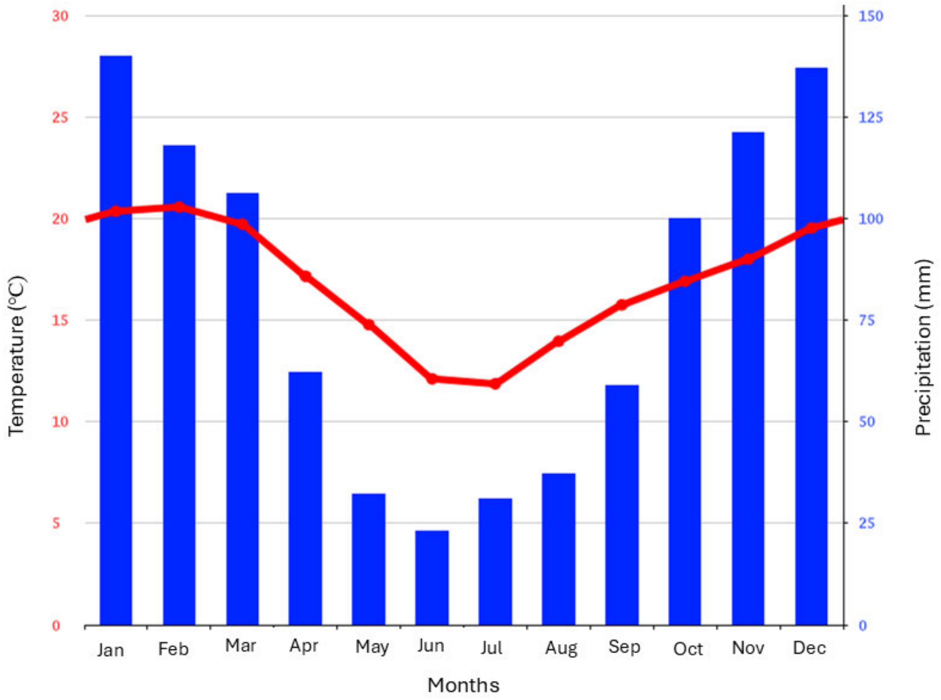

Figure 1.1: Mean monthly temperature (°C) and precipitation (mm) in Cumberland (Data: 1991-2021). The figure was adopted and modified from https://en.climate-data.org/africa/south-africa/kwazulu-natal/pietermaritzburg-634/

Topography, drainage, and geology

Cumberland Nature Reserve is crossed by two river systems and additionally has wetlands and marshy areas. The Rietspruit stream is a tributary of the uMngeni River, and passes through the reserve, while the uMngeni forms part of the eastern boundary of the reserve. The Rietspruit stream and uMngeni river have carved out valleys, creating diverse habitats. Cumberland is situated in the Ecca Group shale and sandstone and the dominant rock types include sandstone and shale (University of KwaZulu-Natal, n.d.). Ecca shale is typically dark-coloured as they are carbon-rich due to the high vegetation content of the original sediments (University of KwaZulu-Natal, n.d.). The reserve has varied landscape terrain including valleys, hills, and plateaus with elevation ranging from 500 to 1200 m above sea level.

Vegetation type

Cumberland consists of grassland and savanna vegetation described as Dry Coast Hinterland Grassland and the KwaZulu-Natal Hinterland Thornveld vegetation types (Rutherford et al., 2006). The Dry Coast Hinterland Grassland lies on undulating plains and hilly landscapes which are mainly associated with drier coast hinterland valleys in the rain-shadow of the rain-bearing frontal weather systems from the east coast (Zdanow and van de Haar, 2018). The vegetation is usually associated with low plant species diversity and is characterized by a sparse cover of sour and wiry grass dominated by the unpalatable *Aristida junciformis,* commonly called Ngongoni grass (Goodall, 2000). In good condition the vegetation is usually dominated by *Themeda triandra* and *Tristachya leucothrix* (Scott-Shaw and Escott, 2011). The conservation status of the Dry Coast Hinterland Grassland and the KwaZulu-Natal Hinterland Thornveld vegetation types is considered vulnerable in KwaZulu-Natal (Mucina and Rutherford, 2006).

The KwaZulu-Natal Hinterland Thornveld is adapted to dry, hot climate with rainfall ranging between 500 and 800 mm per year and is dominated by drought-tolerant species and fire-resistant vegetation (Gillham et al., 2017). KwaZulu-Natal Hinterland Thornveld comprises open thornveld dominated by thorny, deciduous trees including *Acacia* species (Gillham et al., 2017; Ward et al., 2020). The shrub layer includes *Euphorbia* and *Capparis* species (Gillham et al., 2017). The grass layer is dominated by *Hyparrhenia rufa*, *A. junciformis, T. triandra, T. leucothrix*, and *Heteropogon contortus* (Tsvuura and Kirkman, 2013; Ward et al., 2017a, b). Additionally, this vegetation type is threatened by habitat fragmentation, overgrazing, and invasive species (Jewitt, 2018). However, it is currently listed as least concern (Jewitt, 2018).

Flora and fauna

Cumberland is home to 30 species of mammals including several ungulate species such as blesbok (*Damaliscus pygargus phillipsi*), impala (*Aepyceros melampus*), oribi (*Ourebia ourebi*), and recently there have been sightings of a cattle herd of about 30-40 animals. The reserve is also home to over 300 bird species, and over 300 species of wildflowers. Patches of wooded vegetation in the area are often confined to valleys and ridgelines embedded within the Sub Escarpment Grassland assemblages (Malachite Specialist Services, 2017). Termitaria support bush clumps within the grassland and savanna units whose main tree species include *Vachellia sieberiana*, *Cussonia spicata*, *Ehretia rigida*, *Grewia occidentalis* and *Coddia rudis*

(Scott-Shaw, 2016). Bush clumps in Cumberland mainly occur on mounds of *Odontotermes* species and *Macrotermes natalensis* (Muller and Ward, 2013, Figure 1.2). Herbaceous species richness is not as abundant as adjoining vegetation units such as KwaZulu-Natal Sandstone Sourveld and Moist Coast Hinterland Grassland, but the main species include *Aristida junciformis, Themeda triandra*, and *Tristachya leucothrix.*

Figure 1.2: (a) Woody vegetation assemblages on a medium sized termite mound, and (b and c) Typical savanna matrix vegetation assemblages in Cumberland. Photo credit: Vukani Ngcobo

Uitkomst Conservation Area

The Uitkomst Conservation Area, formerly Bartlett Estate (30°37’29”E, 29°46’21S), is located in the Hammersdale, eThekwini Metropolitan Municipality. The area is 516 ha in extent and consists of four sections whose origins are the farms acquired by the Durban municipality at different times for conservation, namely Nature 1, Nature 2, Vacant land and Hamilton section. The Uitkomst Conservation Area form part an important network of protected areas within the eThekwini (Durban) municipality that all fall under the Durban Metropolitan Open Space System (D’MOSS) (Biodiversity Management Department eThekwini Municipality, 2022/2023). The mean annual rainfall in Uitkomst is 632 mm, with most rainfall occurring between October and March (Figure 1.3). Uitkomst experiences a hot, wet season (October to April) with average temperatures ranging between 16℃ and 21℃ (Figure 1.3).

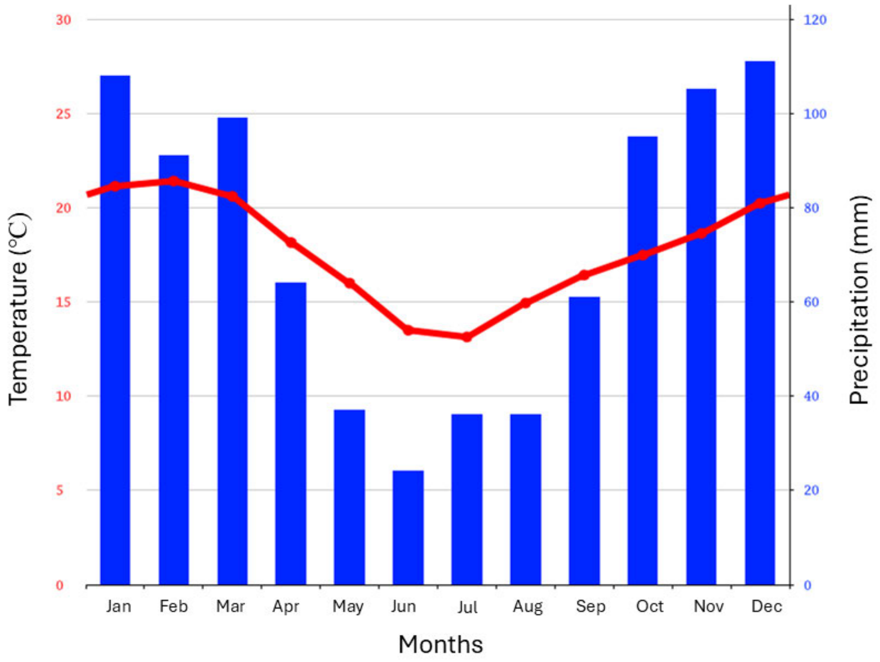

Figure 1.3: Mean monthly temperature (℃) and precipitation (mm) in Uitkomst (Data: 1991-2021). The figure was adopted and modified from https://en.climate-data.org/africa/south-africa/kwazulu-natal/mpumalanga-27228/

Topography, drainage, and geology

Uitkomst includes plateau top flatlands, cliff edges, sheer cliff faces, and undulating slopes (Biodiversity Management Department eThekwini Municipality, 2022/2023). The dominant underlying geologies are Natal Group Sandstone and Dwyka Tillite. There are two important drainage lines draining into the Sterkspruit River on the northern boundary of the area (Biodiversity Management Department eThekwini Municipality, 2022/2023). The first is a rocky bottom watercourse which divides Portion 185 Uitkomst and Doornrug No. 852 and the second is a valley bottom wetland fed by a hillslope seep located across Portions 467, 468 and 469 Uitkomst and Doornrug 852. The conservation properties contain one minor rocky bottom watercourse, and a somewhat degraded unchanneled valley bottom wetland, both located on Portion 394 Uitkomst and Doornrug 852 and a major wetland system occurs in Portion 25 Uitkomst and Doornrug 852, however this section is highly degraded following illegal sand mining.

Vegetation type

Uitkomst conserves a large portion of relatively undisturbed critically endangered KwaZulu-Natal Sandstone Sourveld (KZNSS) with a national conservation status of *Endangered* in terms of section 52 of the National Environmental Management: Biodiversity Act (NEM: BA, Act 10 of 2004) and Provincial status of *Critically Endangered*, as well as pockets of Eastern Scarp Forest (*Vulnerable*), Eastern Valley Bushveld and Wetland Systems (Biodiversity Management Department; eThekwini Municipality, 2022/2023). The KZNSS is a grassland that is dominated by short graminoids, legumes, forbs, shrubs and trees (Hlanguza, 2015; Mutanga et al., 2016). The KZNSS is a fire dependent ecosystem that thrives on regular burning for maintaining the biodiversity and integrity of the grassland (Rouget et al., 2016; Buthelezi, 2017). Fire benefits the KZNSS by suppressing the establishment of woody plants and the spread of alien invasive plants (Rouget et al., 2016; Makhaya et al., 2022). Fire also removes dead plant material, stimulates grass growth and flowering of wildflowers and can cue germination by breaking seed dormancy (Rouget et al., 2016).

Flora and fauna

Uitkomst Conservation Area supports a number of endemic and endangered plant species including *Cineraria atriplicifolia*, *Dierama pallidum*, *Eriosemopsis subanisophylla* and *Helichrysum pannosum*. The oribi (*Ourebia ourebi*) is a keystone species and one of the most threatened mammals occurring on site. Reports also highlighted that bushbuck (*Tragelaphus sylvaticus*), grey duiker (*Sylvicapra grimmia*), large spotted genet (*Genetta tigrine*), porcupine (*Erethizon dorsatum*), and possibly caracal (*Caracal caracal*) may be some of the medium sized mammals present in the area (Biodiversity Management Department; eThekwini Municipality, 2022/2023). Moreover, Uitkomst is largely impacted by soil erosion, woody plant encroachment, and invasive alien plants. The main alien plant species include *Lantana camara*, *Eucalyptus grandis*, *Acacia mearnsii* and, in the closed woodland/forest sections, *Solanum mauritianum* (Figure 1.4). Other threats to conservation include poaching, illegal harvesting of medicinal plants, unauthorized grazing, and sand mining.

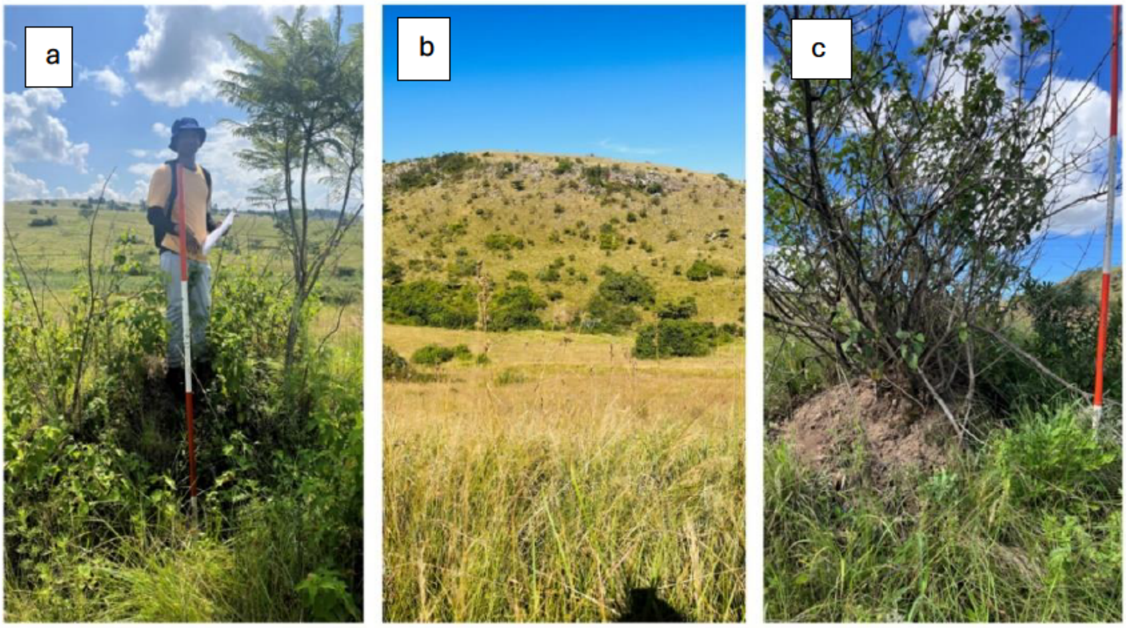

Figure 1.2: (a) V. Ngcobo standing on a vegetated termite mounds showing an early bush clump initiation stage, (b) Typical grassland vegetation assemblages and well-developed bush clumps, some of which have merged to form small continuous woodland patches, and (c) *L. Camara* shrub growing on a typical small termite mound in Uitkomst. Photo credit: Vukani Ngcobo and Philani Shabangu

Thesis Structure Statement

This thesis is presented in the form of publication-ready chapters. It begins with a general introduction that outlines the background, aim, specific objectives, and research questions guiding the study. To avoid repetition, the description of the study areas is included in the general introduction rather than repeated in each chapter. A comprehensive literature review follows, providing the conceptual and empirical context for the research. Each research objective is addressed in an individual results chapter, written in the format of standalone scientific papers. While efforts were made to minimize redundancy, some repetition of background information and methods across chapters was unavoidable. The thesis concludes with a synthesis chapter that integrates key findings across all chapters and discusses their broader ecological implications.

Chapter outlines

Chapter 2: literature review

In **chapter 2**, I provide a detailed literature review. I conducted a review of relevant literature discussing trends and causes of woody plant encroachment in grassy ecosystems. Furthermore, I assessed the effects of termite mounds on soil properties across African savannas, evaluating evidence that termite mounds act as localized patches of improved resource availability. This review explores the mechanisms by which termite mounds generate spatial heterogeneity in grassy ecosystems, contributing to variations in soil nutrients and moisture.

Chapter 3: Long term dynamics of bush clump development in the Uitkomst Conservation Area, KwaZulu-Natal

In chapter 3, I utilized historical aerial photographs to study long term dynamics of bush clump initiation and development in Uitkomst. This chapter is presented is a “short communication” format. In this chapter, I determine the growth rates of bush clumps over time across different land-use history (grassland vs former cropland) and test how bush clump expansion may differ across grassland and former croplands over a time period of 60 years.

Chapter 4: Termite mounds increase the spatial heterogeneity of microhabitats for woody vegetation in grassy ecosystems

In **chapter 4**, I examine the influence of termite mounds on woody plant assemblages, specifically by comparing woody species composition and structure on termite mounds and in the grassland matrix. This analysis aims to clarify the role of termite mounds in promoting woody plant establishment, thereby acting as catalysts for woody encroachment.

Chapter 5: The effects of termitaria size and density on woody vegetation assemblages

Chapter 5 explores how mound size influences woody species composition and structure. I examine changes in woody vegetation species richness, diversity, density, and composition in relation to mound size. Additionally, I assess whether the size and spatial distribution of mounds affect the composition and distribution of bush clumps.

Chapter 6: Processes during woody vegetation succession in termitaria-facilitated bush clump development

Chapter 6 investigates the formation and development of bush clumps on termite mounds, exploring the role of founder species and the successional dynamics of woody plant communities during bush clump formation. This part of the study provides insights into the processes that drive the transition from isolated woody plants to more complex bush clumps on termite mounds.

Chapter 7: Synthesis, conclusions and recommendations

This chapter aims to provide a comprehensive summary of the thesis and integrate the findings presented in the preceding chapters. It also provides an opportunity to discuss the new findings this thesis contributed to the current understanding woody plants encroachment and how the presence of termite mounds within the landscape may initiate and facilitate the process of vegetation transitions to woody plants in grassy ecosystems. This chapter also provide directions for future research on the role of termite mounds in shaping woody vegetation community composition and patterns in grassy ecosystems.

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CHAPTER 2

Literature review

Grasslands and savannas (the grassy ecosystems)

Grassy ecosystems dominated by grasses with the C3 photosynthetic pathway first appeared 11–24 million years ago and rapidly expanded across the globe (Edwards and Smith, 2010; Bond and Parr, 2010). However, about 6 - 8 million years ago, grasses with the C4 photosynthetic pathway replaced and dominated the C3 grasses in warm, seasonally arid areas resulting in grasslands and savannas being the most prominent landscapes in the tropics (Bond and Parr, 2010). Grasslands are terrestrial ecosystems where herbaceous vegetation, mainly grasses and grass-like plants dominates, typically containing less than 10% tree and shrub cover and maintained by climatic constraints or disturbances like fire or grazing. Savannas are mixed woody–grass ecosystems defined by a continuous C4 grass understory beneath a discontinuous canopy of trees or shrubs, with coexistence sustained by factors such as fire, herbivory, and seasonal moisture variation (Scholes and Archer, 1997). Today, grasslands and savannas – the grassy ecosystems, are one of the largest and most important terrestrial biomes (Van Coller et al., 2018). Grasslands and savannas are widely distributed throughout the tropics in all continents, but particularly in northern and southern America, Australia and Africa (Solbrig, 1996), and they cover a combined area of nearly 20% to 40% of the total global terrestrial land surface (Blair et al., 2014; Strydom and Midzi, 2019).

Ecosystem services

Grassy ecosystems provide a wide range of ecosystem services and functions, thus, they significantly impact human livelihoods, as well as biodiversity (Osborne et al., 2018). For example, the miombo and mopane woodlands which constitute the dominant land cover in southern Africa, support the livelihoods of approximately 100 million rural people and more than 50 million urban dwellers, and millions of others beyond the region (Syampungani et al. 2009). Ryan et al. (2016) reported that provisioning services of the miombo and mopane savanna contribute approximately ZAR315 billion (approx. 16.4 billion US$) to rural livelihoods annually and provide up to 76% of the energy used in the region. Additionally, Boone et al. (2018) reported that savanna rangelands contribute 20% - 40% of small ruminant meat production, up to 55% of beef production globally, and in sub-Saharan Africa, up 25% of cattle milk production. In South Africa, savanna rangelands support 52% of the cattle population, as well as 72% and 17% of the goat and sheep populations, respectively (Palmer and Ainslie, 2006; Beyene et al., 2014). Moreover, southern African savannas may also have a significant role in wild fruit production, for which there is potential to support commercialisation. For example, Akweni et al. (2022) reported that up to 13 tons of *Strychnos madagascariensis* and up to 17 tons of *Strychnos spinosa* fruits are produced in the wild in Umhlabuyalinga Municipality in the northern part of KwaZulu-Natal province, South Africa.

Savannas and grasslands are regarded some of the most important ecosystems in global biogeochemical cycles (Archer et al., 2001). For example, southern African savannas and grasslands store an estimated 18-24 gigatonnes of carbon annually (Ryan et al., 2016). Moreover, studies have also shown that water recycled by vegetation in southern African grassy ecosystems is responsible for 10-25% of precipitation in the region, making them important to rain-fed agriculture systems, and overall freshwater resource systems in the region (Ribeiro et al., 2020). Grassy ecosystems are home to a unique and diverse flora and fauna. For example, the miombo and mopane savanna harbours a high species diversity of avifauna including a number of endemic species such as *Monticola angolensis*, *Cinnyris shelleyi* and *Agapornis liliana*, thereby attracting tourist revenue from birdwatchers (Ryan et al., 2016). However, recent studies have indicated that the productivity and ecosystem functioning of grassy ecosystems is threatened by land degradation (Crawford et al., 2019; Liao et al., 2020).

Land degradation can be defined as the reduction or loss of ecosystem function as a result of human and natural processes (Venter et al., 2020). Reduced ecosystem functioning can result in the loss of biodiversity and ecosystem services that support human livelihoods (Venter et al., 2020). For example, Musekamp et al. (2015) estimated that the global ecosystem losses as a result of land degradation is about ZAR115.54-194.4 trillion (approx. 6 – 10.1 trillion US$) per year, which equates to the reduction of the world’s gross domestic product by 10 – 17% annually. This loss affects more than two billion people living in drylands. Land degradation is often associated with a reduction of vegetation cover and loss of natural habitat commonly as a result of deforestation and land clearance for agriculture, infrastructure- and urban development (Wassie, 2020). However, in some environments such as in savannas and grasslands, land degradation can be caused by an increase in woody vegetation density (Belay et al., 2013).

Woody plant encroachment

Over the past 60 years, there has been accumulating evidence to suggest that African savannas are being altered by a phenomenon known as woody plant encroachment (Ward, 2005; Skowno et al., 2017). Woody plant encroachment is the expansion in cover and density of woody communities within a predominantly grassy community (Wiegand et al., 2006). Woody plant encroachment is commonly seen as a form of land degradation (Ludwig et al., 2016) as it significantly inhibits the growth of high-value herbaceous species and decreases indigenous plant species diversity and homogenises habitat structure. This may result in a fundamental shift in grassy ecosystem functioning (O'Connor et al., 2014). As a result, woody plant encroachment has widespread consequences for agricultural productivity, biodiversity and provision of ecosystem services in grasslands and savanna rangelands (Eldridge et al., 2011). Woody plant encroachment and homogenised habitat structure have negative impacts on forage production (Archer, 2010), rangeland carrying capacity, species that are adapted to open areas (Sirami et al., 2009), carbon sequestration (February et al., 2020), hydrology (Honda and Durigan, 2016) and soil erosion (Grellier et al., 2012).

Broad-scale trends in woody plant cover in sub-Saharan Africa

In sub-Saharan Africa, woody vegetation cover has increased by 7.5 million km^2 from 1986 to 2016, with the western parts of this region experiencing 90% reduction of its savanna rangeland as a result of woody plant encroachment (Venter et al., 2018). Similarly, studies have also reported severe cases of woody plant encroachment in East Africa (Yusuf et al., 2011; Graw et al., 2016). For example, in Ethiopia, the density of woody plants increased by 39% in 38 years, corresponding to 149 km^2 decline in grassland cover reported by Mesele (2007) in the same locality. Recently, Kabeta et al. (2020) reported a 9.8% decline per ha in total grassland cover while the total area covered by woody vegetation increased by 21.4% per ha over the last 30 years in the western escarpment of the Great Rift Valley in Ethiopia. In southern African, Botswana, Zimbabwe, Namibia and South Africa are among some of the countries that are currently affected by woody plant encroachment (Shikangalah and Mapani, 2020). Recent studies have reported that more than 32% of Namibian rangelands have been affected by woody plant encroachment, including 50% of the protected areas (Muroua, 2013; Shikangalah and Mapani, 2020). Furthermore, in South Africa, woody plant encroachment has affected approximately 10 – 20 million ha, reducing grazing capacity to only 50%, and further threatening another 27 million ha of rangelands (Symeonakis and Higginbottom, 2014). The main encroaching species in South Africa include *Vachellia* spp., *Hakea* spp., *Pinus* spp. and *Senegalia* spp. (Lesoli et al., 2013). For example, Turpie (2019) reported that in just 50 years, *Senegalia mellifera* became the main encroaching species in 3.5% - 14% of the Northern Cape and Northwest provinces in South Africa.

Evaluating drivers of woody plant encroachment

Environmental change

Woody plant encroachment appears to result from multiple global and local drivers and interactions between them (Wigley et al., 2010; Eldridge et al., 2011; O'Connor et al., 2014; Archer et al., 2017. There is general agreement that elevated CO_2 concentration in the atmosphere, can promote growth of woody species via the C_3 photosynthetic pathway (Archer and Stokes, 2000; Stevens et al., 2016). Studies suggest that C_3 trees benefit from increased CO_2 due to reduced photorespiration, higher water-use efficiency, and faster post-fire regrowth, allowing them to outcompete grasses, especially in fire-prone ecosystems (Higgins et al., 2000). Higher CO2 concentration results in an increased root biomass that ensures rapid regrowth of woody plants following loss of above-ground biomass to disturbances such as fire or herbivory (O'Connor et al., 2014). Palaeoecological evidence supports this view, showing that tree cover increased in interglacial periods with high CO_2 concentration and declined during glacial periods with low CO_2 concentration (Cerling et al., 1993; Bird and Cali, 1998; Ehleringer et al., 1998).

Climate change, particularly changes in precipitation patterns have also been discussed as one of the prominent drivers for woody plant encroachment in arid and semi-arid savannas (Knapp et al., 2008), with studies providing evidence that woody plant cover and density tend to increase with increasing mean annual precipitation (Sankaran et al., 2005). For example, ecohydrological models used to simulate African savanna dynamics along a gradient of 520 – 780 mm year^{-1} mean annual rainfall, revealed alternative states of grassland and savanna across the rainfall gradient (Synodinos et al., 2018). Under semi-arid conditions (520 mm year^{-1}), increasing inter-annual rainfall variability significantly reduced tree cover whereas in wetter conditions (580 – 780 mm year^{-1}), the same rainfall variability helped maintain tree cover (Synodinos et al., 2018). Moreover, in semi-arid savannas, dry extremes induced a loss of tree cover which could not be recovered during wet extremes as a result of high resource competition with grasses and increased fire frequency and intensity due to increased fuel load

(Synodinos et al., 2018). Similarly, during the dry season trees became water stressed and tree cover decreased whereas during the wet season trees experienced no water stress and increased in cover in arid savannas in the Kalahari Transect in southern Africa (D'Odorico et al., 2007). Moreover, increased soil moisture availability, particularly when there was limited competition from grasses, allowed woody plant seedlings to survive and grow into bush thickets (Kgosikoma and Mogotsi, 2013). Additionally, increases in atmospheric nitrogen (N) content due to increasing industrial emissions and changes in land use can potentially increase the deposition, storage and cycling of N in the soil (Pillay et al.,2021). As a result, the growth of N fixing woody plants, usually members of the Fabaceae, can be promoted which later can facilitate establishment of other woody species commonly of adjacent forest origin.

Land use change and change in disturbance

As the world's human population grows rapidly, regional drivers such as cattle numbers, grazing practices, and fire management are changing and likely contribute to woody plant encroachment (Archer et al., 2017). Over-grazing by livestock alters the timing and intensity of grass defoliation as well as recovery periods, thereby allowing woody seedlings to dominate (N'Guessan and Hartnett, 2011). For example, Koch et al. (2023) reviewed the role of livestock management on plant-herbivore feedback in savannas and reported that increased grazing pressure due to large numbers of cattle resulted in an increase in woody vegetation cover. Similarly, Tefera et al. (2008) reported that, in Lowveld savannas of eSwatini (formerly Swaziland), woody plant encroachment was prevalent in areas with a history of high stocking density. Mbatha and Ward (2009) reported that high levels of selective grazing resulted in woody plant encroachment and low plant quality despite rotational grazing and low stocking density in commercial ranches in semi-arid savannas of the Northern Cape province, South Africa. Consistent with these studies, Su et al., (2015) demonstrated that long-term fire suppression and livestock exclusion resulted in increased cover of native woody plants in sandy rangelands of northern China.

Changes in natural fire regimes and/or the suppression of fire induced by anthropogenic land management, and physical disturbance of soil may also be important factors driving woody plant encroachment (Kambatuku et al., 2013). For example, Venter et al. (2018) used high-resolution satellite imagery to study woody vegetation cover over sub-Saharan Africa and noted a decline in burned area along warmer and wetter climates, which was correlated with woody plant encroachment. Similarly, Gordijn et al. (2012) reported increased woody plant cover and density between 1985 and 2007 in sites that experienced a decrease in fire frequency from biennial to no fires in Ithala Game Reserve in northern KwaZulu-Natal, South Africa. The same patterns have been observed in grassland sites where > 50 years of fire suppression led to invasion by exotic plant species such as *Acacia melanoxylon, Jacaranda mimosifolia, Melia azedarach, Lantana camara,* and *Solanum mauritianum* (Ward et al., 2023), as well as some indigenous species including *Vachellia karroo, V. nilotica* and *Lippia javanica* (see Titshall et al., 2000).

Degraded landscapes and disturbed soils are common in abandoned farmlands or old fields (van Gils et al., 2008), and these are commonly vulnerable to woody plant encroachment noticeably by alien invasive shrubs and trees (Tesfai, 2010). Old fields provide more favourable conditions for establishment of invasive alien species than native species due to the poor representation of native species in the soil seed bank (Cramer et al., 2008). Moreover, the high seed productivity and dispersal ability of invasive species make them outcompete native plant species for high nutrient conditions arising from fertiliser applications, thereby facilitating dominance by exotic species in disturbed landscapes. For example, the increase in woody vegetation cover in old fields in the Eastern Cape province was driven by *Acacia mearnsii* invasion (Ruwanza, 2017; Scorer et al., 2019). Moreover, Blair et al. (2018) reported that woody vegetation increased up to 0.16% per year in abandoned fields in former homeland areas in South Africa. Similar patterns of old field invasion by alien and native species have been reported in many parts of Africa and beyond (e.g., Zimmerman et al., 1993; Tognetti et al., 2010; Kuebbing et al., 2014).

Models of woody plant encroachment

There is an increasing general agreement that climate change and elevated atmospheric CO_2 concentration are key global drivers of woody plant encroachment in grassy ecosystems (D’Odorico et al., 2012; Venter et al., 2018). These drivers often interact with regionally variable factors, such as fire suppression, herbivory, and land-use changes, to shape the dynamics of tree-grass coexistence. Understanding bush encroachment in savannas is therefore closely tied to the conceptual framework of tree-grass interactions (O’Connor et al., 2014), with recent literature highlighting that both resource availability (e.g., soil nutrients and water) and disturbance regimes (e.g., fire and herbivory) interact in complex and spatially variable ways to influence vegetation structure (Stevens et al., 2017; Scogings and Sankaran, 2020). Two main theoretical perspectives have been proposed to explain the coexistence of trees and grasses in savannas: competition-based models, which emphasize below-ground and above-ground competition for resources, and demographic bottleneck models, which focus on the role of disturbances in limiting tree recruitment and survival (Sankaran et al., 2004; Stevens et al., 2017).

Competition

Competition-based models of tree–grass coexistence in grassy ecosystems emphasize that spatial and temporal separation in resource acquisition allows these functional groups to coexist. A foundational concept within this framework is the Walter's two-layer soil water model, which propose that grasses and trees partition water use by rooting at different soil depths, grasses predominantly in the upper layers and trees accessing deeper soil moisture (Walter, 1971). This model is particularly relevant in semi-arid and arid savannas, where water availability is strongly stratified and limits plant growth. In such systems, grasses often dominate the upper soil profile during the rainy season, while trees rely on residual moisture at depth during dry periods (Ward et al., 2013). However, more recent research has shown that in mesic savannas, root overlap is common, and the degree of niche separation may be dynamic, varying with rainfall, soil type, and plant life stage (Kulmatiski and Beard, 2013). Importantly, tree–grass interactions are not static but vary across the life stages of woody plants. Tree seedlings and juveniles often experience strong competitive suppression by grasses due to limited access to light, nutrients, and water near the surface (Holdo, 2007; Bond, 2008). Once woody individuals grow above the grass layer, competition shifts and is often reduced. Moreover, disturbances such as fire and herbivory can alter this balance by reducing grass cover, promoting deeper water infiltration, and facilitating seedling recruitment (Kambatuku et al., 2013; Wiegand et al., 2006).

Plant-available soil water and plant-available soil nutrients determine several growth strategies and limitations for trees and grasses (Mishra and Young, 2020), and competition for these resources determine different tree-grass ratios (Kulmatiski and Beard, 2022). For instance, grasses would suppress trees through competition for water and nutrients in the upper layer of the soil as a result of their dense root network in the upper soil horizon, however, the lateral and vertical root system may allow trees to have exclusive access to water and nutrients at greater soil depth if the soil profile is deep enough (Holdo et al., 2018). Differences in the physiology of trees and grasses also impact the rate at which they respond to changes in resource availability and consequently affect tree-grass ratios in savannas (Staver et al., 2021; Laris et al., 2021). For example, grasses tend to respond faster to changes in plant-available water and nutrients because they do not have to invest in a woody stem, whereas trees would need to store sufficient resources below ground for re-sprouting after tissue loss to disturbances (Biro et al., 2024). In addition to water and nutrient availability, light is another key resource over which grasses and woody seedlings compete in grassy ecosystems. For example, dense grass cover can significantly limit the establishment and growth of tree seedlings by reducing light availability at ground level, creating a demographic bottleneck (Scholes and Archer, 1997; Higgins et al., 2000). Competition for light is particularly important during the seedling stage, where light interception by grasses can suppress tree growth. However, once woody seedlings escape the grass layer, they often gain a competitive advantage by shading out grasses beneath their canopy, contributing to the development and persistence of bush clumps.

Disturbance

Demographic bottleneck models focus on climatic variability and disturbance impacting tree seed germination, growth, and mortality as opposed to competition between trees and grasses in determining tree-grass coexistence in savannas (Higgins et al., 2000). Higgins et al. (2000) proposed that woody cover increases in mesic or moist savannas as the fire return period increases, allowing juvenile trees to grow beyond the flame zone. For example, drought suppresses tree seedling recruitment, whereas the growth of saplings to mature trees has been suggested to be a determinant of tree population structure, therefore, frequent, high intensity fires limit saplings' ability to escape the flame zone, resulting in a demographic bottleneck (O’Connor et al., 2014). As a result, bush encroachment is determined by the growth rate of individual trees in relation to fire-return duration and is facilitated by factors that reduce fire frequency or severity while facilitating sapling escape. For example, high levels of grazing significantly decrease grass biomass thereby reducing fuel for fire occurrence (O’Connor et al., 2014).

Grazing and browsing can interact in various ways to maintain the dynamic balance of grasses and woody plants in savannas (Venter et al., 2017). For example, if grazing levels are sufficiently high to decrease grass biomass, it might result in greater woody plants recruitment, permitting woody seedlings to establish and grow tall to adult stage (Venter et al., 2017; Smit and Coetsee, 2019). Similarly, decreased grass biomass reduces tree-grass competition thereby allowing woody plants to gain a competitive edge, whereas increased browsing may lower the canopy cover of mature trees thus decreasing the competitive impacts of trees over grasses (Smit and Coetsee, 2019). Herbivory can influence savanna structure and function through removing trees or suppressing seedling establishment and by removing grass biomass, which decreases fire intensity and consequently the impact of fire on woody plants (Van Langevelde et al., 2019). Alternatively, herbivory might cause positive feedback when reduced fire intensity results in less tree mortality and hence increased woody plant cover, which in turn decreases herbaceous plant cover due to competition for resources (Gillson and Ekblom, 2020). However, grazing is likely to limit tree seedling establishment due to trampling and exposing seedlings to being eaten by browsers (Smit and Coetsee, 2019).

Mixed feeder mega-herbivores restrict woody plants reproduction while simultaneously preventing high intensity fire by lowering grass biomass levels below those that can sustain large fire (Gillson and Ekblom, 2020), thereby maintaining a dynamic balance between trees and grasses. According to Gillson and Ekblom (2020), reduced herbivory combined with greater water availability is likely to allow shifts from open-canopy to close-canopy savannas, especially if increasing water in the landscape allowed water-dependent herbivores to disperse, easing pressure on plants near water sources. For example, Kohli et al. (2021) reported more than 70% decline in herbaceous cover in ungrazed plots when simulated rainfall was increased, giving competitive advantage to woody plants in Asian montane rangelands. Moreover, increased herbivory reduced grass quantity by 57% and woody plants abundance by 30.6% in African savannas, according to a synthesis of plant responses to herbivore exclusion experiment (Staver et al., 2021).

Mechanisms of woody plants succession

There are two ideas concerning the development of bush clumps and the state-transition to woody vegetation. First is the facilitation pathway, where light-demanding pioneer species facilitate the establishment of shade-tolerant species with forest functional traits. Here, facilitation describes a biological mechanism involved in secondary succession of woody vegetation (Vieira et al., 2013). It consists of positive interactions that occur among plants as a result of changes in the abiotic environment or interference by other organisms (Callaway and

Walker, 1997). The second idea is the nucleation pathway, where savanna-originating tree species establish on fire and herbivore refugia in grassland, resulting in the formation of forest from bush clumps.

Facilitation

Facilitation is described as the process where early-establishing woody individuals improve microhabitat conditions for the subsequent establishment of other species (Abreu et al., 2021). Seeds of early-establishing woody individuals may arrive via animal-mediated dispersal, particularly by birds and mammals, which deposit seeds to safe nutrient-rich patches in the open grassland. Once germinated, recruits of early-establishing species face intense competition from grasses and high disturbance from fire and/or herbivores. As a result, successful establishment often requires overcoming these filters, which may make it more challenging compared to nucleation, where conditions are relatively more favourable due to fire refugia and enhanced nutrients (Adie et al., 2023).

Once established, early-establishment species, which are usually light-demanding pioneer savanna species alter the local environment, facilitating the gradual entry of shade-tolerant woody species. For example, Abreu et al. (2021) reported that existing tree cover in savannas can facilitate seedling establishment of forest and savanna woody species. The isolated individual *Vachellia* trees may facilitate the later entry of forest specialist woody species, including broad leaved, bipinnate microphyllous and evergreen species (Abreu et al., 2021). As tree density and cover increases, conditions become less favourable for shade-intolerant herbaceous vegetation and savanna tree species, while becoming more favourable for establishment of forest tree species (Abreu et al., 2021), resulting in the formation of dense bush clumps. Studies have shown that existing tree cover can facilitate germination and establishment of woody seedlings by attracting seed dispersers which enhances seed arrival (Herrera and Garcia, 2009; Abreu et al., 2021). In this process, the existing tree cover can function simultaneously as perches, attracting birds that are seed dispersers and thereby increasing the arrival of seeds, and nurse trees, enabling seedling establishment under their canopies (Abreu et al., 2021). Therefore, facilitation results in higher colonisation success for woody plants under tree canopies in the absence of shade-intolerant savanna species. Moreover, flammability and the probability of fire is reduced once the tree canopy threshold is reached (Adie et al., 2023). Additionally, the savanna-woodland state transition occurs once the canopy is sufficiently dense, which eliminates shade intolerant grasses and woody species, thereby allowing entry of fire sensitive and shade tolerant species when surface fuel and grass competition is eliminated. In the facilitation pathway trees require longer periods of fire suppression to escape the fire trap (Adie et al., 2023).

Nucleation

The nucleation model was first presented by Yarranton and Morrison (1974) to explain succession patterns on the dunes of Grand Bend, Ontario, Canada. According to the nucleation concept, the initial establishment of woody plants occur in resource-rich or disturbance-free microsites (e.g., termite mounds), which then act as focal points for further recruitment through mechanisms such as seed rain and localized dispersal (Yarranton and Morrison, 1974; McDonnell and Stiles, 1983). During the nucleation process, initiation occurs when seeds of woody species are dispersed by birds that are often observed perching on resource-rich or disturbance-free microsites such as large rocks and termite mounds (Joseph et al., 2011; Yamashina and Hara, 2019). Early colonist species colonize these microsites and escape the shade trap as a result of rapid height growth of woody plants driven by asymmetric competition with neighbouring grasses (Adie et al., 2023). These plants then spread clonally and/or facilitate the establishment of late successional species by providing suitable microsites for seed accumulation and germination, as well as seedling growth (Franks, 2002; Holl et al., 2021). Succession spreads outward from the nucleation centres established by the first arriving colonists, resulting in a clumped distribution of woody plants (Franks, 2002; Ursell and Safford, 2022). Nucleation sites such as termite mounds and large rocks are often excluded from fires due to absence of grass fuel and their elevated terrain, thereby making the process of nucleation independent of fire frequency (Adie et al., 2023). Moreover, high woody plant stem density on nucleation sites further reduces fuel load on the surface thereby reducing the probability of fire occurrence and permitting the establishment of species that are sensitive to fire at recruitment (Adie et al., 2023).

Termites increase spatial heterogeneity and facilitate the establishment of woody plants in grassy ecosystems through mound-building

Mound-building termites increase landscape heterogeneity mainly through the transportation of soil nutrients both vertically and horizontally within the soil matrix (Sileshi et al., 2010), as well as by altering soil structure, soil hydrological dynamics, and overall land topography (Mando et al., 1996). In the process of mound-building, termites produce organo-mineral structures such as crop galleries, crop sheeting, and nests which are formed as a result of intestinal transit mixed with saliva, and these structures serve as microsites where a range of physicochemical changes occur in the soil (Mora et al., 2003). The source of materials used in mound-building have an important influence on the resulting soil nutrient status on termite mounds. For example, soil-eating termites generally build their mounds using their nutrient-rich faeces, while fungus-feeding termites use clay-rich soils that they extract from deeper soil layers and mix with saliva, while their faeces contribute less to the mound's structure (Muvengwi and Witkowski, 2020). These processes may consequently result in positive feedback in the environment such as through enhanced plant growth.

Landscape microtopography and soil hydrology

In many grassy landscapes in Africa, mound-building activities of termites have been widely reported to modify the microtopography (Sileshi et al., 2010; Erpenbach et al., 2017). These mounds vary considerably in size, ranging from just a few centimetres up to a few metres wide, with heights that can reach up to four metres, and mound size can also be an indication of its age and a species that constructed it (Muvengwi and Witkowski, 2020). For example, large mounds that are created mainly by termites of the subfamily Macrotermitinaea, particularly the *Macrotermes* and *Pseudacanthotermes* can reach heights of up to four meters (Muvengwi and Witkowski, 2020), with a basal circumference greater than 15 m (Aiki et al., 2021). Furthermore, termite mounds density can vary between 0.4 ha^{-1} to as high as 6.1 ha^{-1} with the proportion of active mound being usually higher compared abandoned mounds (Muvengwi, et al., 2018). For some termite species such as *Cubitermes* species and *Trinervitermes* species the spatial assemblage of their mounds can reach very high densities of up to a few hundred per hectare (Sileshi et al., 2010). For example, Aike et al. (2021) reported that mounds of *Trinervitermes geminatus* occupied 45% of Sudanian savanna, and mounds of *Macrotermes subhyalinus* occupied 55% of Sahelian savanna. Such spatial assemblages of termite mounds may generate a rough and elevated topography of regularly spaced mounds at a landscape scale (Pringle et al., 2010; Davies et al., 2020), which often provide protection to vegetation from seasonal flooding and wildfires (Groen et al., 2008) and therefore act as safe sites for the establishment of woody plants. The mounds therefore become nucleation sites where bush clumps develop with species diversity of woody plants disproportionately greater than the surrounding landscape.

Termite activities can also influence spatial heterogeneity in drainage, soil moisture, and water dynamics within a landscape (Sileshi et al., 2010; Muvengwi and Witkowski, 2020). Macropores created by termite activities on mounds increased interception of water runoff which resulted in increased water infiltration, thereby increasing plant-available water in deeper soil layers (Mando et al., 1999; Léonard and Rajot, 2001). Similarly, Belsky (1988) reported that termite modification of water infiltration in the Serengeti National Park was one factor causing mosaic vegetation patterns within the landscape. Furthermore, termite mounds contained 33% more available soil water to a depth of 60 cm compared to surrounding savanna matrix soil in the Lamto savanna, Ivory Coast (Konaté et al., 1999). On the contrary to these findings, a meta-analysis by Sileshi et al. (2020) showed low moisture retention on mounds and that infiltration increased with distance from the mound base. They further noted that mound permeability was low which could be attributed to the relatively high soil bulk density on mounds compared to matrix soils. However, other studies carried out in arid and semi-arid savannas in southern and western Africa (e.g., Konaté et al., 1999; Turner et al., 2006) reported that *Macrotermes* colonies provided a source of moisture on mounds by drawing water towards their nests. Termites consume and store water in their abdomen which they carried back to their nest sites and mixed with soil to create mortar for mound building. This water gathering behaviour results in larger quantities of water being storied in soil particles, thereby increasing plant available water on mounds, which can significantly impact the growth and survival of trees and grasses. High plant available water on mounds would allow rapid seed germination, seedling establishment near parent trees, and increase leaf retention by trees particularly during the dry season.

Soil fertility

Mound-building activities by termites involves the redistribution of soil particles which often influences mineral composition and fluxes of nutrients, resulting in patches of high-quality resources in nutrient poor African savannas (Seymour et al., 2014; Muvengwi et al., 2016; Muvengwi et al., 2017). Termites translocate large amounts of soil from deeper soil profile to the surface, which can also have a significant role in soil nutrient transfer. For example, Ndiaye et al. (2004) reported that *Macrotermes subhyalanus* and *Odontotermes nilensis* bring to the surface 0.70 – 0.95 tons per ha of soil sheeting which contained higher organic carbon and mineral nitrogen than matrix soil annually in Senegal. Hewitt et al. (1990) reported that *Hodotermes mossabicus* translocate up to 0.70 tons per hectare of soil to the surface containing up to five times more nitrogen than matrix soil annually in a South African savanna. In a meta-analysis of African studies, Sileshi et al. (2010) found that termite mounds were richer in carbon (16%), total N (42%), P (306%), Mg (154%), and were 75% more enriched in clay than the surrounding matrix soil. Moreover, Seymour et al. (2016) found that the amount of P, Zn, and Se was 58 times higher in large mounds relative to inter-mounds soil matrix, whereas soil pH also increased by 8% on termite mounds. Similarly, Sall et al. (2002) reported that C and N content on *Cubitermes niokoensis* mounds at Sara Yorobana in Senegal were five and up to 15 times higher, respectively, than that in non-mound soil. The high content of exchangeable bases and high pH on mounds may be the result of the ability of termites to transport cation-rich clay minerals from deep soil layers to the subsurface during the process of mound building, thereby improving soil fertility which may in turn favour rapid seed germination and increasing woody seedling growth rate. Therefore, resulting in high concentration of woody plants on termite mounds.

Termite mounds interaction with fire and herbivory

Termite-fire interactions can also influence vegetation assemblages. High fire frequency can almost totally restrict tree establishment in grassy ecosystems; however, termite mounds can act as a buffer against severe tree burn in such systems (Moe et al., 2009; Joseph et al., 2013b). For example, Erpenbach et al. (2013) reported that termite mounds through the provision of elevated topography lowered the impact of fire in humid protected areas in Burkina Faso and Benin, which resulted in a high abundance of evergreen woody species that are commonly sensitive to burning, such as *Capparis sepiaria*, *Wissadule amplissima*, and *Combretum aculeatum*. The fuel load, which is commonly grass biomass and dead plant litter, generally determines the intensity of wildfire. However, termite foraging can generate spatial patchiness in the fuel load since termites consume large quantities of grass and plant litter (Mitchell, 2002). For example, Buxton (1981) reported that termites were responsible for 90% of dead wood decomposition in Kenya's Tsavo National Park. Similarly, Sileshi et al. (2010) indicated that termites removed about 60% of dead trees, 3% of tree leaf litter, and 60% of grass litter in West African savannas annually. Concentration of trees on termite mounds have also been noted to significantly suppress grass cover (Sileshi et al., 2010), as result modifying fire intensity on termite mounds.

Termite mounds provide a wide range of benefits for animals through harbouring highly nutritious plants, which makes them preferred foraging patches for herbivores, and the provision of nesting sites for birds (Yamashina and Hara, 2019 Holdo and McDowell, 2004). For instance, Muvengwi et al. (2019) reported that grazing intensity was high on large mounds compared to surrounding areas in granite-derived nutrient-poor savanna soils in the Gonarezhou National Park in Zimbabwe. Such increased grazing intensity on mounds may in turn significantly reduce the competitive ability of grasses against woody plants protected from fire (Erpenbach et al., 2013), and tolerance to herbivory and may ultimately result in woody plants dominating the patches, which can be enhanced by endozoochory by mammals. Large herbivore exclusion resulted in increased diversity of birds and their use of termite mounds, which in turn strengthens their functional role of dispersing seeds and regulating herbivorous insect populations by feeding on them (Moe et al., 2017). However, the contribution of animal seed dispersal on the more distinct and diverse woody plant community found on termite mounds have not been extensively defined, with few studies that reported high community weighted mean (CWM) of woody species exhibiting traits related to mammal and bird dispersal (Yamashina and Hara, 2018).

Woody plant assemblages on termite mounds

Woody plant diversity

While fire and herbivory are widely reported to maintain and amplify savanna patterns and processes (Van Langevelde et al., 2019; Sankaran et al., 2005), mound-building termites play a vital role in generating savanna vegetation patterns and dynamics at a landscape scale (Erpenbach et al, 2013). Termite mounds in African savannas and grasslands have also been noted to harbour a diverse community of woody species (Joseph et al., 2015; Muvengwi and Witkowsk, 2020) and have higher woody species richness compared to surrounding savanna matrix (Erpenbach et al., 2014). For example, Eldridge et al. (2001) reported that only 2.7% of land covered by termite mounds supported up to 8.2% of the shrubs, resulting in a diversity of woody plants that was five times higher than that of the surrounding matrix in northern Burkina Faso. Similarly, Yamashina and Hara (2019) found that termite mounds exhibited species richness, alpha diversity, and species evenness of woody plants that was approximately 35%, 25%, and 20%, respectively, higher than that of surrounding areas between the Kwando and Zambezi drainage basins in Namibia. This suggests that termite mounds may act as hotspots of plant diversity and safe sites for regeneration of woody plants in savannas and grasslands (Davies et al., 2016).

Woody plant density

Termite mounds are also associated with higher densities of woody plants compared to the inter-mound matrix (Moe et al., 2009). For example, Yamashina and Hara (2019) reported that the density of woody plants on mounds was 48% higher than the surrounding areas in the Zambezi region in Namibia. On the contrary, Davies et al. (2016) reported that the overall tree density increased with the distance from the mounds in the Kruger National Park in South Africa. However, in the same study, some woody species such as *Combretum imberbe* and *Phalaenopsis violacea* were reported to occur in high densities on the mounds (Davies et al., 2016), suggesting that termite mounds may favour some species over others. Therefore, more research is required to determine the role of termite mounds on woody plant functional traits that can be supported on mounds.

Mechanisms driving woody plants nucleation on termite mounds

Several mechanisms have been proposed to explain the nucleation of woody plants on termite mounds. The literature highlights how termite activity alters the abiotic environment, particularly through their foraging and mound-building activities, which concentrate organic matter and nutrients (Muvengwi et al., 2016, 2017; Wildermuth et al., 2021), leading to termite mounds acting as nutrient hotspots that promote woody plant establishment (Seymour et al., 2014; Muvengwi et al., 2017). It is important to integrate this with biotic mechanisms that underlie woody plant recruitment. Nucleation of woody plants on termite mounds involves successful seed dispersal and seedling establishment. Termite mounds may enhance seed deposition by serving as perching sites for birds and other animals, thereby increasing the likelihood of seed dispersal onto mounds (Dean et al., 1999; Joseph et al., 2013a).

The relatively bare or grass-suppressed surfaces of mounds further reduce competition with grasses, increasing the chances of woody seedling emergence and survival. Moreover, the stable and nutrient-enriched microsites on mounds provide favourable conditions for the germination and early growth of woody seedlings, which might otherwise be outcompeted in the matrix. Termite mounds also act as refugia from disturbance (Joseph et al., 2013a), as they are less likely to burn or are burned at lower intensity due to reduced grass fuel loads, thereby protecting fire-sensitive woody recruits from mortality (Joseph et al., 2013b). This creates a safe site for establishment in fire-prone savannas. Moreover, as bush clumps mature, competitive interactions among woody plants may further shape species composition, promoting those that are better adapted to the mound microenvironment or that benefit from early arrival and rapid growth.

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Chapter 3

Long term dynamics of bush clump development in the Uitkomst Conservation Area, KwaZulu-Natal

Abstract

This study investigated the growth rate and development pattern of bush clumps in Uitkomst using historical aerial photographs. This study presented evidence that bush clumps initiated on termite mounds, and there was clear evidence of the identities of the species that initiated the bush clumps. Overall, bush clump area significantly increased from 1964 to 2024, indicating that bush clumps were expanding in size from when they first appeared which is an indication of woody plant encroachment. The growth rate of bush clumps was higher in the grassland area between 1964 and 2003. However, post 2003, the expansion rate of bush clumps was rapid in the former cropland area. This occurred after the area was abandoned from agricultural activities. The rapid growth rate of bush clumps in the former cropland area may be due to the fact that these bush clumps are colonized by alien invasive shrubs which are fast growing.

Key words: Abandoned cropland, bush clumps, grassland, historical data

Introduction

Bush clumps are a common feature of many grassy landscapes in southern Africa (Jamison-Daniels et al., 2021; Adie et al., 2023; Nell et al., 2024). The origin and development patterns of bush clumps have recently gained noticeable research interest as a form of woody plant encroachment in grassy ecosystems. Woody plant encroachment is an increase in cover and density of woody plants in grass-dominated or tree-grass co-dominated landscapes (Ward, 2005). Woody plant encroachment is widely reported to be driven by various factors including changes in rainfall patterns, reduced seasonal variability in precipitation, fire suppression, and increased grazing intensity (Stevens et al., 2016; Skowno et al., 2017; Stevens et al., 2017; Venter et al., 2018).

Bush clumps commonly initiated on a fire refugia such as termite mounds, rocky outcrops, or under large savanna trees (Gower et al., 1992; Bloech, 2008; Carlucci et al., 2011; Joseph et al., 2013; Abreu et al., 2021). This process often begins after the establishment of a founder individual tree which then later facilitate the entry of other woody plant species over time (O'Conner and Chamane, 2012; Jamison-Daniels et al., 2021), subsequently leading to bush clumps increasing in size over time. This study aims to investigate the growth rates and pattern of termite mound facilitated bush clumps expansion using data derived from long term historical aerial photographs in Uitkomst Conservation Area in KwaZulu-Natal, South Africa.

Materials and Methods

Study Area

The study was conducted in Uitkomst Conservation Area, within KwaZulu-Natal, South Africa. Uitkomst (29°46'39"S, 30°37'04"E) covers 516 ha situated near the Cato Ridge and Hammardale areas of the eThekwini Metropolitan Municipality, southeast of Pietermaritzburg.

Historical imagery data

The aerial photographs for 1964 and 1983 were acquired from the Chief Directorate of National Geo-spatial Information (NGI) (www.ngi.gov.za) of South Africa. The 2003 true colour orthophoto was acquired from eThekwini Municipality, while the 2024 true colour orthophoto was downloaded from the current map of the study area on Google Earth. All images were not georeferenced, as a result, the 2024 image was georeferenced using the Quick Map Service, OMS standard plugin in Quantum Geographic Information System (QGIS). Aerial photographs for 2003, 1983, and 1964 were than georeferenced to the 2024 image. The 2024 image had the finest resolution, as a result, all other images were resampled to match the spatial resolution of the 2024 image using the nearest neighbour method, and all layers were aligned to the 2024 image.

Bush clumps sampling

Well established bush clumps (n = 20) were randomly selected from the 2024 image and their area was measured from 2024 back to 1964 in QGIS. Bush clumps that disappeared on the earlier images from 2024 were recorded as having an area of zero throughout the remaining time period until 1964. As a result of differences in land use types within the study area, bush clumps were sampled separately for each land use type (undisturbed grassland and former cropland). As a result, 11 bush clumps were sample in an undisturbed grassland, while nine bush clumps were sampled in an abandoned cropland area. The growth rate of bush clumps was computed as the absolute growth rate (AGR) using the following equation:

$$AGR = \frac{A2 - A1}{t2 - t1}$$

where *t1* is the initial time when bush clump area *A1* was recorded, and *A2* is the bush clump area at *t2*.

Statistical Analysis

A Gamma regression model with a log link function was used to analyse bush clump expansion patterns over time across different land-use types. A Gamma regression model was used due to its ability to handle non-negative and positively skewed data, which is normally the case for data such as bush clump area over time (Figure 3.1). Moreover, a lognormal regression model was used to assess how time and land-use type affected the growth rates of bush in Uitkomst,. All statistical analysis were performed in R statistical computing and graphing program, version 4.4.0 (R Core Team, 2024).

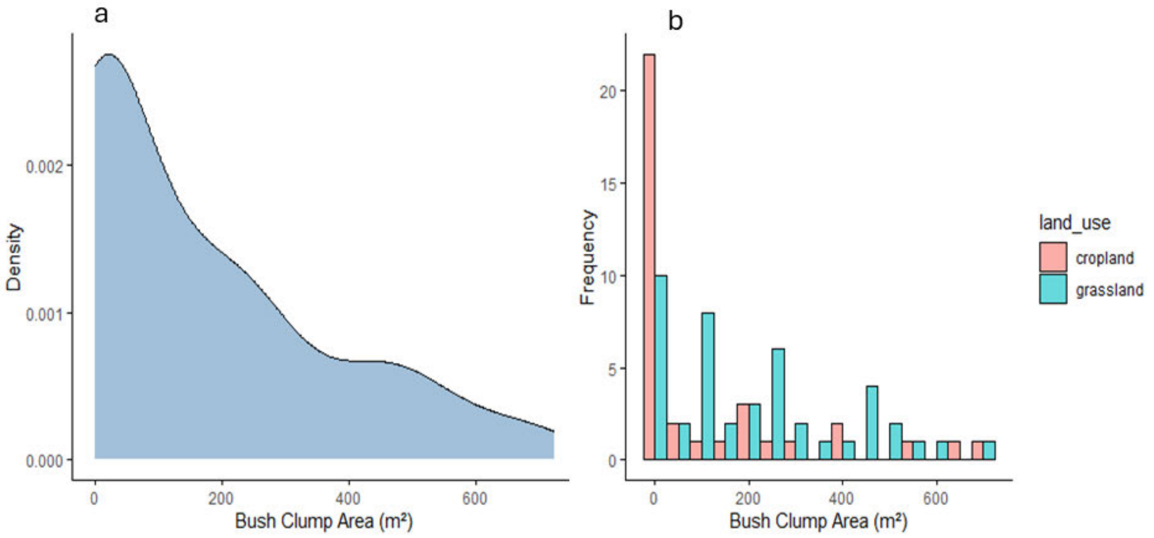

Figure 3.1: Right-skewed bush clump size distribution in Uitkomst between 1964 and 2024 across both the grassland area and the former cropland area.

Results and discussion

Bush clumps in Uitkomst always had a termite mound origin, similar to those reported in KwaZulu-Natal (Gower et al., 1992) and other areas (Blosch, 2008; Moe et al., 2009). Well developed and developing bush clumps reported in this study occurred on termite mounds. Studies (e.g., Gower et al., 1992; Blosch, 2008) highlighted that bush clumps initiated on abandoned mounds. In this study, however, there was no evidence to suggest that the mounds were abandoned. One of the explanations behind the initiation and development of bush clump on abandoned mounds could be that in these mounds damage is not repaired by the termites, therefore, they provide a good seed bank (Blösch, 2008). Another reason why bush clumps initiate may lie on the return period of fire. However, this could not be tested due to the absence of data on fire practice within the area. Furthermore, the absence of browsing herbivores in the area may also have contributed to the successful establishment of woody seedlings in the area. As a result, they grow taller, escape the fire trap if the return period of fire is long enough. Termite mounds can be noted in the year 1964 image as patches that are slightly different from the surrounding landscape such that they create a somewhat rough surface in the landscape (Figure 3.2). As time progressed towards year 2024, a noticeable proportion of these distinct patches were covered by woody vegetation.

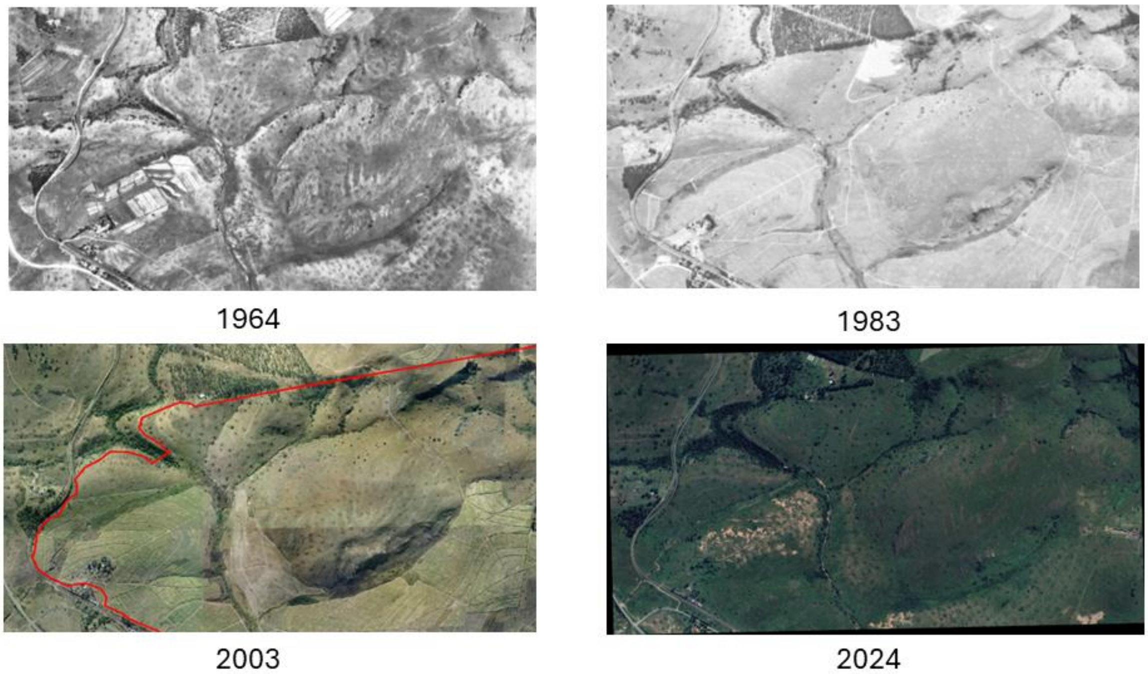

Figure 3.2: A time series of bush clump initiation and development between 1964 and 2024 in Uitkomst. The time series show how the land area in Uitkomst changes in 60 years. In 1964, a few small bush clumps were observed in the grassland area, while they were in the cropland area and in areas that turned into croplands in 1983 to 2003. Between 1983 to 2003 bush clumps also appeared more on the grassland area. However, after the abandonment of the cropland areas after 2003, the 2024 image show a substantial increase in bush clump occurrence in these former cropland areas

In 1964, bush clumps in Uitkomst were generally in the initial bush clump development stage (small) and some of the bush clumps present in year 2024 were absent in 1964 in both the grassland area and the former cropland area (Figure 3.2). The mean bush clump area during this time ranged between 21.1 m^2 and 102 m^2 across both land-use types (Table 3.1). The mean bush clump area in 1983 was 12.9 m^2 in the former cropland area and 169 m^2 in the grassland area (Table 3.1, Figure 3.3). This indicates a decrease in the average bush clump area in the former cropland area from year 1964 to 1983. This time period corresponds with increase in cropland area in Uitkomst, and this area was being actively utilized for sugarcane farming. As a result, consistent disturbance from farming activities may have suppressed woody vegetation in this area, which was not the case in the grassland area that was not used for agricultural activities, which could explain why bush clump area in the grassland kept on increasing throughout the years.

Table 3.4: The mean (±SD) termite mound bush clump area (m^2) in grassland areas and former cropland areas between the year 1964 and year 2024 in Uitkomst.

	Grassland	**Former cropland**
Year	**Mean ± SD**	**Mean ± SD**
1964	102 ± 163	21.1 ± 63.2
1983	169 ± 170	12.9 ± 25.2
2003	225 ± 188	30.3 ± 60.8
2024	356 ± 187	398 ± 187

A Gamma regression model with a log function revealed that bush clump area increased significantly between 1964 and 2024 ($\beta = 2.21$, $t = 3.01$, $P = 0.006$, Figure 3.3). This suggests that overall bush clumps increased regardless of where they occurred (grassland vs former cropland) which is an indication of woody plant encroachment. Moreover, bush clumps in close proximity to each other can merge to form small forest or woodland patches as they expand in size over time. For example, the absence of disturbances such as frequent fire and browsing has been shown to promote bush clump expansion and their eventual coalescence into closed-canopy woody patches or secondary forests (Wigley et al., 2010; O'Connor et al., 2014; Stevens et al., 2017). At Uitkomst, bush clumps that initiated before 1964 were observed to have undergone substantial expansion and, based on an average post-2003 growth rate of ~17.5 m^2 per year, many clumps in the former cropland area may merge with neighboring clumps within the next 30–50 years, while it may take longer for bush clumps in the grassland area (50 – 100 years). Generally, bush clump area was significantly higher in grassland areas compared to former cropland areas ($\beta = 1.79$, $t = 2.73$, $P = 0.01$). The interaction effect between land use type (grassland and former cropland) and time (years) was significant in 2024, indicating that bush clump expansion in grasslands did not continue at the same rate as in croplands ($\beta = -2.04$, $t = 2.55$, $P = 0.0179$). For example, over a 60-year period, the mean bush clump area in grasslands areas increased from 102 m^2 in 1964 to 356 m^2 in 2024 at an overall rate of 4.7 m^2 $year^{-1}$ (Figure 3.1). In former cropland area, bush clump growth was slow between 1964 and 2003 (0.15 m^2 $year^{-1}$), until a sharp increase from 2003 to 2024 (17.51 m^2 $year^{-1}$, Table 3.1, Figure 3.3).

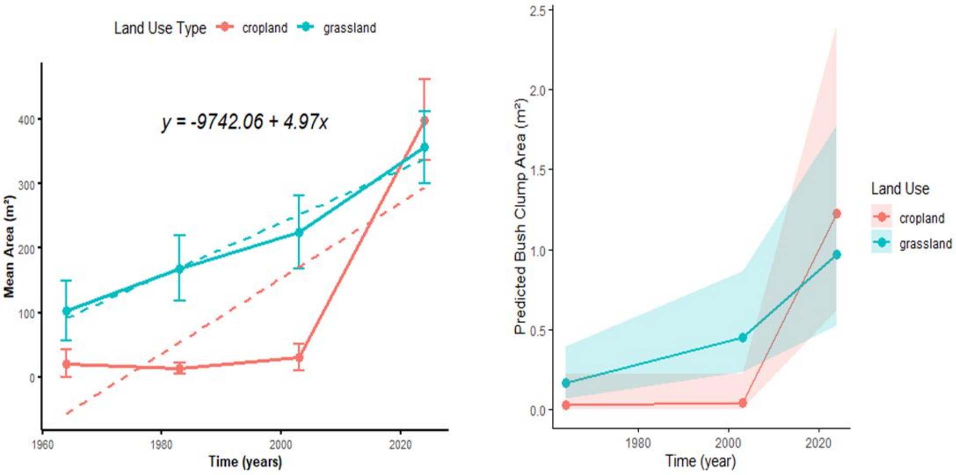

Figure 3.3: Bush clump development pattern in grassland area and former cropland area in Uitkomst.

A lognormal regression model revealed a significant increase in the absolute growth rate (AGR) of bush clumps in 2024 ($\beta = 376.21$, $P < 0.001$), indicating that the expansion of bush clumps increased in the last time period. The AGR of bush was significantly higher in grassland area compared to former cropland area between 1964 and 2003 ($\beta = 74.76$, $P = 0.041$). However, the negative significant interaction effect between land-use (grassland vs former cropland) and 2024 suggests that recent bush clump growth rates were higher in former the cropland area than in the grassland area ($\beta = -311.91$, $P < 0.001$). In 2003 towards 2024, the cropland area was abandoned. Abandoned cropland areas are commonly cited to be vulnerable to woody plant encroachment. For example, Blair et al. (2018) reported that woody vegetation increased up to 0.16% per year in abandoned fields in former homeland areas in South Africa. Furthermore, the increase in woody vegetation cover in abandoned crop fields in the Eastern Cape province was facilitated by *Acacia mearnsii* invasion (Ruwanza, 2017; Scorer et al., 2019). Similar patterns of old field invasion by alien and native species have been reported in many parts of Africa and beyond (e.g., Zimmerman et al., 1993; Tognetti et al., 2010; Kuebbing et al., 2014). Similarly, bush clumps in the abandoned cropland area in Uitkomst were dominated by the invasive shrub *Lantana camara*, and other invasive plants including *Jacaranda mimosifolia, Melia azedarach,* and *Solanum mauritianum* (V. Ngcobo Per. Obs.).

Alien invasive plants are generally fast growing; hence they reproduce faster (Ruwanza, 2020), which may explain the rapid growth rate of bush clumps in the former cropland area after agricultural activities stopped after 2003. This pattern raises concerns about the long-term persistence of grassy ecosystems, particularly where bush clumps are dominated by invasive species. To mitigate the risk of complete woody encroachment, including by alien species, proactive management interventions such as prescribed burning, mechanical clearing of invasive plants, and the restoration of herbivory regimes are recommended (Trollope et al., 2002; Shackleton et al., 2017).

Conclusions

The aim of this study was to assess bush clump development patterns and growth rates over a 60-year period in Uitkomst across two different land-use types. Observation from the historical aerial images of the area provided evidence that bush clumps in Uitkomst initiated and developed on termite mounds. Evidence of the species responsible for initiating the bush was lacking from the imagery data. The area covered by bush clumps increased significantly between 1964 and 2024 in both the grassland area and the former cropland area, which is an indication of a trend towards woody plant encroachment. The growth rates of bush clumps were high in the grassland area between 1964 and 2003. However, after 2003 high growth rates of bush clumps were noticeable in the abandoned cropland area. Moreover, bush clumps in the abandoned cropland area were dominated by fast growing alien invasive shrubs, which explains the rapid growth rates post 2003 where agricultural activities were stopped in the area.

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CHAPTER 4

Termite mounds increase the spatial heterogeneity of microhabitats for woody vegetation establishment

Abstract

Spatial heterogeneity of microhabitats and resource availability is a key determinant of species richness, abundance, and the coexistence of plant assemblages in grassy ecosystems. Termites, through their mound-building and foraging activities, enhance soil fertility and moisture retention, thereby creating resource-rich patches that promote the establishment and growth of woody plants. These localized effects contribute significantly to small-scale heterogeneity and may facilitate woody plant proliferation at the landscape level by enhancing regeneration. This study investigated how termite mounds influence woody species composition, diversity, and community structure, as well as the underlying mechanisms driving variation between termite mound vegetation and the surrounding matrix. Woody vegetation was sampled on 62 termite mounds and 71 adjacent matrix plots in Cumberland Nature Reserve and Uitkomst Conservation Area in KwaZulu-Natal, South Africa. The results revealed that the species composition of woody plants was different between termite mounds and matrix plots, with clear evidence that termite mounds harboured unique woody vegetation assemblages characterized by high species richness, diversity, and density compared to the matrix assemblages. Out of 55 woody species reported in this study, ~ 70% of were restricted to termite mounds, and *Lantana camara*, *Cussonia spicata*, and *Searsia pyroides* were significant indicators of termite mound assemblages. Woody stem density on termite mounds was approximately two times higher than in the matrix, whereas the species richness and density of saplings were both approximately two times higher on termite mounds. Density of mature trees was approximately four times greater on termite mounds than in the matrix. The community-weighted means of bird-dispersed species producing drupe-type fruits were higher on termite, whereas pod producing, and mammals dispersed woody species were common in the matrix.

Keyword: African savanna, animal seed dispersal, functional traits, perch, termite mounds, woody plant encroachment

Introduction

Within grassy landscapes, resource heterogeneity has been reported to be a primary force driving plant species richness, abundance, and the overall vegetation assemblages (du Toit et al., 2003; Sileshi et al., 2010). Typically, the interaction of rainfall and topography often leads to varying soil characteristics at different positions along hillslopes. For example, rainfall run-off moves clay particles downslope, resulting in sandy, nutrient-poor soils on the slope summit to the backslope position while clay and nutrient rich soils consistently accumulate in lowland areas (Scholes and Walker, 1993; Khomo et al., 2011). This creates diverse plant species assemblages along hillslope positions, particularly with dense woody vegetation cover concentrated in lowland habitats (Venter et al., 2018; Baldeck et al., 2014). Moreover, patch dynamics can influence plant community assemblage, composition, and structure (Joseph et al., 2013). For example, when nutrient rich patches develop under larger savanna trees which is facilitated by increased animal activities and altered nutrient cycling, leads to fertile islands with plant assemblages that differs from the matrix (Abreu et al., 2021).

In African grassy ecosystems, termite mounds mostly constructed by the genus *Macrotermes* are common on well-drained soils on hill crest slope positions. In these localities, termite activities including foraging and mound-building, redistribute soil particles, moisture, and nutrients within the soil column (Levick et al., 2010; Sileshi et al., 2010; Davies et al., 2014). This results in termite mound soils having a higher concentration of clay minerals and plant available soil nutrients, along with improved water-holding capacity compared to surrounding soils (Dangerfield et al., 1998; Seymour et al., 2014). Subsequently, this creates randomly distributed patches of bare soil with conditions comparable to those in lowland areas within the landscape, and these patches are commonly susceptible to colonization by various species of woody plants. Moreover, vegetation on termite mounds is generally less exposed to fire (Sileshi et al., 2010), therefore, the mounds support fire sensitive plants typically characterized by fruit-bearing and evergreen species (Joseph et al., 2011), Furthermore, vegetation on mounds often originate from nutrient rich habitats such as riparian ecosystems, forest margins, or lowland habitats (Joseph et al., 2013).

Early vegetation studies across several regions of tropical Africa, supported by recent surveys (e.g., Sileshi et al., 2010; Joseph et al., 2012; Muvengwi et al., 2017) consistently reported the unique vegetation assemblage found on termite mounds compared to the matrix. For example, in the Hluhluwe-iMfolozi Park in South Africa, Van der Plas et al. (2012) found that of the 67 woody plant species identified on mounds and matrix plots, 23 species were only found on termite mounds. Similarly, in the Seke communal areas of Zimbabwe and the Plain of Lubumbashi in the Democratic Republic of Congo, Muvengwi et al. (2016) and Cuma Mushagalusa et al. (2020) recorded 46 and 16 woody species that occurred strictly on termite mounds out of the 54 and 71 species, respectively, recorded for the entire study area. However, the mechanisms behind the unique plant cover on termite mounds remain largely unclear. A reciprocal transplant experiment by Cuma Mushagalusa et al. (2018) provided evidence of local adaptation among termite mound species. Their findings showed that seedlings of termite mound species transplanted to the surrounding woodland soil had higher mortality rates during the dry season, indicating greater susceptibility to water stress (Cuma Mushagalusa et al., 2018).

Vegetation composition on termite mounds exhibits greater variation than that observed in matrix plots. For example, as observed in Pendjari National Park, northern Benin, woody vegetation composition on termite mounds exhibited greater variation than that observed in matrix plots for all savanna types studied (Erpenbach et al., 2017). Similarly, studies in Lake Mburu National Park in the southwest of Uganda (Moe et al., 2009), Chizarira National Park in north-western Zimbabwe (Joseph et al., 2013), and Gonarezhou National Park in south-eastern Zimbabwe (Muvengwi et al., 2017) noted higher woody plant species richness and diversity on mounds, potentially explaining the increased variation in species composition on mounds. However, some studies (e.g., Erpenbach et al., 2013) suggest that species richness is not always high on mound vegetation compared to savanna vegetation. The low species richness observed on mounds might be due to competitive exclusion, leading to dominance by a few species (Muvengwi et al., 2022). As a result, Erpenbach et al. (2017) argued that the high within-group variation in vegetation composition observed for both savanna plots and mounds may be enhancing the contrast in variation between the mound and the savanna matrix.

Research indicates that while termite mounds only constitute ~5% of the savanna landscape, high tree densities associated with them significantly enhance the small-scale regeneration of woody plants, thus the overall woody vegetation cover (Moe et al., 2009). For example, Loveridge and Moe (2004) and Moe et al. (2009) reported high woody plant densities on *Macrotermes* mound communities compared to surrounding savanna matrix in Iwaba Wildlife Estate, Zimbabwe, and Lake Mburu National Park, southwest of Uganda, respectively. In Hluhluwe-iMfolozi Park, South Africa, Van der Plas et al. (2012) found that termite mounds had more than four times more trees with a canopy height above 2 m compared to control matrix plots. Seymour et al. (2014) reported high densities of *Maerua prittwitzii, Capparis* *tomentosa, Euclea divinorum, Diospyros quiloensis, Manilkara mochisia* and *Combretum mossambicense* trees occurring in termite mounds compared to the matrix savanna land in Miombo woodland in Chizarira National Park. Similarly, Yamashina and Hara (2019) reported that the density of woody plants on mounds was 48% higher than the surrounding areas in the Zambezi Region, Namibia.

Previous studies on the impacts of termite mounds on savanna vegetation have only highlighted alterations in vegetation structure, nutrient composition, and overall biodiversity, including plant species richness (Moe et al., 2009; Sileshi et al., 2010; Joseph et al., 2013; Muvengwi et al., 2017). However, the overarching role of termite mounds in the development of bush clumps and the implications for vegetation transition to woody plants in grassy ecosystems are still unclear. Therefore, the aims of this study were to assess the influence of termite mounds on woody species establishment, examine the role of bird-mediated seed dispersal, and evaluate the contribution of termite mounds to woody plant encroachment to understand the feedback mechanisms promoting woody plant encroachment facilitated by termite mounds. The objectives of the study were to (1) investigate the effects of termite mounds on woody species richness, diversity, community composition, and structure; (2) explore the contribution of birds to seed dispersal on termite mounds, particularly the dispersal of fleshy-fruited woody species, and how this influences the formation of bush clumps; and (3) determine the role of termite mounds as focal points for bush clump formation and their contribution to woody plant encroachment, leading to the expansion of woody vegetation in grassland areas.

Materials and Methods

Sampling Design

Data collection was carried out between November 2022 – August 2023. This study focused on vegetated termite mounds and nearby matrix vegetation to quantify and understand the effects of termite mound on the vegetation composition and structure, and their role as a source of woody plant heterogeneity in grassy ecosystems.

Termite mounds with well-developed woody vegetation at least 10 m apart were selected randomly. Subsequently, a 10 m × 10 m plot centred on each mound was established. In order to compare an equal area on and off termite mounds, a control plot (10 m ×10 m) was established along a randomly selected bearing radiating out from the perimeter of each mound, but at least 10 m from the termitaria edge to minimize the influence of termite activities (Levick et al., 2010; Okullo and Moe, 2012).

Vegetation survey

Sixty-two vegetated termite mounds (Cumberland Nature Reserve, n = 16, and Uitkomst Conservation Area, n = 45) were sampled. Plots were used to standardise the vegetation survey area within vegetated termite mounds, and between termite mounds and matrix plots, also to capture the immediate effect of the mound. Seventy-one matrix plots were randomly selected at least 10 m from the mound in a random direction in the savannas at both sites.

In each plot, woody plant structural parameters—including stem circumference (cm) at rooting point and tree height perpendicular to the ground surface—were measured using a 2-meter ranging rod. Tree canopy cover *c* was computed using the following equation:

$$c = \pi\left(\frac{d_1}{2}\right)\left(\frac{d_2}{2}\right)$$

where d_1 is the largest diameter of the tree crown, and d_2 is the perpendicular short diameter measured using a tape measure. Woody plant stems for each woody plant surveyed were systematically counted and stem diameter were computed using:

$$D\ (stem) = \frac{C(stem)}{\pi}$$

where *C(stem)* is the woody stem circumference measured at various heights above the ground depending on how tall the surveyed plant was. Additionally, stem diameters of woody plants with multiple stems were computed as the sum *D(stem)* computed for each individual stem of the same plant using the following equation:

$$Dtotal(stem) = \big(D1(stem)\big) + \big(D2(stem)\big) \ldots + (Dn(stem))$$

The basal area (*BA*) of an individual woody plant was computed based on their *C(stem)* using the following equation:

$$BA = \frac{C(stem)^2}{4\pi}$$

the basal area of woody plants with multiple stems was computed as the sum basal area of each woody stem. Woody plants were categorised into two size class groups as mature plants (≥ 1.5 m) and saplings (< 1.5 m).

All woody plants > 1.5 m inside the plots were identified to species level and their abundance on termite mounds and on matrix plots were recorded, while woody plants < 1.5m were sampled on 5 m × 5 m subplots placed on the corners of the main plot. Species identification was done using field guide of woody plants of the region (Pooley, 1993), which was supplemented by consulting iNaturalist (https://www.inaturalist.org/) and PlantNet (https://identify.plantnet.org/).

Plant functional traits selection and coding

Plant traits such as the type of fruit a species produces can give insights into the species dispersal modes, which may indicate the species propagation potential (Joseph et al., 2014). This can also allow estimates of distance seeds can be dispersed and the number of seeds that are likely to be dispersed (de Jager et al., 2018; Gelmi-Candusso et al., 2019), whereas the nutrient uptake strategy of a species may reflect its adaptation to different levels of nutrient availability (Joseph et al., 2014). To assign functional traits related to seed dispersal and nutrient uptake strategies for woody species recorded on termite mounds and matrix sites, relevant literature and a range of regional and international tree databases were consulted (Appendix 3.1). Traits reflecting seed dispersal included dispersal mode (bird or mammal) and fruit type (drupe or pod). A species-by-trait matrix was constructed, with traits coded using binary values: a value of one was assigned if a species exhibited a given trait, and zero if the trait was absent. For nutrient uptake strategy, species were categorized based on the presence or absence of nitrogen-fixing bacteria in their roots. Each functional trait assigned to a species was validated using information from at least two independent sources (Appendix 3.1).

Statistical analysis

All statistical analysis was performed in R statistical computing and graphing program, version 4.4.0 (R Core Team, 2024), using packages; *vegan* (Oksanen et al., 2013), *ggplot2,* and *dplyr,* (R Core Team, 2024). The adequacy of sampling for woody plants on termite mounds and matrix plots was evaluated using sample-based rarefaction curves using the *specaccum* function on the *vegan* package in R. Thereafter, the data were tested for normality, and where appropriate the data were transformed using the square root or log transformation before conducting further analysis.

To analyse the species composition of woody plant on termite mounds and matrix plots, a Bray-Curtis dissimilarity matrix was constructed based on a data matrix of woody species abundance, which was square root-transformed to weight rare and common species more equally (Clarke and Warwick, 2001). Differences in the species composition of woody plants between termite mounds and matrix, while accounting for differences in site location were then assessed with a permutational multivariate analysis of variances (PERMANOVA) based on a Bray-Curtis dissimilarity matrix of the species abundance data. PERMANOVA is a non-parametric test of significant differences between groups that operates on a distance matrix. In this case, the groups were habitat (termitaria and matrix), location (Cumberland and Uitkosmt), and the interaction between habitat and location. PERMANOVA compares the centroids of the groups in multivariate space and tests the null hypothesis that there are no differences in the relative magnitude of a set of variables among objects from different treatments or groups (Anderson and Walsh, 2013). Additionally, P-values are calculated using permutation tests.

To assess the effects of termite mounds on woody species richness, Shannon-Wiener diversity index, species evenness, woody plant density, woody stem density, and woody plants height, while accounting for differences in the site location (Cumberland and Uikomst). A series of two-way analysis of variance (ANOVA) tests with an analysis of covariance (ANCOVA) design were conducted. These tests were conducted to determine whether woody plant diversity, density, and growth significantly differed between termite mounds and matrix habitats. Where data did not meet the assumptions of a two-way ANOVA test, an Aligned Rank Transform ANOVA test was used. ART ANOVA is a non-parametric alternative of a two-way ANOVA which also allow the inclusion of factorial designs. Model assumptions were tested using Leven's test for homogeneity of variances and Shapiro-Wilk test for normality. Additionally, the analysis for density and species richness were undertaken separately for saplings and mature trees.

Height distributions of woody plants on termite mounds and matrix plots were compared using a two-sample Kolmogorov-Smirnov test. Furthermore, paired-sample *t*-tests were used to compare the community-weighted means of woody plants trait related to dispersal mechanism, fruit-type, nutrient uptake strategy between termite mounds and matrix plots. Indicator species of termite mounds and matrix plots were identified using the indicator value method. Species with significant indicator values ≥ 60% were classified as indicator species of termite mounds or matrix.

Results

Species accumulation curves indicated that sampling was adequate off the termite mounds (matrix), but species richness of woody plants continued to increase on the termite mounds (Figure 4.1). Woody species were observed on all 62 termite mounds in Cumberland (n = 16) and Uitkomst (n = 46), with each mound vegetation system supporting more than one species. In contrast, woody species were found in 71 matrix plots, and only ~ 59% of these plots contained more than one species. A total of 2432 individual woody plants were identified across termite mounds and matrix plots. On termite mounds, 1636 woody individuals represented by 54 species and 31 families were identified, whereas 796 woody individuals represented by 17 woody species distributed across 15 families were recorded in the matrix plots (Appendix 4.1).

Thirty-nine species were found exclusively on the termite mounds including *Ziziphus mucronata, Gymnosporia buxifolia, Grewia accidentalis, Celtis africana, Indigofera natalensis*, whereas only *Morus indica* was unique to the matrix plots, and 15 other woody species were found in both mound and matrix plots (Figure 4.2). *Lantana camara,* and *Lippia javanica* shrubs were abundant in both termite mound and matrix plots, whereas *Rubus ulmifolium, Cussonia spicata*, and *Searsia pyroides* were more abundant on termite mound plots (Figure 4.2). *Vachellia sieberiana, Aloe ferox*, and the invasive *Acacia mearnsii* and *Solanum mauritianum* were more prevalent in matrix plots.

Fourteen woody species were identified as indicator species for termite mounds and matrix habitats. However, only species with indicator values greater than 60% were classified as significant indicator species. As a result, the significant indicator species for termite mound vegetation were, including *L. camara* (indicator value = 76.2%), *C. spicata* (indicator value = 75.2%), and *S. pyroides* (indicator value = 64.8%). There were no significant indicator species for matrix vegetation. Notably, all the termite mound significant indicator species produced fleshy fruits and were bird-dispersed (Appendix 4.1). Furthermore, one of three of termite mound significant indicator species was an alien invasive shrub.

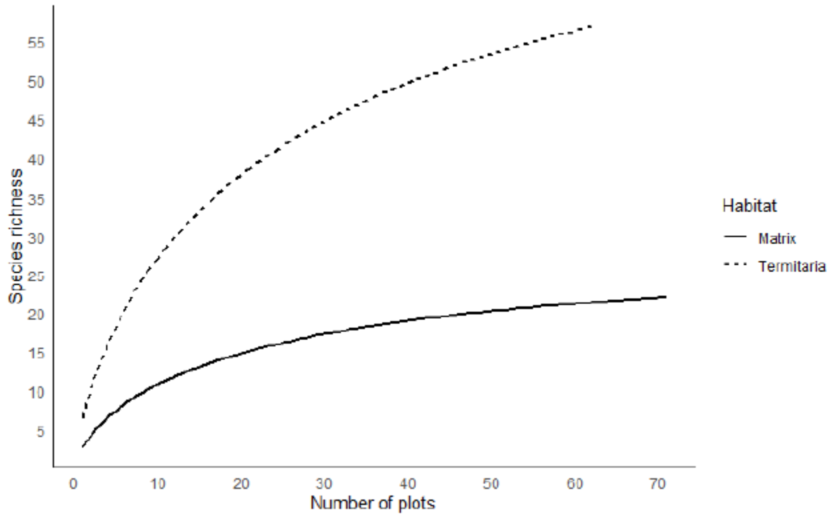

Figure 4.1: Sample based species accumulation curve for woody plants on termite mounds and matrix plots in Cumberland and Uitkomst

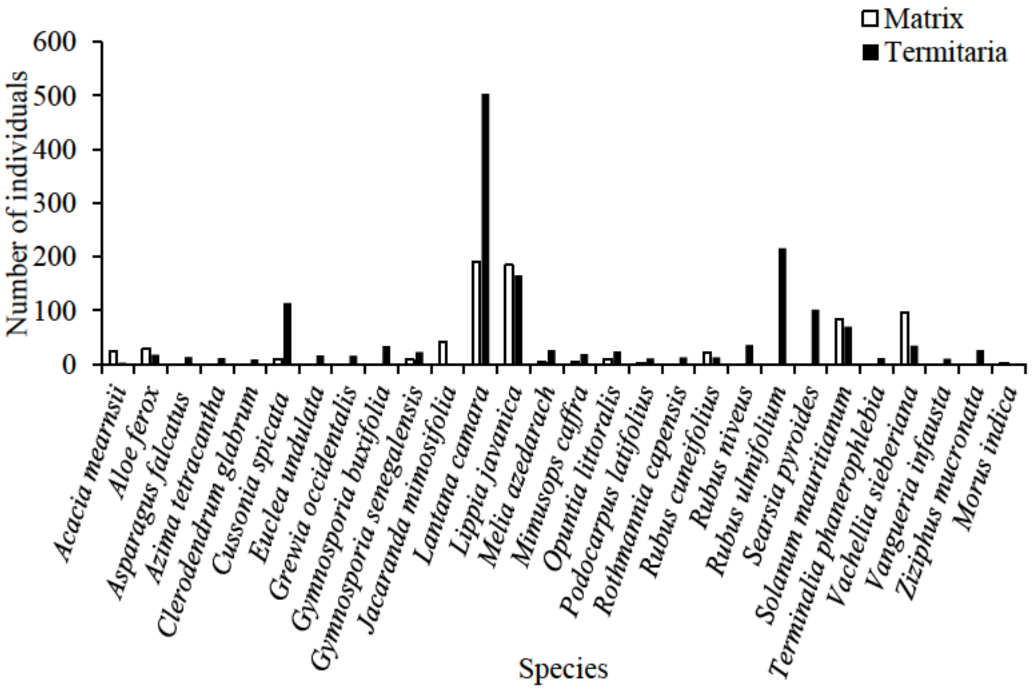

Figure 4.2: Abundance of common woody plant species occurring on termite mounds (n = 62) and matrix plots (n= 71) in Cumberland and Uitkomst. The species are listed in an alphabetic order.

Figure 4.3: (a) Typical matrix savanna vegetation and, (b, c) vegetation on termite mounds, one with a dense bush clump in Cumberland, KwaZulu-Natal. Photo credit: Vukani Ngcobo

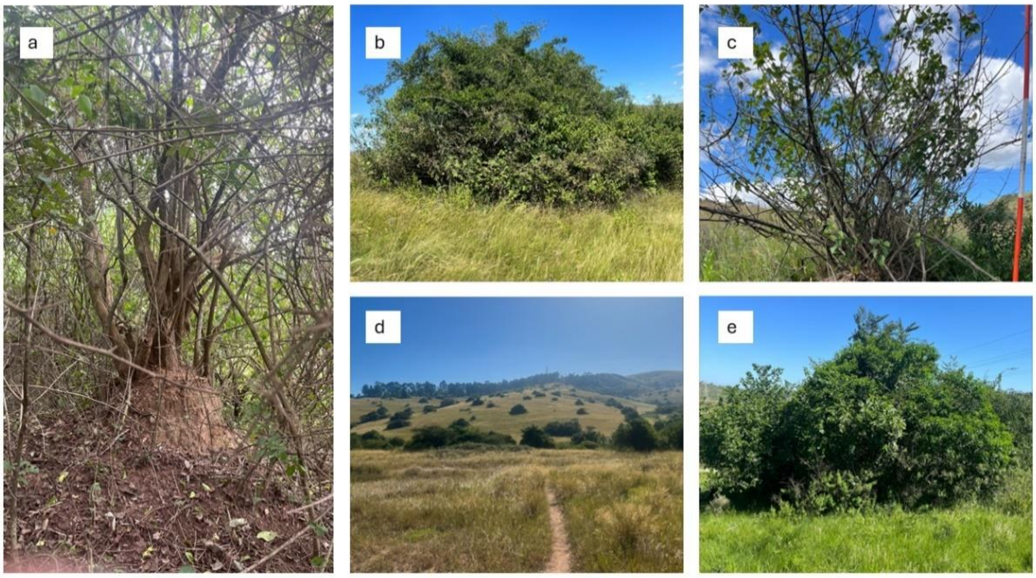

Figure 4.4: Woody vegetation on termite mounds showing different stages of bush clump development, (a, c) initial stages of bush development, (b, e) dense bush clumps, and (d) matrix vegetation assembles and dense bush clumps within the landscape in Uitkomst, KwaZulu-Natal. Photo credit: Vukani Ngcobo.

The species composition of woody plants was significantly different between Cumberland and Uitkomst (PERMANOVA: $R^2 = 0.15$, $F = 25.43$, $P = 0.001$), and between termite mounds and matrix plots ($R^2 = 0.07$, $F = 11.8$, $P = 0.001$). There was also a significant interaction of habitat (termite mound and matrix) and site location ($R^2 = 0.03$, $F = 4.93$, $P = 0.001$), suggesting that the effects of habitat on species composition significantly differed in Cumberland and Uikomst. Additionally, the nMDS results illustrated distinct assemblages of woody species in termite mounds compared to the matrix across the two study locations (Figure 4.5).

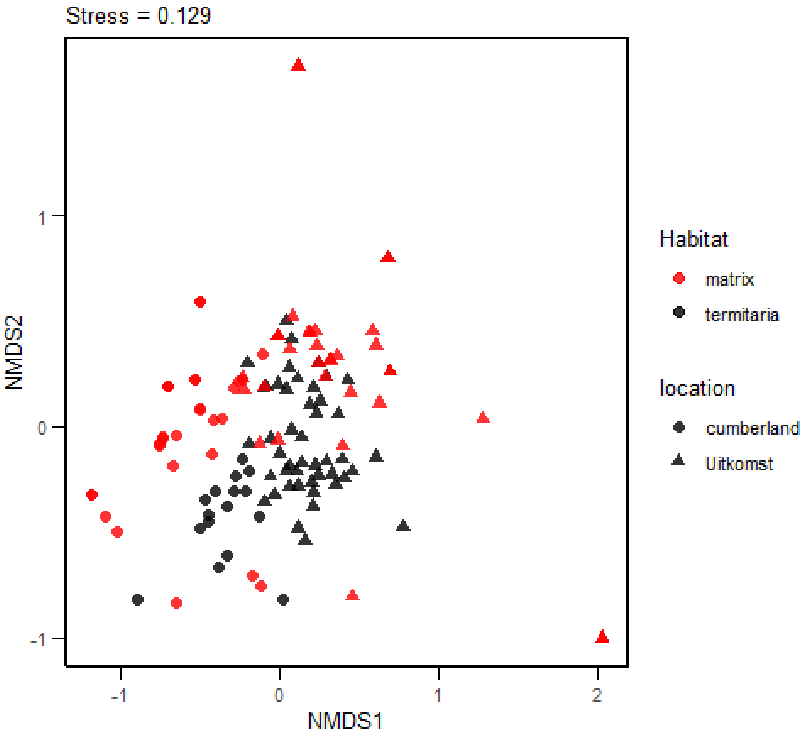

Figure 4.5: Non-metric multi-dimensional scaling ordination of woody plant assemblages occurring on termite mounds and matrix plots in Cumberland and Uitkomst

Woody species richness was significantly different between termite mounds and matrix plots ($F_{(1,129)} = 98.5$, $P < 0.0001$, Table 4.1). The effect of location and the interaction between habitat and location were not significant ($P > 0.05$), indicating that the species richness of woody plants was not significantly between Cumberland and Uitkomst, and the effect of habitat on the species richness was the same across both locations. Shannon-Wiener diversity index of woody plants significantly differed between termite mounds and matrix plots ($F_{(1,129)} = 134.09$, $P < 0.0001$, Table 4.1). The main effect of location was also significant, suggesting that Shannon-Wiener diversity of woody plants was significantly different between Cumberland and Uitkomst regardless of habitat ($F_{(1,129)} = 11.45$, $P = 0.0001$), however the interaction of habitat and location was not significant ($P > 0.05$), indicating that habitat influenced Shannon-Wiener diversity the same way across both locations. Similarly, the species evenness was significantly different between termite mounds and matrix plots ($F_{(1,129)} = 35.81$, $P < 0.0001$, Table 4.1) and between Cumberland and Uitkomst ($F_{(1,129)} = 11.01$, $P = 0.001$), however, the interaction between habitat and location was not significant ($P > 0.05$), indicating a consistent effect by habitat across both locations.

Woody plant density significantly differed between termite mounds and matrix plots ($F_{(1,129)} = 28.19$, $P < 0.0001$, Table 4.1), however the main effect of location and the interaction between habitat and location was not significant ($P > 0.05$), which indicates that woody plant density did not significantly differ between Cumberland and Uitkomst, and the effect of habitat on woody plant density was similar across both locations. Similarly, woody stem density was significantly different between termite mounds and matrix plots ($F_{(1,129)} = 8.42$, $P = 0.004$, Table 4.1), while location and the interaction between habitat and site location had no effect on woody stem density ($P > 0.05$). Moreover, a similar trend was also observed on woody plant height ($F = 9.99$, $P = 0.0015$, Table 4.1).

Table 4.5: Mean (± SE) species richness, Shannon-Wiener index, evenness, woody plant density, woody stem density, and woody plants height between termite mounds (n = 62) and matrix plots (n =71) (two-way ANOVA and ART ANOVA).

Parameter	**Termitaria**	**Matrix**	***P***
Species richness	5.68 ± 0.40	1.85 ± 0.10	< 0.0001
Shannon-Wiener index	1.27 ± 0.07	0.39 ± 0.04	< 0.0001
Evenness	0.78 ± 0.02	0.45 ± 0.05	< 0.0001
Tree density (100 m^2)	30.74 ± 3.24	12.37 ± 1.56	< 0.0001
Stem density (100 m^2)	109.44 ± 16.29	52.00 ± 11.87	0.004
Woody plant height (m)	2.1 ± 0.6	1.55 ± 0.4	0.0015

Sapling species richness was significantly different between termite mounds and matrix plots (*F* $_{(1,129)}$ = 51.05, *P* < 0.0001, Table 4.2). The main effect of location was also significant (*F* $_{(1,129)}$ = 5.38, *P* = 0.021). suggesting that sapling species richness significantly differed between Cumberland and Uitkomst when habitat was not considered. However, the lack of interaction between habitat and location (*P* > 0.05) indicates that effect of habitat was constant across the two locations. The species richness of mature trees (> 1.5 m) was significantly different between termite mounds and matrix plots (*F* $_{(1,129)}$ = 97.09, *P* < 0.0001, Table 4.2), however the main effect of location, and the interaction between habitat and location were not significant (*P* > 0.05). Similar results were obtained for sapling density (*F* $_{(1,129)}$ = 4.99, *P* = 0.027, Table 4.2). Moreover, the density of mature trees was significantly higher on termite mounds than in matrix plot both in Cumberland (*F* $_{(1,46)}$ = 54.38, *P* < 0.0001, Figure 3.6) and Uitkomst (*F* $_{(1, 83)}$ = 35.33, *P* < 0.0001, Figure 4.6).

Table 4.6: Mean (± SE) species richness and density (100 m^2) of woody plants in different growth stages on termite mounds (n = 62) and matrix plots (n = 71) (two-way ANOVA and ART ANOVA)

Parameter	**Termitaria**	**Matrix**	***P***
Species richness (< 1.5 m)	2.65 ± 0.19	1.18 ± 0.10	< 0.0001
Species richness (> 1.5 m)	4.89 ± 0.37	1.32 ± 0.11	< 0.0001
Density (< 1.5 m)	15.63 ± 2.77	8.61 ± 1.62	0.027

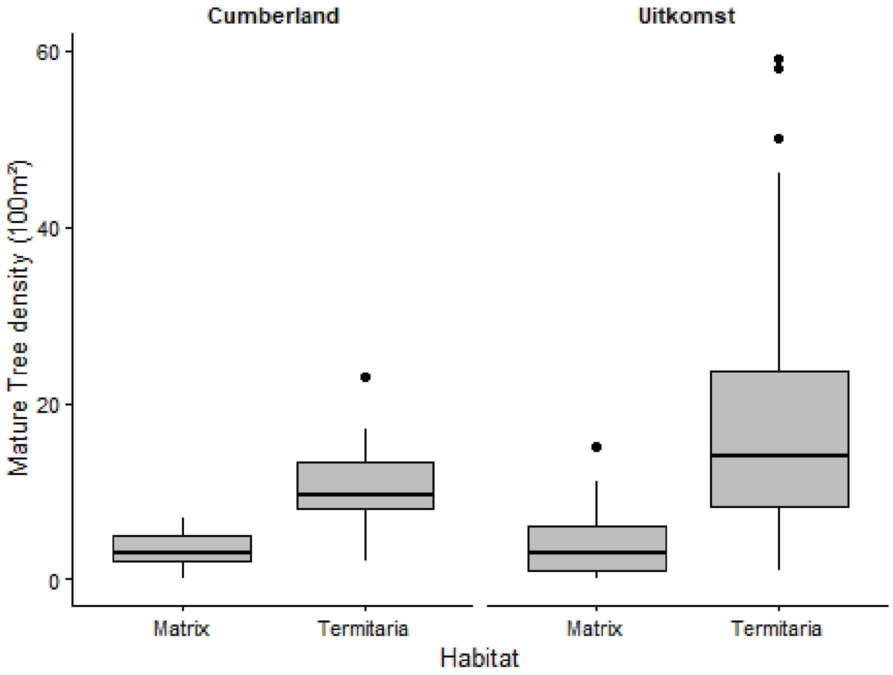

Figure 4.6: Mature tree density on termite mounds and in matrix habitats across Cumberland and Uitkomst.

Woody plant height was significantly different between mound and matrix plots vegetation (*D* = 0.29, *P* = 0.001, Figure 4.6a and 4.6b), which suggests that tree height was influenced by the presence of termite mounds. In matrix plots the height of woody plants showed a near perfect reverse J-shaped curve, whereas the reverse J-shaped curve was less realised for woody plants on termite mounds (Figure 4.6a and 4.6b). Woody plants with heights ranging from 1.5 m to 6.5 m were underrepresented in matrix plots than on termite mound plots (Figure 4.6a). Moreover, the number of woody plants < 1.5 m height was almost equally represented in both termite mound and matrix plots (Figure 4.6).

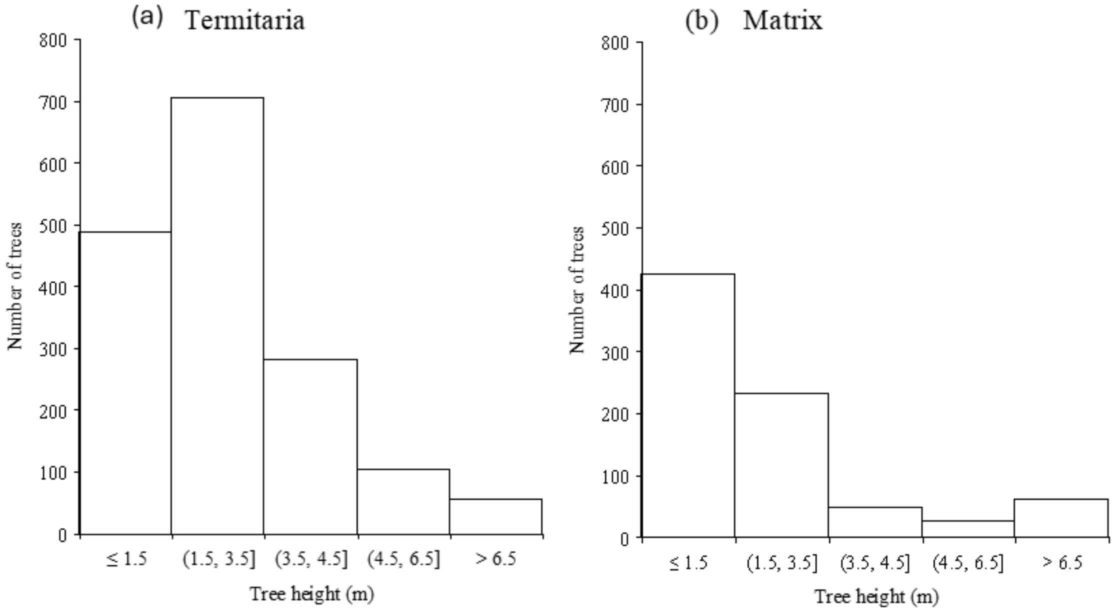

Figure 4.7: Height distribution of woody plants on (a) termite mounds and (b) matrix plots in Cumberland and Uitkomst (Kolmogorov-Smirnov test, $D = 0.29$, $P < 0.001$).

The community-weighted means of woody species exhibiting bird-dispersed traits was higher on termite mounds compared to matrix plots ($t = 3.9$, $P < 0.001$, Figure 4.8a), while the community-weighted mean of mammal-dispersed species was higher in matrix plots than on termite mounds ($t = 5.2$, $P < 0.001$, Figure 4.8a). In terms of fruit types, the community-weighted mean of woody species bearing drupe-type fruits was higher on termite mounds than in matrix plots ($t = 4.7$, $P < 0.001$, Figure 4.8b), whereas the community-weighted mean of species with pod-type seeds was higher in the matrix than on the mounds ($t = 5.1$, $P < 0.001$, Figure 4.8b). Moreover, the community-weighted mean of nitrogen-fixing species was significantly higher in matrix plots than on termite mounds ($t = 5.14$, $P < 0.0001$, Figure 4.9b).

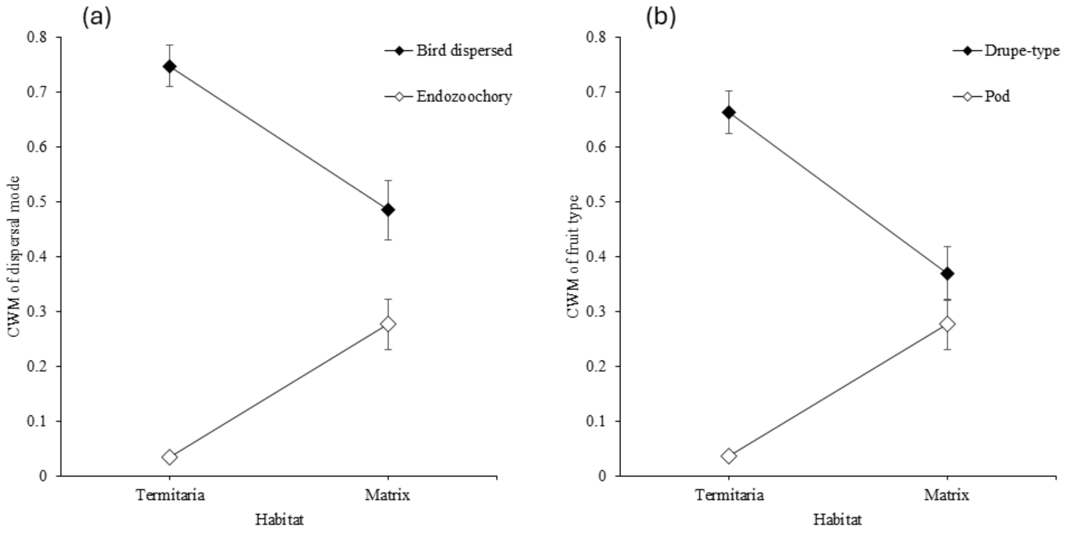

Figure 4.8: The CWM (± SE) of (a) seed dispersal mode, and (b) fruit type on termite mounds (n = 62) and matrix (n = 71) vegetation (Welch two sample *t*-tests).

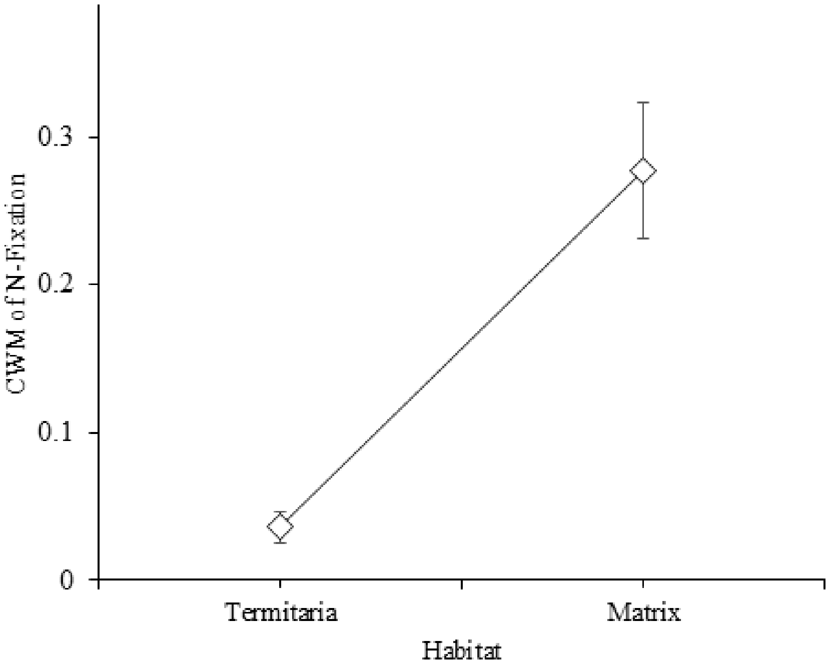

Figure 4.9: The CWM (± SE) of N-fixation by woody species on termite mounds (n = 60) and in matrix (n = 71) plots (Welch two sample *t*-tests).

Discussion

In this study, termite mounds supported woody species composition different from the matrix habitat, consistent with findings in other savanna environments (e.g., Traoré et al., 2008; Moe et al., 2009; Joseph et al., 2013; Van der Plas et al., 2013; Davies et al. 2014; Muvengwi et al., 2016; Erpenbach et al., 2017). Although 15 woody species were shared between termite mounds and matrix plots, the majority of species (39) were found exclusively on termite mounds, while only a single species was restricted to the matrix. Termite mounds are elevated patches of soil (Moe et al., 2009; Joseph et al., 2014), as a result, they may be less subjected to fire. The absence of fire disturbance on termite mounds may facilitate the establishment and growth of saplings belonging to fire-sensitive species, particularly those of forest margin or forest origin, which would otherwise be eliminated by frequent fires in the surrounding matrix. In this study, fire adapted species such as *Vachellia sieberiana* dominated the matrix, while species that are sensitive to fire such as *Cussonia spicata* and *Clerodendrum glabrum* were restricted to termite mounds. Moreover, nitrogen-fixing woody species were common in the matrix than on termite mounds. This may be due to the generally nutrient-poor, N-limited conditions of the matrix, and their ability to form symbioses with N-fixing bacteria provides a competitive advantage in matrix sites (Scholes and Archer, 1997). On the contrary, termite mound soils have high concentrations of nitrogen due to termite activities (Konaté et al., 1999), which reduces the need for N-fixation, allowing species that are not N-fixing to dominate on termite mounds. Additionally, this study showed that N-fixing species such as *V. sieberiana* were common in matrix vegetation and are known to thrive in the matrix's frequent fire and herbivory (Bond, 2008), and their deep root systems help them access water and co-exist with grasses in the matrix (Goheen et al., 2004).

Woody species in termite mounds had higher values of the Shannon-Wiener index, species richness, and evenness compared to the matrix. Similar results were reported for other savanna environments, such as the miombo woodlands in Zimbabwe (Loveridge and Moe 2004), in the Lake Mburo National Park in Uganda (Moe et al., 2009), and Hluhluwe-iMfolozi Park in South Africa (Van der Plas et al., 2013). Many studies have also linked the changes in woody plant diversity to improved micro-habitat conditions on termite mounds (e.g., Konaté et al., 1999; Jouquet et al., 2006; Joseph et al., 2013; Muvengwi et al., 2016). For example, due to increased soil resources, termite mounds act as resource islands in relatively nutrient poor savanna environments, thereby increasing habitat heterogeneity and productivity within the landscape (Moe et al., 2009, but see Konaté et al. 1999; Joseph et al., 2013; Muvengwi et al., 2017). Plant species richness generally increases with increasing productivity (Moe et al., 2009). Moreover, since woody cover and density in savannas generally increase with water availability (Scholes and Archer, 1997), high water retention may result in the dominance of woody plants on termite mounds. In particular, the conditions on mounds may allow the establishment, recruitment and growth of tree species that have higher water and nutrient requirements compared to the savanna species (Joseph et al., 2013; Davies et al., 2016).

Consistent with findings from previous studies (e.g., Arshad, 1982; Pomeroy, 1983; Loveridge and Moe, 2004; Jouquet et al., 2006; Traoré et al., 2008; Moe et al., 2009), this study found that woody plant density and tree canopy cover were significantly higher on termite mounds than in the surrounding matrix. Density of mature trees was approximately four times higher, whereas sapling and woody stem densities were approximately two times higher on termite mounds than in the matrix. In a study from the miombo woodlands in Zimbabwe, Loveridge and Moe (2004) found that the density of woody plants on termite mounds was two times higher than in nearby matrix areas. In Lake Mburo National Park, southwest Uganda, Moe et al. (2009) found that tree densities were 25 times greater on termite mounds compared to matrix habitats. Similarly, in Hluhluwe-iMfolozi Park, KwaZulu-Natal, South Africa, Van der Plas et al. (2013) found that the density of large trees (> 2 m) on the mounds was more than four times greater than in the matrix, which was also the case for mature trees in this study. Additionally, in a restoration experiment in northern Burkina Faso, Mando et al. (2002) found that woody species established only on termite mounds and the presence of termite mounds increased woody vegetation cover.

Studies propose that the improved woody plants establishment and growth, resulting in dense vegetation cover on termite mounds could be the result of altered soil water status and nutrient concentrations on termite mound soils (Mando et al. 1996; Konaté et al. 1999; Joseph et al., 2013; Muvengwi et al., 2017), resulting from termites' mound-building and foraging activities. In a review and meta-analysis of studies across Africa, Sileshi et al. (2010) and Muvengwi and Witkowski (2020) found that termite mounds soils were enriched with clay and had a relatively high amount of soluble plant nutrients. Similarly, studies in the miombo woodlands of Chizarira National Park (Joseph et al., 2013) and Gonarezhou National Park (Muvengwi et al., 2017), both in Zimbabwe, found a doubling in clay content, and the macro-and micro-nutrients, as well as an increase in pH on termite mounds relative to the matrix areas. Furthermore, Konaté et al. (1999) found that the water storage capacity was higher in termite mound soils than matrix soils, which improved moisture retention and increased soil moisture availability in the Lamto Reserve in Cote d'Ivoire. These conditions combined with others such as increased seed deposition and reduced fire frequencies can facilitate rapid seed germination and establishment of woody plants, also increase their productivity, thereby resulting in high woody plant cover and density on termite mounds, such as that reported in this study.

The presence of large trees on termite mounds may increase seed dispersal to mounds by animals, particularly birds and mammalian herbivores (Acanakwo, 2018; Davies et al., 2024). The species composition on termite mounds was characterized by bird-facilitated seed dispersal and drupe-type fruits, suggesting that avian seed dispersal may have played a significant role in shaping the woody plant assemblages on termite mounds. The indicator woody species of termite mounds were *Cussonia spicata*, *Lantana camara*, and *Searsia pyroides,* which produce drupes-type fruits (Appendix 3.2) at the beginning of the rainy season. These species attract visitation by a diverse avifauna which disperse the seeds to and from nearby communities into termite mounds. Similarly, in a study in the Muyako Community Forest in the Zambezi Region of Namibia, Yamashina and Hara (2019) found that the indicator species of mounds such as *Salvadora persica* and *Capparis tomentosa* produced drupe-type fruits and their seeds were dispersed by birds. Additionally, viable seeds may be carried into mound cavities by rodents, as observed with *Tamarindus indica* seeds in the Central Plateau in Burkina Faso. Moreover, herbivores browsing near mounds (e.g., Loveridge and Moe, 2004; Mobæk et al., 2005), may bring seeds potentially increasing seed accumulation on termite mounds. Increased seed deposition can result in a high seed diversity of soil seed banks on termite mounds (Masocha and Dube, 2019), which later may be reflected by high species richness and diversity following rapid seed germination and seedling establishment due to high resource availability and reduced grass competition on termite mounds.

Conclusion

The results reported in this study showed that termite mounds had an impact on the species richness, diversity, and the overall species composition of woody plants in Cumberland and Uitkomst. The results showed that woody plant assemblages on termite mound had a high number of species and were more diverse relative to the matrix assemblages, thereby emphasizing the role of termite mounds in generating and increasing spatial heterogeneity for woody species establishment and growth in the landscape. The concentration of mature trees on trees on termite mounds may suggest that termite mounds acted as fire refuge woody plants, allowing the grow taller or the resource rich micro habitat on termite mounds increased the growth rates and productivity of trees. Increased regeneration and growth rates of woody plant on a fire refugia leads to an aggregation of trees, resulting in the formation of dense close canopy stands of woody plants (bush clumps) that expand in size, and simultaneously contribute to the increase of woody plant cover and density in a landscape. The results also highlighted the role of seed dispersal by birds on termite mound woody plant assemblages. For example, bird-dispersed woody species dominated termite assemblages, while the matrix was dominated by mammal dispersed species.

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CHAPTER 5

The effects of termitaria size and density on woody vegetation assemblages

Abstract

Termite mounds vary in size and soil nutrient concentrations, which may determine the degree of their influence on woody species composition and community structure. This study examined patterns of woody vegetation change in relation to termite mound size on termite mounds located in Cumberland Nature Reserve and Uitkomst Conservation Area, KwaZulu-Natal, South Africa. Specifically, the study tested: (1) whether the spatial distribution of bush clumps across the landscape is related to termite mound density, (2) whether increases in mound surface area correspond to changes in woody species composition, community structure, and woody cover, and (3) whether the proportion of termite mound indicator species increases with mound size. Termite mound densities ranged from 4.7 to 5.4 mounds per hectare in Cumberland and Uitkomst, with vegetated mounds accounting for the majority (3–3.4 ha^{-1}) and bare mounds ranging from 1.2 to 2.4 ha^{-1}. Mound surface areas varied widely, from 1.46 m^2 to 111.12 m^2. A significant positive relationship was found between termite mound density and bush clump density ($P < 0.0001$), indicating that higher densities of termite mounds are associated with increased bush clump formation. As expected, both species richness and bush clump size increased with termite mound surface area. Although species composition remained relatively constant across mound sizes, species richness on large mounds (>30 m^2) was approximately double that observed on medium (10–30 m^2) and small (<10 m^2) mounds. The Shannon-Wiener diversity index was significantly higher on large mounds than on medium and small mounds. Total woody plant density and sapling density were approximately three times greater on large mounds, while mature tree density was about twice as high. Furthermore, woody stem density was nearly four times greater on large mounds. The proportion of termite mound indicator species also increased significantly with mound size, being highest on large mounds compared to medium and small mounds.

Key words: NMDS ordination, savannas, species pool, termite mounds, woody vegetation

Introduction

Patch-dynamic systems as described in Levin and Paine (1974) can influence species community assemblage, composition and structure. The spatiotemporal patchy distribution of micro habitats and a continuously changing assortment of patches may allow more species to coexist than would be the case in homogeneous landscapes (Levin and Culver, 1971; Levin and Paine, 1974; Nee and May, 1992). Furthermore, changes in the spatial heterogeneity of a landscape can reflect changes within patches, or changes in nearby patches (Burnett et al., 1998). In grassy ecosystems, studies have reported that trees, depending on their population structure, and spatial distribution can increase spatial heterogeneity over the landscape (Belsky et al., 1993; Jeltsch et al., 1996; Janecke, 2020). For example, nutrient rich patches develop under large trees, creating woody vegetation mosaic assemblages under these nursery trees due to altered nutrient cycling and increased animal activities (Hoffmann et al., 2012; Charles-Dominique et al., 2018; Abreu et al., 2021).

Termites also increase resource heterogeneity in nutrient poor grassy ecosystems. This can be done through the re-allocation of nutrients and subsoil particles, particularly fine clay particles during mound building and continuous foraging as mounds undergo a cyclic process of abandonment and recolonization over time (Sileshi et al., 2010; Joseph et al., 2014; Erens et al., 2015). These processes can in turn influence the mineral composition, nutrient fluxes, and soil moisture status in termite mound soils (Sileshi et al., 2010; Joseph et al., 2013; Seymour et al., 2014). For example, studies have shown that termite mound soils are characterized by higher clay content, exchangeable base cations, pH, total nitrogen, and soil moisture content compared to adjacent matrix soils(Arshad, 1982; Smith and Yeaton, 1998; Traoré et al., 2008; Muvengwi et al., 2017). Furthermore, these soil resources tend to increase as the mound increase in size (e.g., Joseph et al., 2013; Seymour et al., 2014).

Irrespective of the importance of termite mounds to spatial heterogeneity (e.g., Moe et al., 2009; Sileshi et al., 2010; Van der Plas et al., 2013; Davies et al., 2014; Muvengwi and Witkowski, 2020), studies investigating the effects of mound size on woody vegetation assemblages, particularly how the woody species composition, diversity, and density may change as termite mound size increases are lacking. Large termite mounds may provide more space and resources, and a relatively stable environment than matrix habitats and smaller mounds, allowing them to capture more plant species (Holdo and McDowell, 2004; Sileshi et al., 2010; Muvengwi et al., 2016), which may be due to reduced competition between and within different plant life forms as a result of increased resource abundance. For example, Joseph et al. (2013) found that soil nitrogen concentration on large mounds was ~ 70 times higher than in matrix soil and about ~ 60 times higher than small and medium-sized mounds. Similarly, as termite mounds grow larger, their clay content doubles (Turner et al., 2006), which also improves the water holding capacity of the soil on mounds (Groen et al., 2008), which may increase establishment of woody plants on termite mounds (Moe et al., 2009; Sileshi et al., 2010; Muvengwi and Witkowski, 2020)

Large termite mounds may also function as fire refugia by presenting a stronger structural barrier than smaller mounds, thereby creating sites that are stable for establishment and growth of seedlings (Sileshi et al., 2010; Joseph et al., 2015). Furthermore, many large termite mounds are encircled by a wide, barren zone of eroded soil, with less grass biomass than the surrounding matrix habitats and can potentially serve as a natural firebreak (Konate´ et al., 1999; Sileshi et a., 2010; Joseph et al., 2013). Additionally, due to being relative elevated compared to the surrounding matrix, large termite mounds may be less exposed to frequent high intensity fires which may reduce the impacts of fire on termite mound vegetation (Joseph et al., 2013). As a result, vegetation on large termite mounds would experience less fire damage, whereas elsewhere this damage would be greater resulting in killing off of tree seedlings (Blösch, 2008; Moe et al., 2009).

Within the areas of this study, termite mounds varied in vegetation cover — some supported well-developed woody plant assemblages, while others were bare. As a result, the potential role of termite mound presence in influencing woody plant colonization was explored. This allowed for a comparison between the spatial distribution of all mounds and that of bush clumps, helping to isolate whether mound presence alone is sufficient to facilitate woody colonization. Moreover, since patches of high-quality resources have a great impact in nutrient poor ecosystems such as in African grassy landscapes (Scholes, 1990), it was expected that the larger termite mound patches will have higher species richness and species diversity of woody plants compared to smaller due to increased space and nutrient availability for colonizing species on larger mounds.

The aim of this study was to examine the effects of termite mound size on woody species composition and diversity, and the effects of termite mound density on the spatial distribution of bush clumps within a landscape. The specific questions were: (1) do termite mound densities influence the distribution of bush clumps occurring within the area? and (2) does the increase in termite mound surface area affect woody species composition, diversity and cover?

Materials and methods

Sampling design

This study focused on woody vegetation associated with termite mounds differing in surface area. Specifically, it examined well-established accumulations of woody vegetation, defined as associations of two or more woody plant species with interlocking canopies that are spatially isolated from other woody clusters by the surrounding grassland matrix, following the criteria outlined by O'Connor and Chamane (2012). Therefore, vegetation clusters made up of a single species were ignored so that vegetation was sampled from a total of 62 randomly selected termite mounds of various sizes in Cumberland Nature Reserve ($n = 16$), and Uitkomst Conservation Area ($n = 46$). All woody plants < 1.5 m were sampled in 10 m × 10 m plots centred on the termite mound, while woody plants < 1.5m were sampled on 5 m × 5 m subplots placed on the corners of the main plot.

Termite mound structure

To estimate the size of the termite mounds where individual bush clumps occurred, mound height was estimated by placing a ranging rod level with the top of the termite mound in each of the four cardinal directions and measuring the four heights from the ground to the ranging rod using a tape measure. The long (*d1*) and short diameter (*d2*) of each termite mound was measured at right angles using a tape measure. Additionally, termite mounds were modelled as cones to compute their surface area, using the following equation:

$$A = \pi r(r + \sqrt{h^2 + r^2},$$

where r is the average radius of the mound computed as the sum of half $d1$ and $d2$ divided by 2, and h is the vertical height of the mound. The size of each mound was recorded and ranked according to surface area classes: small-sized mounds (> 10 m^2), medium-sized (10 - 30 m^2) and large-sized mounds (> 30 m^2) (Joseph et al., 2013; Muvengwi et al., 2017).

Figure 5.1: Example of vegetated termite mounds of different sizes. (a) *Lantana camara* growing on a small termite mound in Uitkomst, (b) a cluster of trees on a large termite mound, and (c) woody plants occurring on a medium-sized termite mound in Cumberland. Photo credit: Vukani Ngcobo

Vegetation survey

Within each vegetated termite mound plot, all individual woody plants were identified to species level using Pooley (1993), which was supplemented by iNaturalist (https://www.inaturalist.org/) and PlantNet (https://identify.plantnet.org/) for additional validation. Height of each woody plant within the sampling plot was measured from the ground level using a 2-m ranging rod, and the number of woody stems per individual plant was systematically counted.

The number of saplings (< 1.5 m) and mature trees (≥ 1.5 m) of each species was counted per termite mound plot. The 1.5 m threshold to distinguish between saplings and mature trees was selected, aligning with the range used in other studies differentiating saplings and trees in forests (Janse-Ten Klooster et al., 2007). This threshold is lower than that used for savanna trees (2–4 meters, Higgins et al., 2000), as saplings on termite mounds would have experienced minimal or no flame exposure, and a higher cut-off would have resulted in an insufficient number of trees for comparing sapling and tree assemblages between termite mounds of various sizes. Additionally, species richness for both trees and saplings was calculated for each termite mound plot. Species diversity and species evenness of woody plants was estimated using the

Shannon-Wiener index (*H'*) and by dividing the Shannon-Wiener index by the natural log of the species richness, respectively.

Termite mound density survey

To assess how termite mounds density is related to the spatial distribution of bush clumps found in Cumberland and Uitkomst, the total number of termite mounds and bush clumps was estimated from 100 m × 100 m plots ($n = 41$) randomly located in different parts of the open area. The total number of bare termite mounds and vegetated mounds (bush clumps)were counted in the 100 m x 100 m plot.

Statistical Analysis

All statistical analysis were performed in R statistical computing and graphing program, version 4.4.0 (R Core Team, 2024).

A linear regression model was used to examine the relationship between termite mound density and bush clump density. A linear regression model was used because both the predictor (termite mound density) and the response (bush clump density) variables were continuous, and data met the assumptions of the model. To account for site-specific differences between Cumberland and Uitkomst, location was included as a categorical covariate, therefore treating the model as an Analysis of Covariance (ANCOVA) design. As a result, the model allowed for the assessment of the effect of termite mound density on bush clump density, the effect of location on bush clump density independent of termite mound density, and the interaction effect between termite mound density and location.

Species abundance data were square root transformed before the analyses were performed. The square root transformation of species abundance data helps weight common and rare species more equally. To examine the woody plant species composition among termite mounds of different sizes, a similarity matrix for the transformed species abundance data was constructed based on the Bray-Curtis distance matrix using the *vegan* function in R. Furthermore, woody species composition among large, medium, and small termite mounds were compared using permutational multivariate analysis of variance (PERMANOVA) with an interaction effect between termite mound size and location to account for differences study site location (Cumberland and Uitkomst). PERMANOVA can deal with nonparametric ecological community data, which rarely meet the requirements of parametric multivariate approaches

(Anderson 2001). The model splits the variance and calculates a pseudo-*F* statistic using any metric or semi metric distance matrix such as Bray-Curtis similarity matrix and estimates *P* values using permutations.

A lognormal regression model with a log link function and a Gaussian distribution was used to assess the relationship between termite mound area and species richness of woody plants. The model was fitted with an ANCOVA design by including location as a covariate, thereby controlling for site-specific differences while testing for the effect of termite mound size on species richness and whether the effect of termite mound size on species richness is same for both Cumberland and Uitkomst. A lognormal regression model applies a log transformation to the response variable (species richness) to allow data to meet the model assumption.

To compare Shannon-Wiener index, species richness, density, stem density, species evenness of woody plants, and the proportion of termite mound indicator species representatives across termite mound size classes, two-way Analysis of Variance (ANOVA) models were fitted with an ANCOVA design to account for site-specific differences between Cumberland and Uitkomst by including location as a covariance. The model assumptions were tested using Shapiro-Wilk tests for normality and Levene's tests for homogeneity of variances. Where model assumptions were not met ($P < 0.05$), an alternative non-parametric Aligned Rank Transform ANOVA (ART ANOVA) test was used. Pairwise post hoc tests were conducted using Tukey and Wilcoxon rank-sum tests where appropriate. The comparison for species richness and woody plant density were undertaken separately for saplings and mature trees.

A gamma regression model with a log link function was used to assess the relationship between termite mound area and the proportion of termite mound indicator species representatives, while accounting for site differences between Cumberland and Uitkomst by including location as a covariate to the model. A gamma regression model with log link function is appropriate for modelling positive continuous proportions, and data that violates the normality assumption of a linear regression.

Results

Termite mound densities ranged between 4.7 ha^{-1} and 5.4 ha^{-1} in Cumberland and Uitkomst. The densities of termite mounds without woody vegetation (bare mounds) ranged between 1.2 ha^{-1} and 2.4 ha^{-1}, while densities of vegetated mounds ranged between 3 ha^{-1} and 3.4 ha^{-1} (Table 5.1). Termite mounds surface area ranged from 1.46 m^{2} to 111.12 m^{2} across both study areas.

The number of termite mounds had a significant positive effect on bush clump density ($P < 0.0001$, Figure 5.3), suggesting that an increase in the number of termite mounds results in a corresponding increase in bush clumps. The main effect of location, and the interaction between the number of termite mounds and location was not significant ($P > 0.05$), suggesting that the effect of termite mound density was not different between Cumberland and Uitkomst.

Table 5.1: Mean ± SE of bare, vegetated and total termite mound densities (ha^{-1}) in Cumberland and Uitkomst

Mound condition	Cumberland	Uitkomst
Bare mounds	2.4 ± 0.6	1.2 ± 0.3
Vegetated mounds	3 ± 0.6	3.4 ± 0.4
Total	5.4 ± 0.8	4.7 ± 0.4

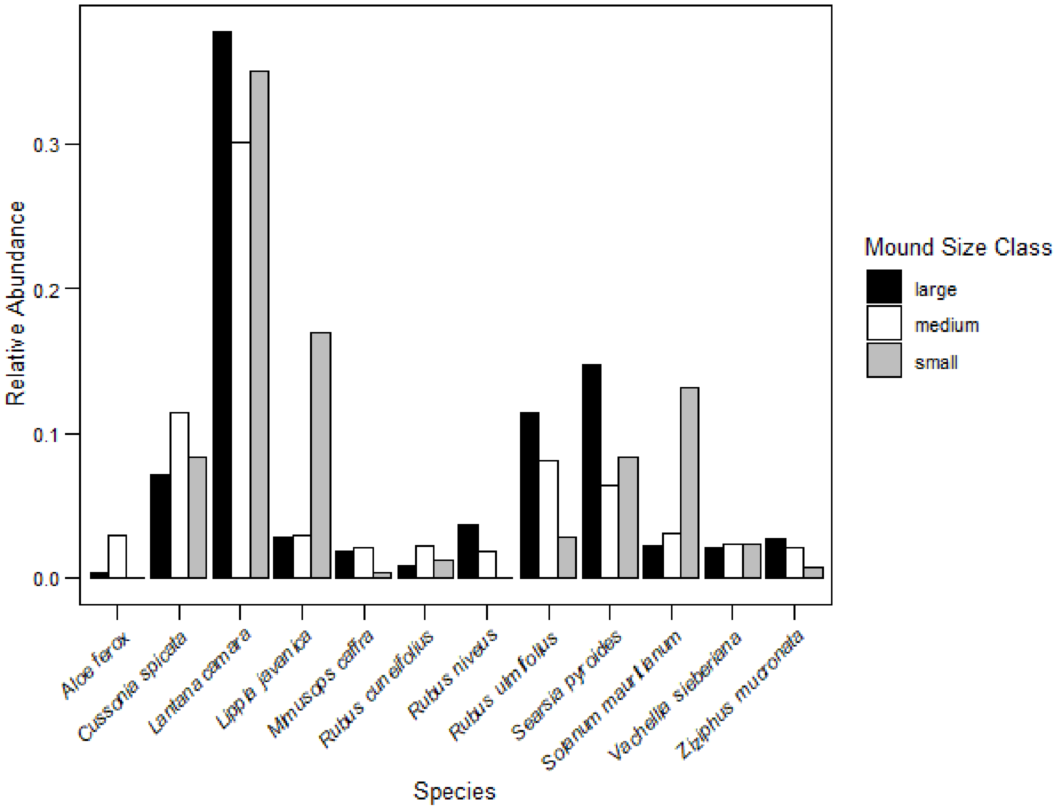

Figure 5.2: The relative abundance per termite mound size class of the most common species on termite mounds in Cumberland and Uitkomst. Species are ordered alphabetically.

A permutational multivariate analysis of variance (PERMANOVA) test showed that location had a significant effect on species composition ($R^2 = 0.42$, $F = 46.09$, $P < 0.001$), suggesting that species assemblages varied between Cumberland and Uitkomst. However, species composition was not influenced by termitaria size ($R^2 = 0.037$, $F = 2.05$, $P = 0.056$) and the effect of termitaria size on species composition did not significantly differ between ($P > 0.5$), indicating that although woody plant assembles differed across both locations the main effect of termite mound size on woody species composition was consistent.

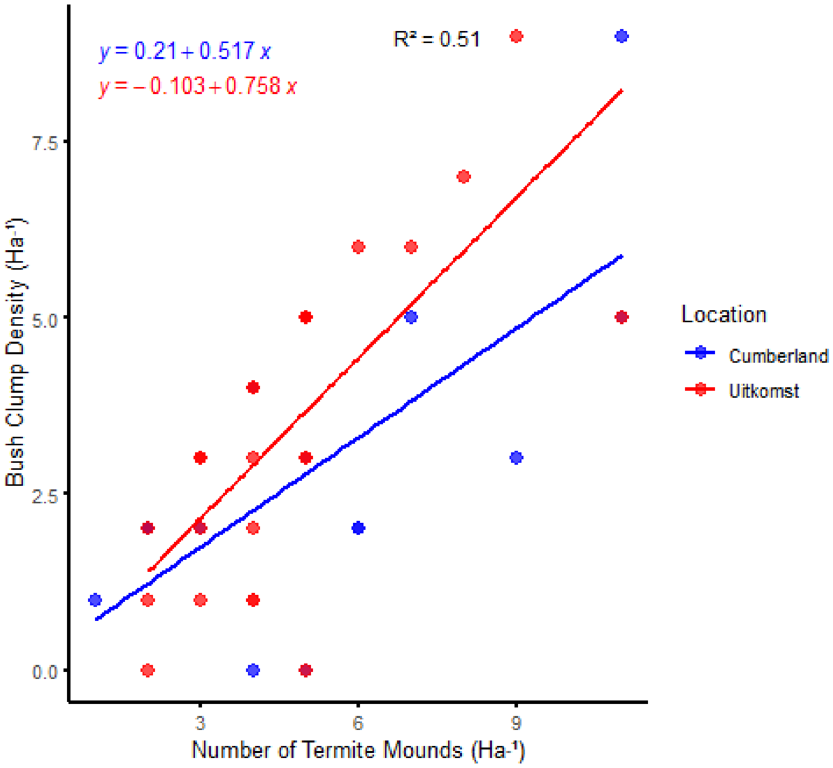

Figure 5.3: The relationship between density of termite mounds and density of bush clumps in Cumberland and Uitkomst. A linear regression model assessing the effects of termite mound density on bush clump density while accounting for location differences explained 51.2% of the variance in bush clump density ($R^2 = 0.512$, $F_{(3, 37)} = 12.92$, $P < 0.0001$).

Termitaria area had a significant effect on the species richness of woody plants across both Cumberland and Uitkomst ($P < 0.001$, Figure 5.4). The interaction term between termitaria area and location was not significant ($P > 0.05$), suggesting that the effect of termitaria area on species richness did not significantly differ between Cumberland and Uitkomst. However, when considering location-specific effects, the relationship was significant in Cumberland (*P* = 0.019, Figure 5.4) but not in Uitkomst.

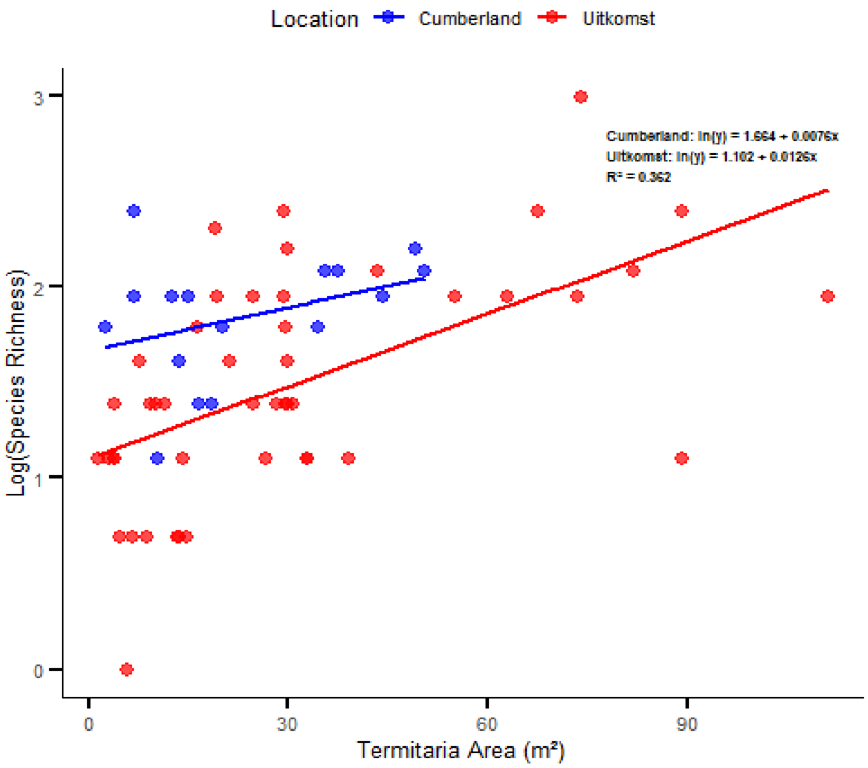

Figure 5.4: The relationship between the species richness of woody plant and termite mound surface area in Cumberland and Uitkomst. A lognormal linear regression model assessing the effect of termitaria surface area on the species richness of woody plants explained 36.2% of the variance in species richness of woody plants ($R^2 = 0.362$, $F_{(3, 58)} = 10.96$, $P < 0.0001$).

A two-way ANOVA showed a significant effect of termite mound size on the species richness of mature trees ($F_{(2, 56)} = 10.31$, $P = 0.0001$), indicating that the species richness of mature trees differs among different termite mound sizes. However, neither location nor the interaction between termite mound size and location were significant ($P > 0.05$), indicating that the species richness of mature trees was not significantly different between Cumberland and Uitkomst, and the effect of termitaria area on the species richness of mature trees was consistent between both locations. Furthermore, a post Tukey post hoc analysis revealed that the species richness of mature trees was significantly higher on large than small termite mounds (*P* = 0.009, Figure 5.5); however, it was not significantly different between medium-sized and both large and small termite mounds (*P* > 0.05). Surprisingly, although the species richness of saplings was similar among termite mound size classes (*F* = 1.35, *P* = 0.267), it significantly differed between Cumberland and Uitkomst (*F* = 65.76, *P* < 0.0001). However, the effect of termite mound size on the species richness of woody saplings was similar across both locations (*P* > 0.05).

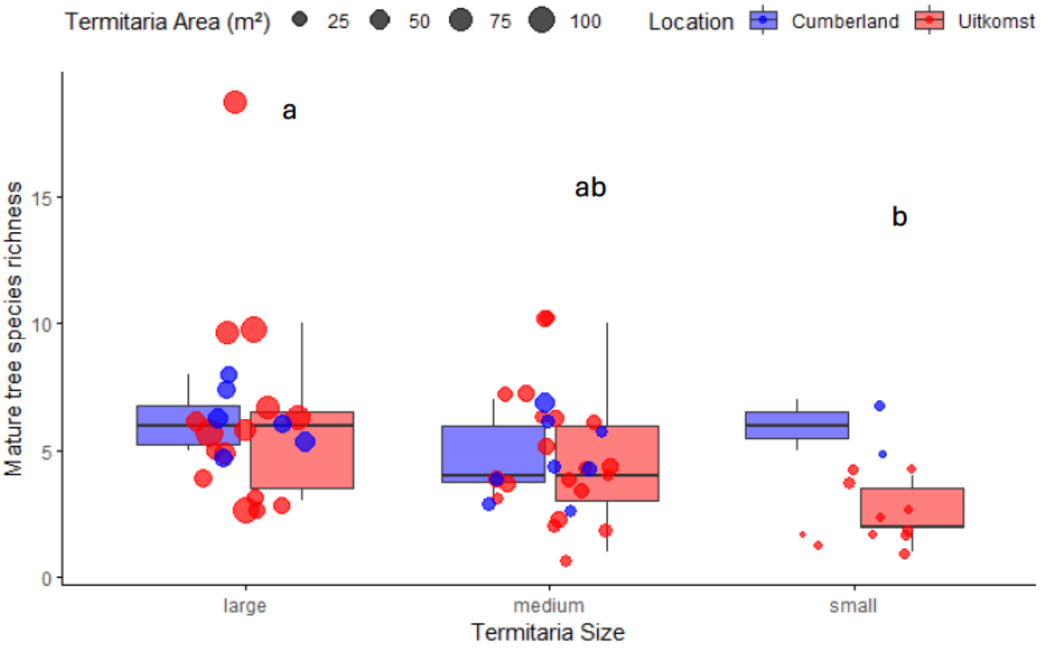

Figure 5.5: Mature trees species richness on different termitaria size classes in Cumberland and Uitkomst. Different letters represent groups that are significant ($P < 0.05$). The points were scaled to reflect termitaria area (m^2).

A two-way ANOVA showed that the Shannon diversity index of woody plant was significantly differed among different termitaria sizes ($F_{(2, 56)} = 6.65$, $P = 0.0003$), and between Cumberland and Uitkomst ($F_{(1, 56)} = 5.73$, $P = 0.02$), however there was a no significant interaction effect between termitaria size and location (*P* > 0.05), indicating that the effect of termitaria size on the Shannon diversity index of woody plants was not different between Cumberland and Uitkomst. A Tukey post hoc test revealed that Shannon diversity index of woody plants significantly differed between small and medium size termitaria (*P* = 0.02, Figure 5.6) and between small and large termitaria (*P* = 0.002, Figure 5.6), however it was not significantly different between large and medium size termitaria (*P* > 0.05). Moreover, the species evenness of woody plant was not significantly affected by termitaria size, location, and their interaction (*P* > 0.05).

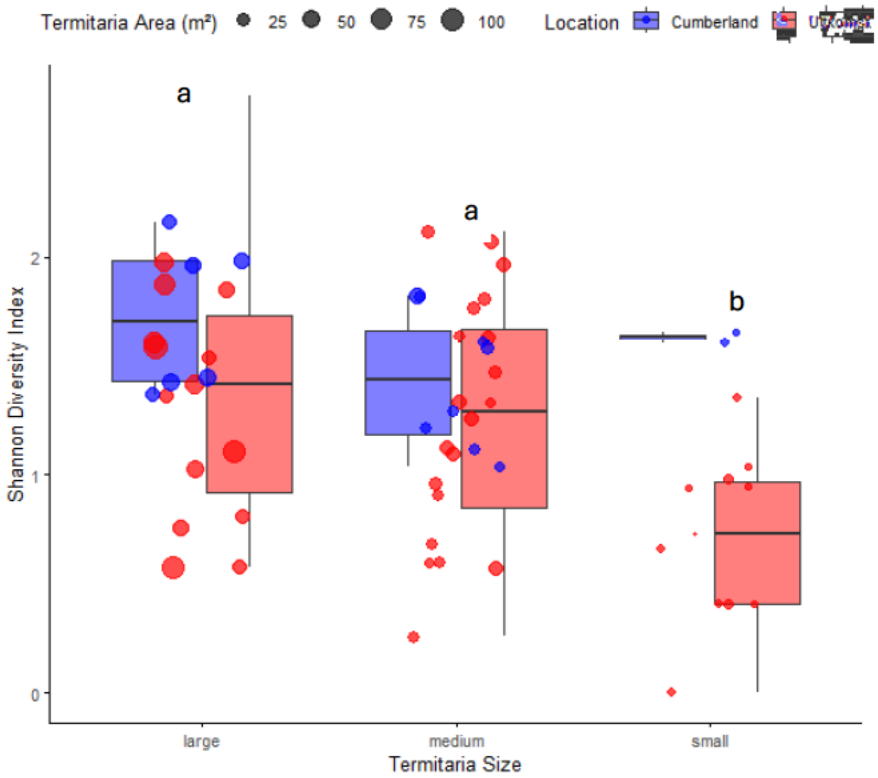

Figure 5.6: Shannon diversity index of woody species in different termitaria size classes in Cumberland and Uitkomst. Different letters represent significant different ($P < 0.05$). The points were scaled to reflect termitaria are (m^2).

Woody stem density significantly differed among termite mounds size classes ($F = 10.613$, $P < 0.001$), however it was not significantly affected by location nor the interaction between termitaria size and location ($P > 0.05$), indicating that woody stem density was similar between Cumberland and Uitkomst regardless of the termitaria size and the effect of termitaria size across each location was consistent. Furthermore, a post hoc pairwise Wilcoxon rank-sum test showed that woody stem density was significantly higher on large termitaria compared to medium-size ($P < 0.001$, Figure 5.7) and small mounds ($P = 0.002$, Figure 5.7), while there were no significant differences observed between small and medium sized mounds ($P > 0.05$).

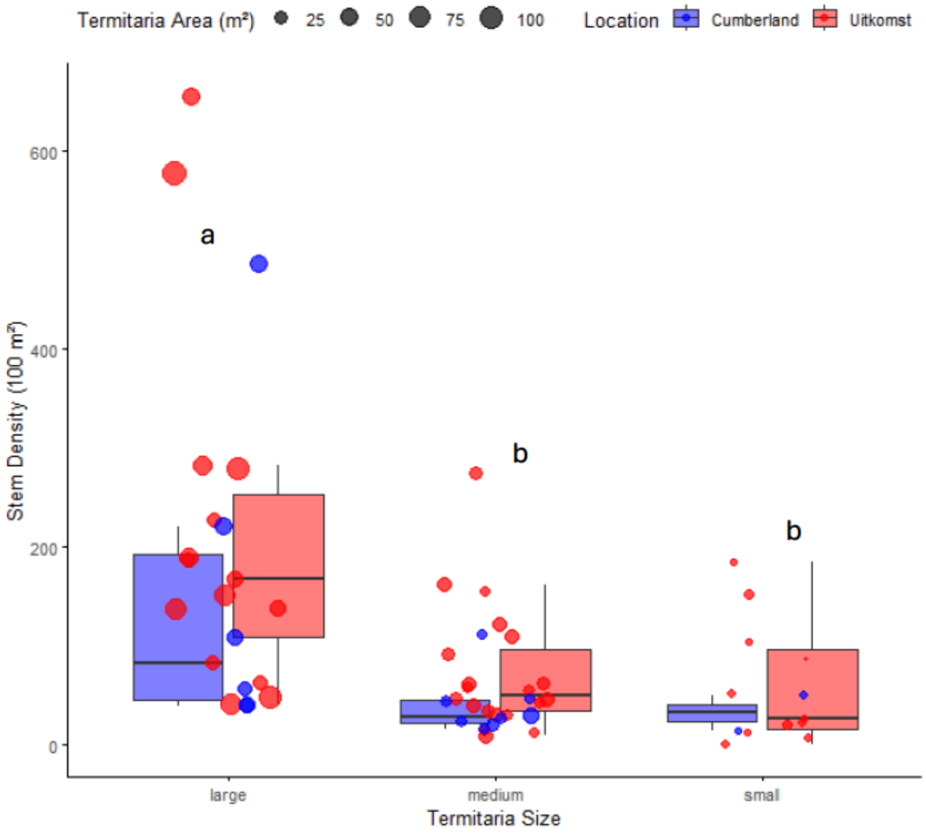

Figure 5.7: Woody stem density of woody plants surveyed across termite mounds of different size classes in Cumberland and Uitkomst. Different letters represent significant difference among termitaria size classes ($P < 0.05$). Points were scaled to reflect termitaria area (m^2).

Although sapling density differed significantly between Cumberland and Uitkomst ($F = 66.95$, $P < 0.001$), the main effect of termitaria size and the interaction between location and termitaria size was not significant ($P > 0.05$), suggesting that the influence of termitaria size on sapling density was similar across locations despite the significantly higher sapling density observed in one location. Mature tree density differed significantly among different termite mound sizes ($F = 8.982$, $P < 0.001$), however location nor the interaction between termitaria size and location ($P > 0.05$) significantly affected mature tree density. Furthermore, a post hoc pairwise Wilcoxon rank-sum test showed that mature tree density was significantly higher on large termitaria compared to medium size ($P = 0.007$, Figure 5.8) and small termitaria ($P = 0.003$, Figure 5.8), however it was not significantly different between small and medium size termitaria ($P > 0.05$).

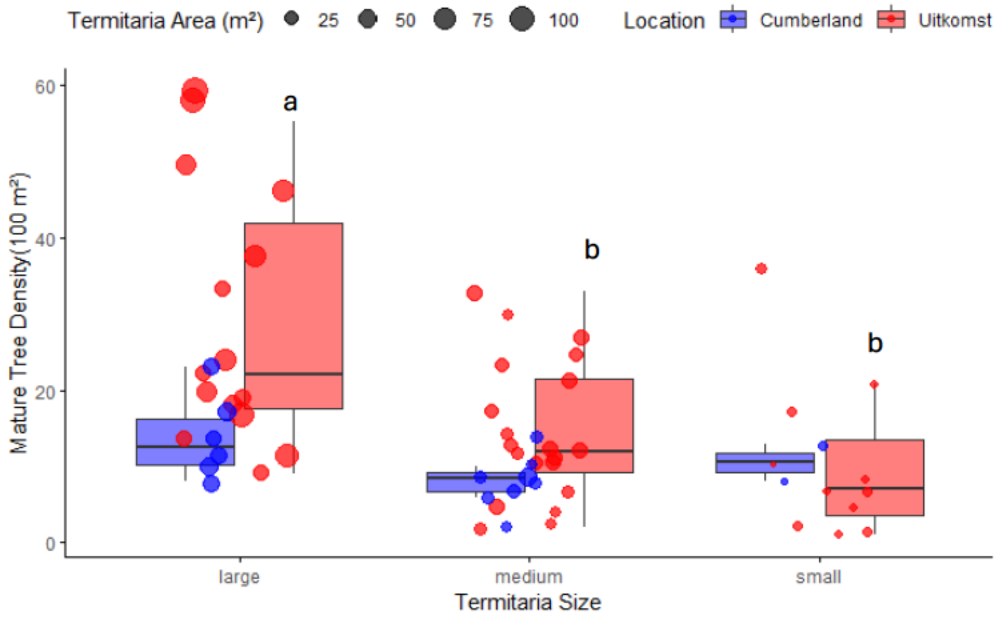

Figure 5.8: Mature tree density among different termitaria size classes in Cumberland and Uitkomst. The points were scaled to reflect termitaria area.

A two-way ANOVA showed that the proportion of termite mound indicator species representatives was significantly affected by termitaria size ($F = 7.33$, $P = 0.001$) and location ($F = 45.675$, $P < 0.001$), however the interaction of termitaria size and location was not significant ($P > 0.05$). Thereby indicating that the effect of termitaria size on the proportion of termitaria indicator species representatives did not differ between Cumberland and Uitkomst. Furthermore, a Tukey HSD test revealed that the proportion of termitaria indicator species representatives was significantly higher larger termitaria compared to medium size ($P = 0.02$, Figure 5.8) and small termitaria ($P = 0.001$, Figure 5.9), while termitaria indicator species were represented equally on small and medium size termitaria ($P > 0.05$). Additionally, a Gamma regression model revealed that as the size of termite mounds increased, the proportion of termite mound indicator species representatives also increased ($t = 2.03$, $P = 0.047$, Figure 5.10). Although termite mound indicator species were more represented in Uitkomst ($t = 4.86$, $P < 0.001$), the effect of termite mound size on the proportion of termite mound indicator species representatives did not significantly differ between Cumberland and Uitkomst ($P > 0.05$).

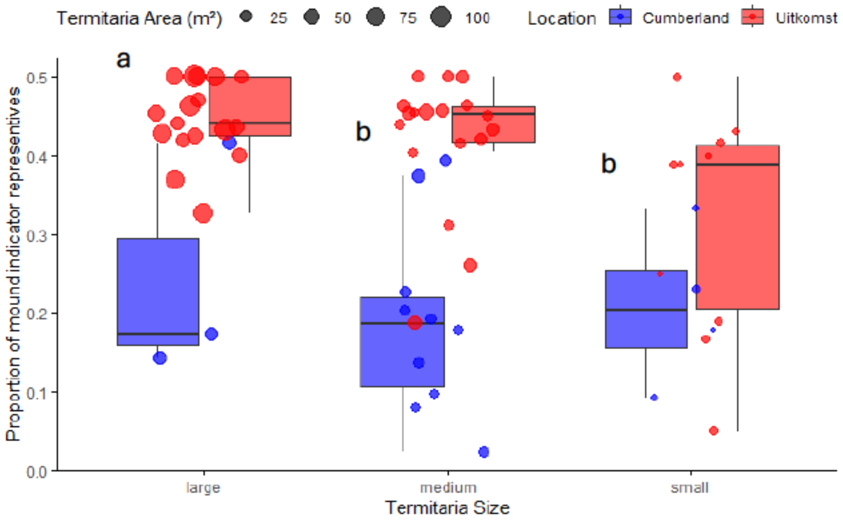

Figure 5.9: The proportion of termite mound indicator species representatives in termitaria of different size classes in Cumberland and Uitkomst. The points were scaled to reflect termitaria area (m^2).

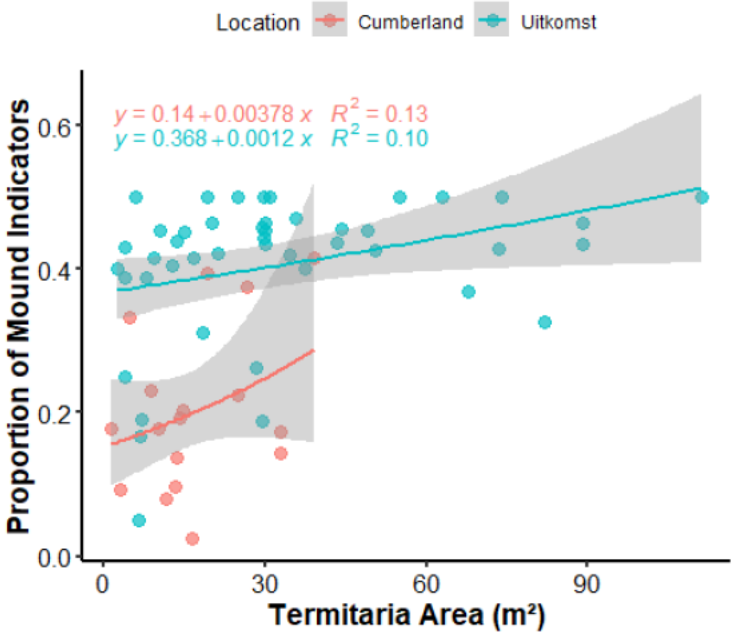

Figure 5.10: The relationship between the proportion of termitaria indicator species representatives and termitaria area in Cumberland and Uitkomst.

Discussion

Termite mound distribution and size have been reported to influence woody vegetation patterns and composition in African savannas (e.g., Blösch, 2008; Moe et al., 2009; Joseph et al., 2013). The termite mound densities reported here (5.4 mounds ha^{-1} at Cumberland) and (4.7 mounds ha^{-1} at Uitkomst) are comparable to those reported in Pomeroy (1977) for most parts of Uganda, Trapnell et al. (1976) for Chitememe in Zambia, and Moe et al (2009) in Lake Mburo National Park, Uganda. Elsewhere, termite mound densities have been reported to be as low as 0.46 mounds ha^{-1} in N'waswitshaka River catchment (Davies et al., 2014), 0.7 mounds ha^{-1} in southern Kruger National Park (Levick et al., 2010), and 0.73 mounds ha^{-1} in northern Kruger National Park (Meyer et al., 1999).

The low densities reported in some of the studies cited may be due to the methods used for estimating mound densities. For example, remote sensing studies often cover large spatial extent, therefore the reported densities could be a true representation the entire area as it can easily capture the spatial variations in the number of mounds per area depending on the spatial resolution data used, whereas field-based studies such as the present one used few plots to estimate mound densities of the entire landscape. However, low mound densities could also reflect failure of remote sensing equipment such as Light Detection and Ranging (LiDAR) (Levick et al., 2010; Davies et al., 2014) to detect smaller mounds due to their spatial resolution, which they can be easily detected and counted in field-based sampling. Additionally, some studies argue that termite mound densities may be influenced by the region (Moe et al., 1999), soil type (Van der Schijff, 1965), and mean annual precipitation (Davies et al., 2014) of the areas in which they occur.

Termite mound densities within a landscape may affect the magnitude of their influence on spatial heterogeneity in savannas. For example, in this study the occurrence of bush clumps was related to the density of termite mounds. This could suggest that high mound densities may increase colonization probability of a mound by woody species dispersing from nearby sources, and they also decrease dispersal distance between patches. Similar trends were observed in the Lake Mburo National Park (Moe et al., 2009), and in the southwestern part of the Lake Mburo National Park, which experiences less disturbances from fire and grazing (Hoag et al., 1991). Similar vegetation assemblages formed by termite mounds have also been observed in Central Brazil (Diniz et al., 1986). Moreover, termite mounds significantly influenced bush clump formation in seasonally waterlogged areas (Pomeroy, 1976; Blösch, 2008) and in the Loita plains of Kenya (Glover et al., 1964).

The size and structure of termite mounds in Cumberland and Uitkomst are similar to those observed in other grassy environments. For example, the conical structure of these mounds has been widely reported for other areas (Joseph et al., 2013; Yamashina, 2013), and this structure may reflect the termite's adaptation to high solar energy and wind load (Fagundes et al., 2021), which may be due to the lack of protection from dense and closed canopy vegetation in grassy ecosystems. Termite mounds in Cumberland and Uitkomst varied in size, having an average radius and height of 2 m and 2.2 m, with a surface area of up to 111.3 m^2 respectively.

The size of termite mounds may reflect successive stages of gradual soil and organic matter accumulation (Erens et al., 2015) and erosion (Lepage, 1984) during alternating periods of the mound being colonized, abundant, and recolonized by different colonies of termites or even different termite species over time (Erens et al., 2015). These processes could allow the mound to increase in size (Dangerfield et al., 1998), while also influencing nutrient enrichment (Seymour et al., 2014) and the composition of nutrients on mounds (Joseph et al., 2013). For example, the concentrated decomposition of organic material and relocation of soil in the mound over extended time periods can lead to the accumulation of carbonates, nitrogen, phosphorus, exchangeable cations, and clay on termite mound soil (Jouquet et al., 2004; Joseph et al., 2013; Seymour et al., 2014; Lima et al., 2018). High clay content can increase the soil moisture retention (Jouquet et al., 2016), which can increase microbial activities (Fall et al., 2004) and improve plant growth on mounds (Chauhan et al., 2017). As a result, termite mound size can determine the extent of its influence on plant composition (Muvengwi et al., 2017).

This study revealed that large termite mounds supported a higher number of woody plant species compared to small mounds. Additionally, woody plant diversity and density increased with termite mound surface area, and woody stem density was high on large mounds. However, plant species composition did not change across mound sizes. Similar trends were reported in the miombo woodlands, north-western Zimbabwe where species richness of woody plants increased with the mound surface area (Joseph et al., 2013). In the same study, the composition of woody plants changed with mound surface area (Joseph et al., 2013), which was not the case for this study. While large termite mounds may allow high local plant diversity and density of woody plants due to increased resource availability, reduced competition, and reduced fire intensity (Holdo and McDowell, 2004, Ndiaye et al., 2004, Sileshi et al., 2010; Joseph et al., 2013; Muvengwi et al., 2016), the similarity in species composition among termite mound sizes reported in this study may suggest that even if the species richness and their abundance may vary, however, their presence on termite mounds is relatively constant. For example, termite mound vegetation in this study appeared to be dominated by the same species among mound sizes, where the most common species on mound vegetation (e.g., *Lantana camara, Cussonia spicata, Searsia pyroides*, and *Lippia javanica*) were present in all mound size classes (Figure 5.9). This may suggest that termite mounds create conditions that might favour species that are adapted to specific conditions, resulting in similar composition across mound sizes. For example, some species commonly found on termite mounds are evergreen and tend to be associated with higher clay soils (Fleming and Loveridge, 2003), representatives of riparian communities and are often dispersed by birds (Joseph et al., 2014), while matrix species are adapted to dry, nutrient poor soils (Frost, 1996) and produce dehiscent pods which are dispersed by herbivorous mammals (Joseph et al., 2014). This may also explain why the proportion of representatives of termite mounds indicator species increased with termite mound surface area and were more presented in large mounds compared to smaller mounds.

Over 90% of the woody species in this study are dispersed by animals (Appendix 3.1), and as result, species composition may tend to converge towards dominance of a shared regional species pool, resulting in similar species composition across patches (Tatsumi et al., 2020; He et al., 2023). Similar trends in species composition have been observed in systems with a high level of disturbance (Vellend et al., 2007), as disturbance intensity can strongly determine the outcomes of local extinction and colonization processes (Caswell and Cohen, 1991). For example, intense disturbance such as the establishment of alien species as observed in this study, can selectively exclude species that initially existed, reducing the species pool, which can make nearby patches to become compositionally homogenous (Tatsumi et al., 2020). Alien plant species such as *Lantana camara* have been reported to reduce species diversity and composition in many areas (Ruwanza, 2020; Raphela and Duffy, 2023; Ssali et al., 2024). This may have been the case for this study, where the establishment of alien species may have reduced the number of species available to colonize termite mounds patches, resulting in a constant species composition across mound sizes.

The species richness and alpha-diversity in this study appeared to be not affected by the factors that influenced species composition (beta-diversity). The increase in species richness with termite mound area, and the differences in alpha diversity and woody density among termite mound sizes suggest that large mounds may capture more species from the existing species pool. This may be the result of increased space availability, and improved microhabitat conditions, particularly higher clay content with its associated soil moisture retention, and higher soil nutrient concentration on large termite mounds (Turner et al., 2006; Joseph et al., 2013). For example, studies have shown that large mounds contain more nutrients and clay than small mounds (Joseph et al., 2013; Seymour et al., 2014), and this could also in turn influence woody plants productivity, resulting in high woody density stands in large termite mounds, as reported in this study.

Although the overall woody species richness and species of mature trees only were higher on large mounds, the species richness of saplings was not affected by termite mound size. This suggests that while larger mounds support more mature trees, sapling establishment might be influenced by other factors not directly related to mound size. For example, high density of large trees on large mounds may outcompete saplings, while their establishment may be limited by space and resource availability on smaller mounds. Moreover, rodents and invertebrates can also limit seedling establishment as they can be important seedling predators (Shaw et al., 2002). Studies have also noted the effects of large herbivores on seedling regeneration across African savannas (Moe et al., 2009; Støen et al., 2013). For example, Sharam et al. (2009) and Moe et al. (2009) found impala to be important seedling predators. Similarly, Støen et al. (2013) and Mobaek et al. (2005) found that impala preferred feeding on seedlings on termite mounds in the Lake Mburo National Park. As a result, the species richness of saplings may be kept constant by these factors across termite mound sizes, however, their high density on large mounds suggests a trend towards homogenization on these patches.

Conclusions

Termite mound densities within a landscape determines spatial distribution of bush clumps, while mound size can determine the magnitude of the mound's influence on species composition and diversity. The results reported in this study revealed a position relationship between termite mound density and the density of bush clumps occurring within the study areas, suggesting that woody plant recruitment in an area with a high density of vegetated bush clumps may lead to coalescence of the bush clumps thereby forming a woodland or dry forest. Although the community composition of woody plants remained constant across termite mound sizes, the species richness, diversity, and density of woody plants increased with mound size. This suggests that while large termite mounds captured more woody species and supported more trees, new species were not introduced into the termite mound vegetation system, suggesting that regardless of size, termite mounds present similar soil and microclimatic conditions which may only favour species that are well adapted to conditions presented on mounds or to similar habitats such as in lowlands and riparian habitats. Therefore, resulting in similar species composition. Furthermore, a limited local species pool as a result of the introduction of alien vegetation into termite mounds and nearby communities may also lead to the low woody species richness in the species pool and may trigger a trend towards landscape homogenization where a few species colonize available patches.

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CHAPTER 6

Processes during woody vegetation succession in termitaria-facilitated bush clump development in grasslands

Abstract

Woody plant encroachment, characterized by the increase in cover and density of woody vegetation threatens grassy ecosystems in Africa and beyond. However, patterns and underlying processes of woody plants encroachment into grassland areas are not fully understood. This study investigated the patterns and processes of woody plant succession linked to the formation and development of bush clumps on 62 vegetated termite mounds in Cumberland Nature Reserve and Uitkomst Conservation Area in KwaZulu-Natal Province of South Africa. This study specifically determined: (1) the identities of the woody species responsible for initiating the bush clumps; (2) whether woody plant species richness, diversity, and composition change as bush clumps mature and increase in size; (3) whether the species assemblage of saplings in early-stage bush clumps reflects the species assemblage of mature trees in later-stage bush clumps; and (4) whether the degree of forest specialization among saplings and mature trees within bush clumps increases along a successional gradient. The findings revealed that although bush clumps were simultaneously initiated by multiple species, *Vachellia sieberiana* and *Searsia pyroides* were responsible for initiating approximately 48% of the bush clumps. There was an increase in woody basal area, species richness, diversity, and the number of mature trees with increasing bush clump area. A non-metric multidimensional scaling analysis revealed that the difference in woody species assemblage was closely related to bush clump size. Species that initiated bush clumps decreased in proportion as bush clumps increased in size. Additionally, forest specialization of woody plants showed no relationship to bush clump size; instead, the proportion of the alien invasive species increased as bush clumps matured. This finding raises concerns about the long-term residence of native vegetation on bush clumps occurring on termite mounds.

Keywords: Bush clumps, Forest specialisation, *Lantana camara*, Termitaria, Succession, Woody plant encroachment,

Introduction

Woody plant encroachment, the increase in density and cover of native woody vegetation in grassy ecosystems is an issue of global significance, often resulting in a nearly complete turnover of species, with savanna specialists being replaced by forest-adapted species (Archer et al., 2017; Abreu et al., 2021). While patterns of woody plant encroachment are not yet fully understood, an increasing body of literature has contributed to a broader foundation for improving understanding of the underlying processes (Archer, 1990; Bond, 2008; O'Connor and Chamane, 2012; Jamison-Daniels et al., 2021). For example, in South Africa, Bews (1717) described woody plant encroachment as an increase in *Acacia* species (now known as *Vachellia* or *Senegalia* species) around Pietermaritzburg, with later studies also linking woody plant encroachment to an increase of microphylluos species, which may facilitate the later establishment of other woody species, including broad-leaved, bipinnate microphyllous, and evergreen forest specialist species (Wigley et al., 2010; O'Connor and Chamane, 2012; Jamison-Daniels et al., 2021; Adie et al., 2023; Nell et al., 2024), resulting in the formation of dense clumps of woody species (bush clumps) which subsequently expand in size (O'Connor and Chamane, 2012; Jamison-Daniels et al., 2021).

The formation of bush clumps in grassy ecosystems have been recorded in different sites in southern Africa. For example, in the Eastern Cape Province of South Africa, the encroachment of savannas and grasslands by *Vachellia karroo* and later entry of other species has resulted in the formation of bush clumps under large *V. karroo* trees (Bews, 1917; O'Connor and Chamane, 2012; Nell et al., 2024). Similar patterns were reported in Mpumalanga Province, also in South Africa, where existing tree cover facilitated the entry of other species, resulting in a directional change toward forest-type species in larger and mature bush clumps (Jamison-Daniels et al., 2021). Similarly, coastal forests in eastern South Africa have been reported to have a savanna bush clump origin (Adie et al., 2023). Moreover, termite mounds have also been implicated in the formation of bush clumps in KwaZulu-Natal (Gower et al., 1992), Chizarira National Park, north-western Zimbabwe (Joseph et al., 2013), and Gonarezhou National Park, Zimbabwe (Muvengwi et al., 2017).

Bush clumps initiate on at least partially abandoned termite mounds (Blösch, 2002 and 2008). On active mounds, termites rapidly repair any damage, preventing plant colonization, whereas on abandoned mounds, damage is not repaired, allowing erosion and weakening of the hard soil surface, thereby facilitating plant growth (Glover et al., 1964; Blösch, 2008). The establishment of woody plants on termite mounds is supported by frequent visits from granivores and frugivores that deposit seed of woody plants there (Moe et al., 2009). Moreover, termite mounds may support the growth of bush clumps through fire protection, increased soil fertility, and improved soil drainage (Joseph et al., 2013).

Bush clumps are poorly studied in southern Africa (O'Connor and Chamame, 2012). However, there is strong evidence from existing studies to suggest that bush clump development follows a deterministic succession through facilitation, as described by Connell and Slatyer (1977), where an initial plant species supports the establishment of additional plants via a nucleation process facilitated by animal seed dispersal (Yarranton and Morrison, 1974; Acanakwo et al., 2017; Yamashina and Hara, 2019). Deterministic succession describes a directional change in species composition caused by environmental conditions that support the establishment and persistence of specific species (Jamison-Daniels et al, 2021). For example, on termite mounds deterministic succession can be driven by several mechanisms, including disturbance intensity, soil modification (Okullo and Moe, 2012), microclimatic changes (Traoré et al., 2008), and interactions between species (Connell and Slatyer, 1977). These mechanisms may create a predictable sequence of colonization and community assembly (O'Connor and Chamane, 2012; Jemison-Daniels et al., 2021).

During the formation of bush clumps, woody species often create distinctive associations within bush clumps rather than forming random species assembles (Nell et al., 2024). For example, as density of the woody canopy increases along a successional gradient, species composition changes predictably as soil moisture increases (Schönbeck et al., 2015; Jamison-Daniels et al., 2021). Moreover, the composition of saplings in early successional stages tend to be similar to that of mature trees in later stages, thereby demonstrating a predictable transition from saplings to mature trees (Jamison-Daniels et al, 2021). However, early successional tree composition frequently diverges from sapling communities in later stages, demonstrating the limited establishment of early successional species in mature stages (O'Connor and Chamane, 2012; Jamison-Daniels et al., 2021; Nell et al., 2024).

O'Connor and Chamane (2012), Jamison-Daniels et al. (2021), and Nell et al. (2024) reported that deterministic succession in bush clumps results in mature bush clumps being dominated by late-successional forest species. A decline in light levels reaching the ground surface as succession advances and canopy cover closes results in shade-intolerant savanna species being increasingly replaced by shade-tolerant forest species (O'Connor and Chamane, 2012; Jamison-Daniels et al., 2021; Abreu et al., 2021; Adie et al., 2023). Additionally, Jamison-Daniels et al.

(2021) recorded lower maximum air temperatures, flux density of radiant energy and higher humidity levels in mature bush clumps compared to bush clumps that are in early succession stages. As a result, microclimatic changes during bush clump succession can suppress the establishment of herbaceous vegetation, reduce vegetation flammability due to reduced fuel load and provide ideal conditions for fire-intolerant forest species to establish (Abreu et al., 2021; Adie et al., 2023). Thus, the vegetation succession on bush clumps and the resultant microclimatic alterations (Jamison-Daniels et al., 2021), coupled with elevated levels of plant available nutrients and soil moisture on termite mounds (Muvengwi et al., 2017) are likely to promote the establishment and densification of forest species. As a result, bush clump succession is predicted to increase the number of forest specialists while decreasing the number of species with broad ecological needs (Christensen and Peet, 1984; Palmer and Dixon, 1990; Jamison-Daniels et al., 2021).

In this study, the overall aim was to investigate the patterns and processes of woody plant succession linked to the formation and evolution of bush clumps in termite mound facilitated systems. The specific objectives of the study were to: 1) determine the structure and composition of woody vegetation on termite mound facilitated bush clumps, 2) determine the identities of woody species responsible for initiating bush clumps on termite mounds, 3) test whether woody species assemblage, community composition, and community structure changed as bush clumps matured and increased in size, 3) test whether species assemblage of saplings in early stages of bush clump development reflects the species assemblage of mature trees of bush clumps in late development stage, 4) determine whether the degree of forest specialization among saplings and mature trees in bush clumps increases along a successional gradient, and 5) establish whether the species habitat breadth decrease along successional gradients. It was predicted that the similarity in species composition between saplings in small bush clumps and mature trees in large bush clumps would be higher than the similarity between mature trees in small and large bush clumps, suggesting a pattern consistent with deterministic succession. Furthermore, it was hypothesized that species composition would progressively shift towards forest-type species as bush clumps increased in size, accompanied by a decline in savanna-type founder individuals. Additionally, it was expected that species with narrow habitat breadths would become more prevalent in older or larger bush clumps.

Material and methods

Field Sampling

Data collection was carried out from November 2022 to August 2023. Within the sampling units, small saplings were extensively observed, however, no evidence of seedling germination was observed, and most saplings were in a stunted stage possibly as a result of competition with established woody plants, and this stage can last for several decades until suitable conditions permit rapid growth (Jamison-Daniels et al., 2021). Therefore, the season in which the data was collected was unlikely to have effects on the species composition of saplings.

In this study, a bush clump was defined as an association of two or more woody plant species with connecting canopies that were separated from other woody plants by a matrix of grassland (O'Connor and Chamane, 2012). Therefore, vegetation clusters made up of a single woody species were ignored in this study. As a result, a total of 62 bush clumps occurring on termite mounds of various sizes in Cumberland Nature Reserve ($n = 16$) and Uitkomst Conservation Area ($n = 46$) were randomly selected and surveyed.

Bush clumps occurring on termitaria varied in size, however they all displayed an elliptic shape. Therefore, in that context the size of a bush clump on termitaria was modelled as an area inside the perimeter of bush clump canopy cover. The size of each bush clump was determined by measuring its length along its longest axis, and breadth perpendicular to that axis. Bush clump area was then computed as the area of an ellipse (O'Connor and Chamane, 2012; Jamison-Daniels et al., 2021).

Within each bush clump, all individual shrubs and trees were identified to species level using Pooley (1993), which was supplemented by iNaturalist (https://www.inaturalist.org/) and PlantNet (https://identify.plantnet.org/) for additional validation. Woody plant stems for each woody plant surveyed were systematically counted and stem diameter $D(stem)$ was computed using $D(stem) = C(stem)/\pi$, where $C(stem)$ is the woody stem circumference measured in centimetres. Additionally, the stem diameter of woody plants with multiple stems was computed as the total $D(stem)$ computed for each individual stem of the same plant using $D(stem)_{total} = D\ (stem)_1 + D(stem)_2 \ldots + D(stem)_n$. For each woody plant, height (m) was estimated by measuring its vertical height perpendicular to the ground using a 2-m ranging rod.

The number of saplings (< 1.5 m) of each species was counted per bush clump. The 1.5 m threshold to distinguish between saplings and trees was selected, aligning with the range used in other studies differentiating saplings and trees in forests (Janse-Ten Klooster et al., 2007).

This threshold is lower than that used for savanna trees (2–4 meters, Higgins et al., 2000), as bush clump saplings would have experienced minimal or no flame exposure, and a higher cutoff would have resulted in an insufficient number of trees for comparing sapling and tree assemblages between small and large clumps. It was assumed that tree(s) within the bush clumps that had the largest trunk circumference were the founder individuals, around which the clumps initially established (Jamison-Daniels et al., 2021). The trunks of these founder trees were consistently significantly larger than those of other trees in the clumps. However, this assumption has two important sources of error. First, the founder individual may have died; accordingly, a search was made for stumps. Second, the largest individual may be faster growing than the founder, but unfortunately growth rates of woody plants in these ecosystems are not known (O’Connor and Chamane, 2012).

Basal area (BA)for each tree stem was estimated using the formula $BA = C(stem)^2/4\pi$, where A represents the basal area and $C(stem)$ is the circumference of the stem. For multi-stemmed trees, BA was calculated for each stem individually. The total woody basal area per clump was then obtained by summing the basal areas of all stems and served as a proxy for bush clump maturity. Additionally, species richness for both trees and saplings, as well as a count of trees (trees > 1.2 meters), was calculated for each clump. Species diversity was estimated using the Shannon-Wiener index.

Statistical Analysis

All statistical analysis were performed in R statistical computing and graphing program, version 4.4.0 (R Core Team, 2024).

To analyse the community composition of woody plant species on bush clumps of different size classes (small and large) in the two locations (Cumberland and Uitkomst), data on woody species abundance was square root-transformed to weight rare and common species more equally (Clarke and Warwick, 2001). Differences in the community composition of woody plants between small and large bush clump on each location were then assessed with a one-way ANOSIM based on a Bray-Curtis dissimilarity matrix of the species abundance data.

To determine the effects of bush clump size and location on the composition of woody plants assemblage, a permutational multivariate analysis of variance (PERMANOVA) test was used based on a similarity matrix derived using Bray-Curtis method on the square root transformed species abundance data matrix. PERMANOVA is a non-parametric test of significant differences between groups that operates on a distance matrix such as the Bray-Curtis similarity matrix. In this case, the groups were size classes of bush clumps and location. In cases where the experimental design is unbalanced, like in this study, PERMANOVA is sensitive to heterogeneous dispersions. To address this, data were tested for heterogeneity using the *betadisper* function in the *vegan* package. This involved calculating the distance from the spatial median with 999 permutations and adjusting for bias due to unequal sample sizes. Additionally, patterns in woody plants composition were visually displayed using an NMDS ordination plot.

Linear regression models, and where appropriate lognormal regression models with log link function were used to assess the relationships between bush clump size and species richness, Shannon-Wiener diversity, basal area, and density of woody of woody plants. The models were effectively treated as an ANCOVA design by including location as a covariate to account site-specific variations between Cumberland and Uitkomst. Lognormal models were used when the response variable data violated the normality assumptions of a traditional linear regression model (Shapiro-Wilk test: $P < 0.05$) or when the model performed better in modelling data compared to other candidate models (low AIC). Lognormal regression model applies a log transformation the response variables which allows them to meet the model assumptions.

Similarity of the species composition of saplings and trees was compared between large and small clumps. This was undertaken by identifying from the data set 17 of the smallest clumps and 17 of the largest clumps, with the smallest bush clumps representing early successional stage while the largest bush clumps represented late successional stage. The Morisita–Horn index was used to quantify similarity in species composition between small and large bush clumps. This was undertaken by Morisita–Horn similarity index calculating a Morisita–Horn similarity index for each combination of large and small bush clumps.

In a system undergoing deterministic succussion, founder species tend to be replaced by forest specialist species in the later successional stage of bush clump development. As a result, a beta regression model with a link logit function to test whether the proportion of founder tree species decreased as bush clumps increased in size. Location was included as a categorical covariate to the model to account for any variations that may have been caused by differences between Cumberland and Uitkomst, therefore the model was effectively treated as an ANCOVA design. A beta regression model is specifically designed to handle proportional data, which is bounded between 0 and 1, and violates the normality assumptions of a traditional linear regression model.

A community-weighted mean of forest specialization was calculated for each bush clump using the species abundance and species forest specialization data (Appendix 6.1 and 6.2). High values of the community weighted mean represent bush clumps with high numbers of forest specialist species. Thereafter, a lognormal regression model with log link function was used to test whether the community-weighted mean of forest specialization increased with bush clump size. Potential site-specific variations between Cumberland and Uitkomst were addressed by including location a covariant to the model which allows for the assessment of the effects of bush clump size, location independent of bush clump, and the interaction between bush clump size and location on the community-weighted mean of tree forest specialization.

Habitat breadth was calculated for each species by summing the number of habitats (Appendix 5.1 and 5.2) for which the species was described (see Jamison-Daniels et al., 2021), and it was used to compute the community-weighted mean of tree species habitat breadth. A lognormal regression model with a log link function was used to evaluate the relationship between bush clump size and the community-weighted mean of tree species habitat breadth. To account for potential site-specific differences between Cumberland and Uitkomst, location was included as a covariate thereby effectively treating the model as an ANCOVA model.

Results

Bush clumps

Bush clump area ranged from 4 - 450 m^2 (102.14 ± 10.67 m^2) for both Cumberland and Uitkomst. The total number of woody plants per bush clump ranged between five and 128 (mean ± SE = 28 ± 3) and mean (±SE) number of saplings and mature trees was 11.59 (± 1.69) and 16.3 (± 1.67), respectively. The species richness of woody plant ranged between two and 20 species per bush clump (mean ±SE = 5.6 ± 0.41), and the mean (± SE) species diversity computed as Shannon-Wiener index was 1.27 (± 0.07). Additionally, the mean (± SE) number of woody stems was 107.8 ± 16.38 per bush clump across the bush clumps surveyed from in both Cumberland and Uitkomst.

Vegetation structure and composition

I identified a total of 1636 woody individuals, encompassing 54 woody plant species distributed across 31 families, within 62 bush clumps located in Cumberland and Uitkomst (Appendix 6.1). Remarkably, 100% of these species were present both as mature trees (height ≥ 1.5 m) and saplings (height < 1.5 m). The most abundant species identified were the invasive *Lantana camara* and *Rubus ulmifolium*. Among native species, the top three in abundance were *Lippia javanica*, *Cussonia spicata*, and *Searsia (*formerly *Rhus) pyroides* (Figure 6.1). Species such as *Vachellia sieberiana*, *Ziziphus mucronata*, and *Grewia occidentalis* were found at frequencies below 3% across the 62 bush clumps (Figure 6.1). Moreover, the population size structure of the 11 (of 18) most dominant species was dominated by small individuals, indicating a high degree of regeneration (Figure 6.8).

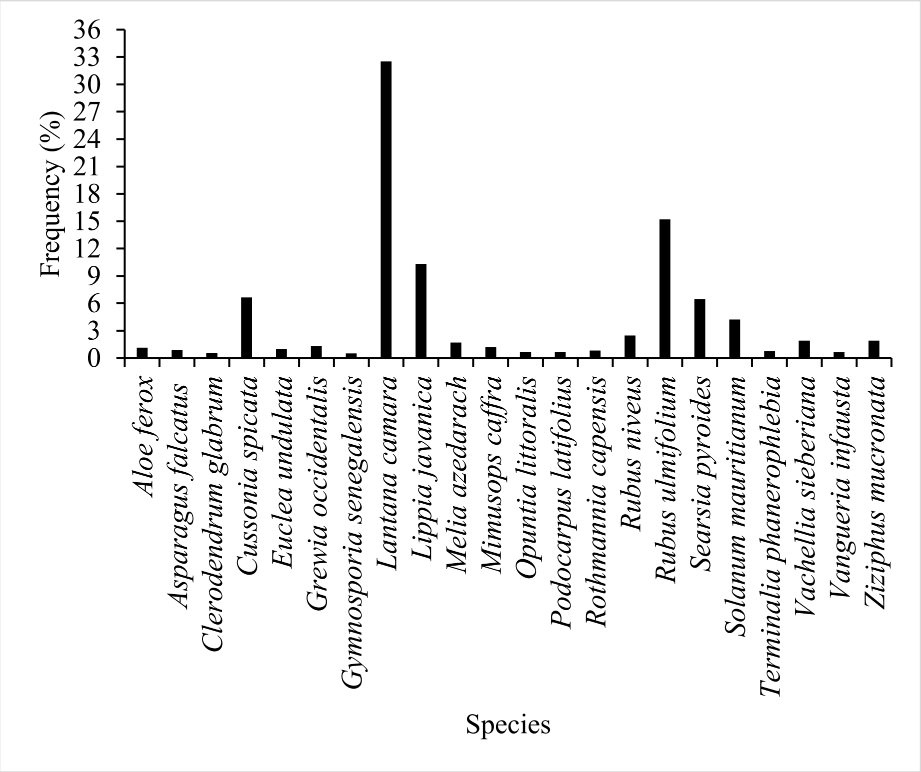

Figure 6.1: Frequency (%) of selected woody species occurring in bush clumps (n = 62).

Bush clump initiation

Representatives of 20 tree species which makes up ~ 42% of the total recorded species were identified as founder individuals across Cumberland and Uitkomst (Table 6.1). The stem diameter of founder individuals per bush clump ranged between 1 cm and 76.9 cm (mean ±SE

= 37 ± 2.8 cm), and their abundance across the bush clumps ranged between one and 57 individuals. Stem diameter of the largest *S. pyroides* and *V. sieberiana* ranged from 14.6 cm to 76.9 cm and 11.8 cm to 76.3 cm, respectively. *S. pyroides* and *V. sieberiana* were the largest individuals in 30 bush clumps (~ 48%), while *Cussonia spicata, Buddleja saligna, Gymnosporia buxifolia, Clerodendrum glabrum, Solanum mauritianum, Vangueria infausta,* and *L. camara* were the largest individuals in 22 bush clumps (~ 35%). The other remaining species were founder individuals in one bush clump each in ~ 16% of the bush clumps (Table 6.1).

Table 6.1: Founder species identified in bush clumps (n = 62) at Cumberland and Uitkomst. Founder species were identified as individuals with the highest stem diameter in a bush clump.

Species	**Family**	**Location**	**Number of bush clumps**
Acacia mearnsii De Wild.*	Fabaceae	Uitkomst	1
Aloe ferox Mill.	Asphodelaceae	Cumberland	1
Buddleja saligna Willd.	Scrophulariaceae	Cumberland	3
Celtis africana Burm.f.	Cannabaceae	Cumberland	1
Clerodendrum glabrum E.Mey.	Lamiaceae	Uitkomst	2
Cussonia spicata Thunb.	Araliaceae	Cumberland , Uitkomst	7
Ekebergia capensis Sparrm.	Meliaceae	Cumberland	1
Grewia occidentalis L.	Malvaceae	Uitkomst	1
Gymnosporia buxifolia (L.) Szyszyl	Celastraceae	Uitkomst	3
Jacaranda mimosifolia D.Don*	Bignoniaceae	Uitkomst	1
Lantana camara L.*	Verbenaceae	Uitkomst	3
Melia azedarach L.*	Meliaceae	Uitkomst	1
Rothmannia capensis Thunb.	Rubiaceae	Uitkomst	1
Searsia pyroides (Burch.) Moffett	Anacardiaceae	Uitkomst	15
Solanum mauritianum Scop.	Solanaceae	Uitkomst	2
Tecoma stans (L.) Juss. ex Kunth*	Bignoniaceae	Uitkomst	1
Terminalia phanerophlebia Engl.	Combretaceae	Uitkomst	1
Vachellia sieberiana (DC.) Kyal. and Boatwr.	Fabaceae	Cumberland , Uitkomst	15
Vangueria infausta Burch.	Rubiaceae	Uitkomst	2

Ziziphus mucronata Willd.	Rhamnaceae	Uitkomst	1

* Indicates alien species

Processes during bush clump development

The multidimensional scaling with a cluster analysis revealed that at broad levels of similarity (70%), two core categories emerged: (1) Cumberland large bush clumps clustered as a group with large bush clumps in Uitkomst, (2) large bush clumps in Uitkomst clustered as a group with small bush clumps in the same locality and large bush clumps in Cumberland (Figure 6.2). At lower similarities (40% and 30%), four categories emerged. The groupings at lower similarities consisted of (1) large and small bush clumps in Uitkomst, (2) large and small bush clumps in Uitkomst and an overlap of large bush clumps in Cumberland. Additionally, only one group combined large and small bush clumps in Uitkomst, large bush clumps in Cumberland, and only one small bush clump in Cumberland.

An ANOSIM revealed that the species composition between Cumberland and Uitkomst was significantly different (R statistics = 0.645, $P = 0.001$), and also between small and large bush clumps in both locations (R statistics = 0.23, $P = 0.002$, Figure 5.3). A PERMANOVA test confirmed that the composition of woody plant assemblages on large bush clumps was distinct from vegetation assemblages in small bush clumps in both locations ($R^2 = 0.19$, $F = 15.1$, $P = 0.001$). The woody plant assemblage in Cumberland was also significantly different from the woody plant assemblage in Uitkomst for both large and small bush clumps ($R^2 = 0.047$, $F = 3.785$ $P = 0.002$). Additionally, the interaction effect of location and bush clump size was also significant ($R^2 = 0.025$, $F = 1.98$, $P = 0.032$), suggesting that the effect of bush clump size on the species composition varied between Cumberland and Uitkomst. Additionally, the mean (± SE) similarity in woody species composition computed as Morisita-Horn index of mature trees in large bush clumps and mature trees in small bush clumps was 0.76 ± 0.034, indicating a high level of similarity between the two groups.

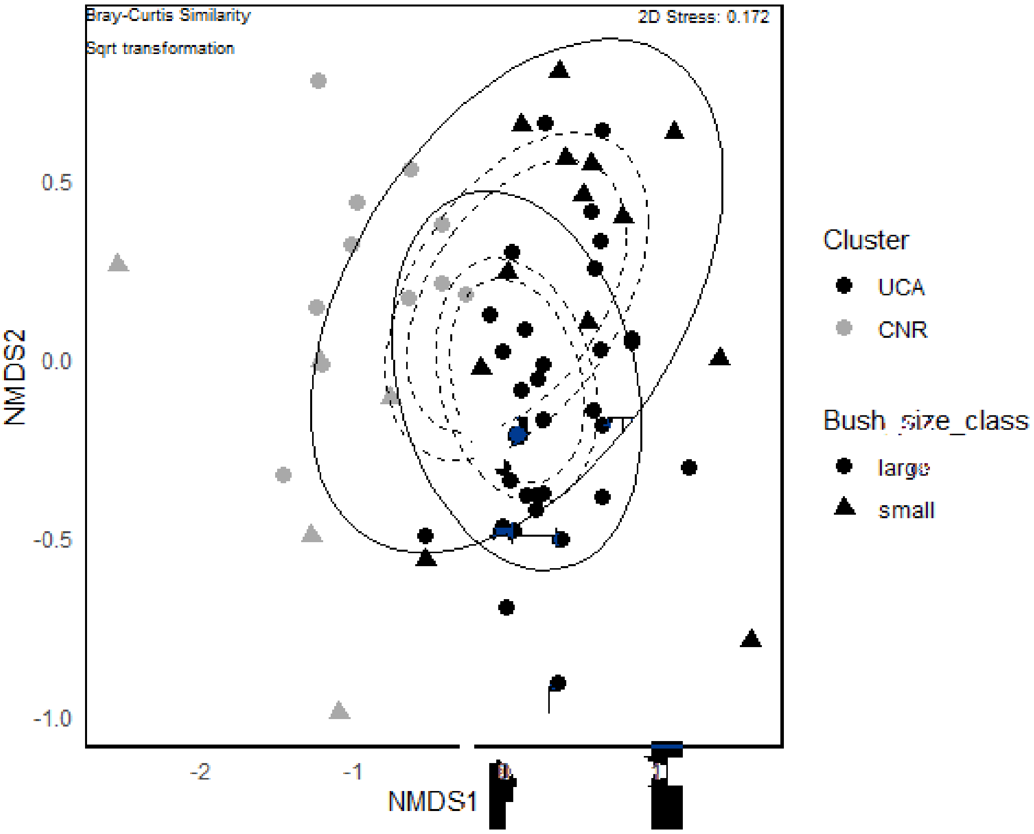

Figure 6.2: NMDS ordination based on Bray-Curtis distance matrix representing assemblages of woody plant species for Cumberland and Uitkomst Conservation in small (< 50 m^2) and large (≥ 50 m^2) bush clump sizes. solid circles represent > 70% similarity, and dotted circles represent 30% and 40% similarity.

A lognormal regression model revealed that bush clump size had a significant positive effect on the number of trees ($t = 7.348$, $P = 0.017$, Figure 6.3), indicating that the number of trees increased along the successional gradient towards bush clump maturity. However, the main effect of location, and the interaction between bush clump size and location were not significant ($P > 0.05$), indicating that the effect of bush clump size on the abundance of trees was consistent between Cumberland and Uitkomst.

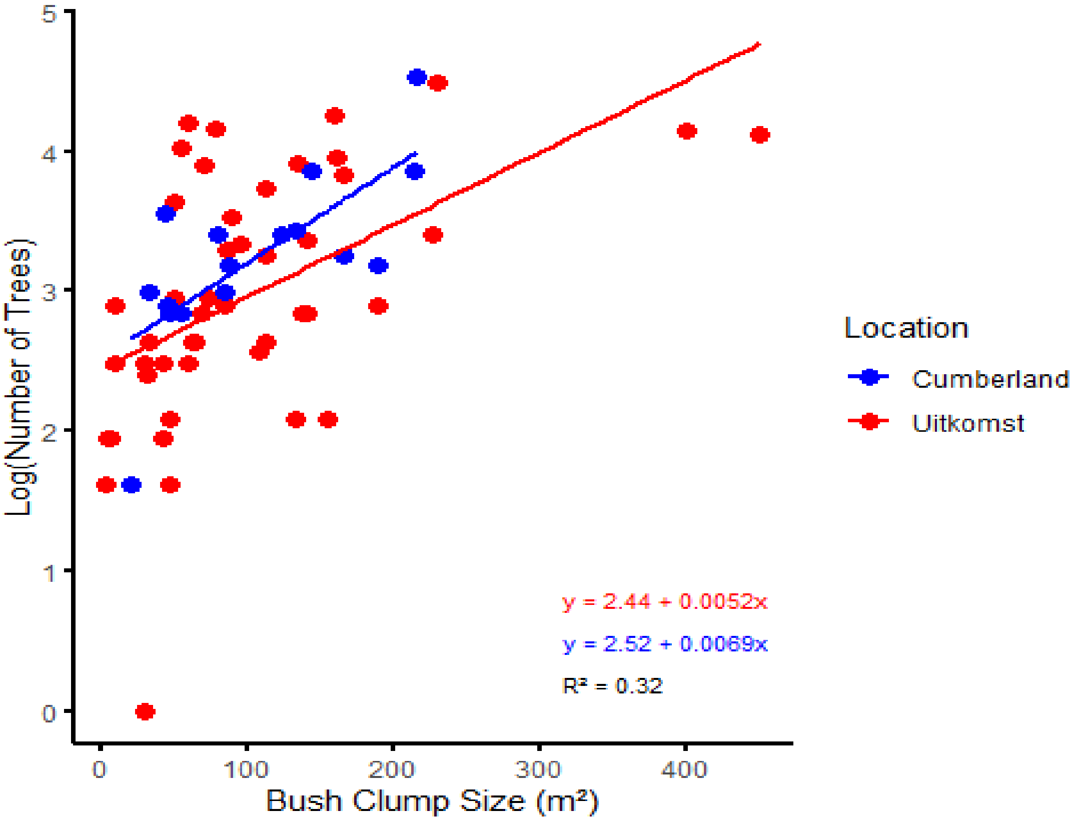

Figure 6.3: Relationship between number of trees per bush clump and bush clump size. The lognormal linear regression model explained 32.05% of the variation in the number of trees ($R^2 = 0.32$, $F_{(3, 58)} = 9.119$, $P < 0.001$).

The was a significant positive effect of bush clump size on Shannon diversity of woody plants ($P = 0.0116$), suggesting that Shannon diversity of woody plants increased as bush clumps matured and increased in size (Figure 6.4a). The main effect of location and the interaction between bush size and location was not significant ($P > 0.05$), indicating that Shannon diversity was not significantly different across both locations and the effect of bush clump size was similar between Cumberland and Uitkomst. Similar patterns were observed for the overall species richness of woody plants (Figure 6.4b) and the species richness of mature trees (Figure 6.4c).

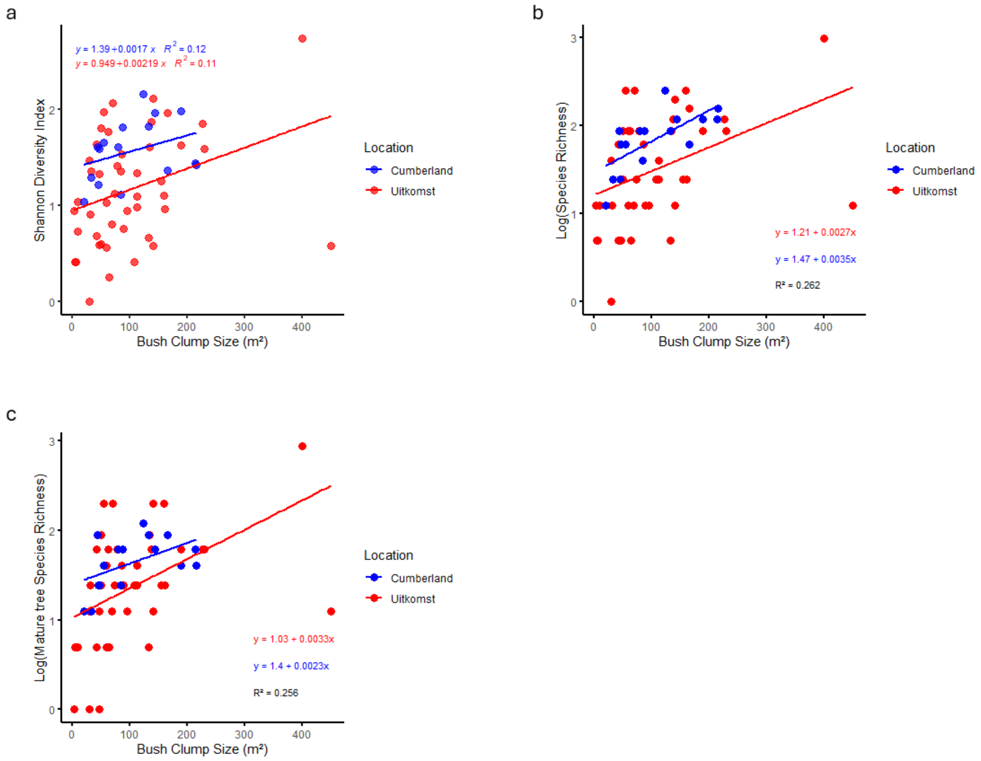

Figure 6.4: (a) The relationship between bush clumps size and Shannon diversity of woody plants in Cumberland and Uitkomst. A linear regression model explained 20.3% of the variation in Shannon diversity ($R^2 = 0.203$, $F_{(3,\,58)} = 4.936$, $P = 0.004$). (b) The relationship between the overall woody plants species richness, the lognormal linear regression model explained 26.2% of the variation in the overall species richness ($R^2 = 0.262$, $F_{(2\,,58)} = 6.862$, $P < 0.001$). (c) The relationship between bush size and species richness of mature trees in Cumberland and Uitkomst and a lognormal linear regression model explained 25.58% of the variation in the species richness of mature trees ($R^2 = 0.256$, $F_{(2,\,58)} = 6.646$, $P < 0.001$).

A linear regression model revealed that there was significant positive effect of bush clump size on sapling species richness ($P = 0.0209$, Figure 6.5), suggesting the species richness of sapling increased with bush clump size. Moreover, there was a significant interaction between bush clump size and location ($P = 0.027$), indicating that the effect of bush clump size was significantly different between Cumberland and Uitkomst, However, the main effect of location was not significant ($P > 0.05$), suggesting that sapling species richness differences across the locations are mainly due to bush clump size rather than inherent differences across the locations.

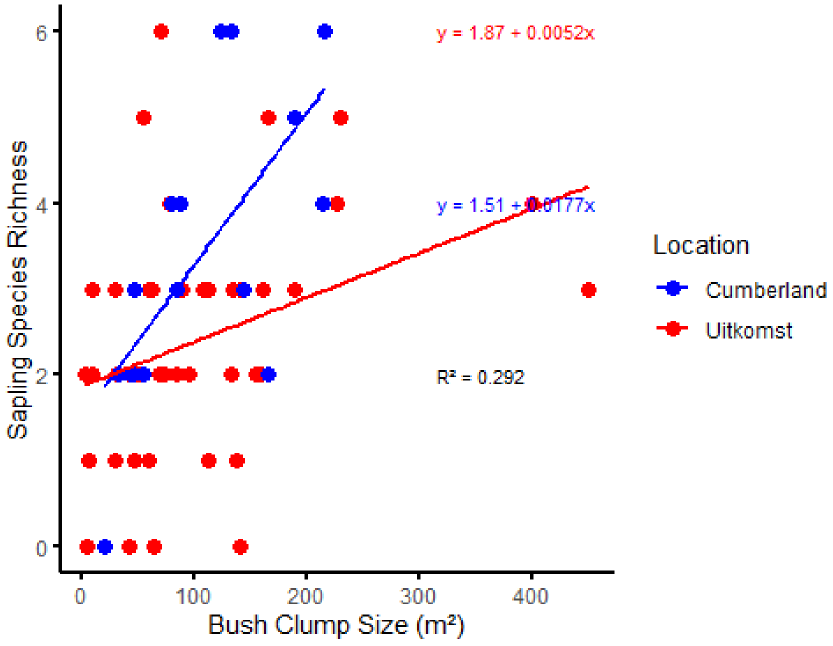

Figure 6.5: The relationship between the bush clump size and sapling species richness in Cumberland and Uitkomst. A linear regression model explained 29.2% of the variation in woody sapling species richness ($R^2 = 0.292$, $F_{(3, 58)} = 7.965$, $P < 0.001$).

Bush clump size had a significant positive effect on woody basal area ($t = 6.42$, $P < 0.001$, Figure 5.6a), indicating that woody basal area increased with bush clump size. The effect of location and the interaction between bush clump size and location were not significant ($P > 0.05$), suggesting that basal area was not significantly different between Cumberland and Uitkomst, and the effect of bush clump size on basal area was consistent across both locations. Similarly, the diameter of largest trees increased with bush clump size ($t = 5.525$, $P < 0.001$, Figure 6.6b), however the main effect of location and the interaction between bush clump size and location was not significant ($P > 0.05$), suggesting that the effect of bush clump size on the diameter of largest trees was the same between Cumberland and Uitkomst. Similar trends were observed for the diameter of largest *S. pyroides* and *V. sieberiana* (Figure 6.6c), and the diameter of largest trees when *S. pyroides* and *V. sieberiana* were excluded (Figure 6.6d)

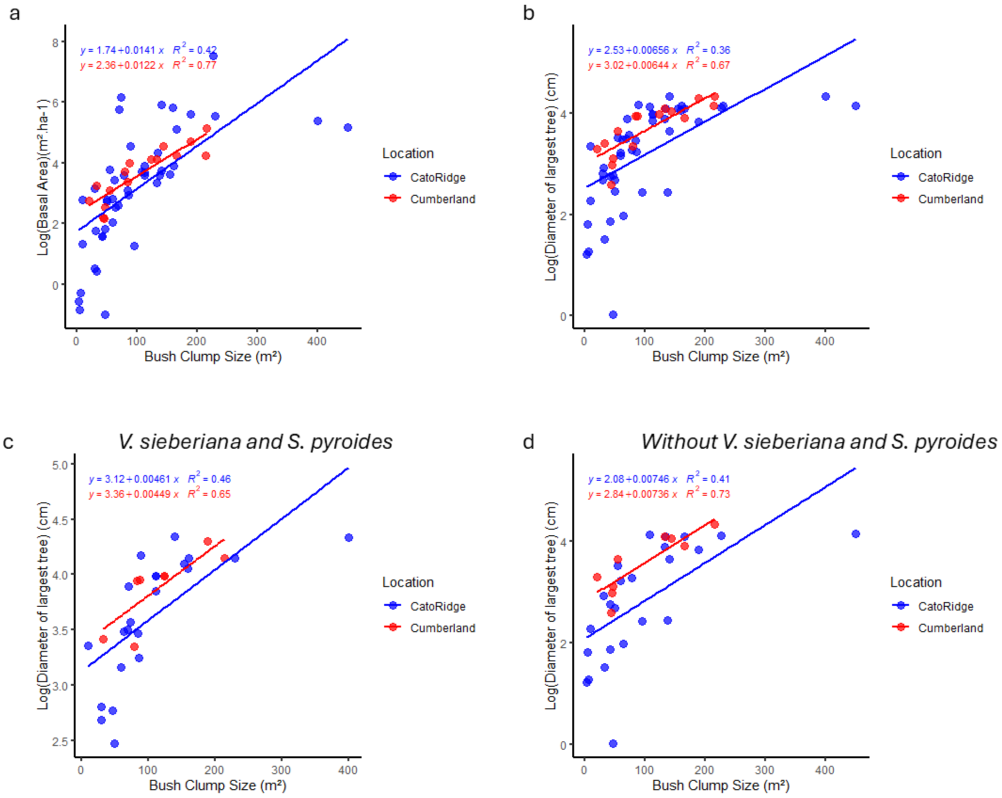

Figure 6.6: Lognormal linear regression models revealed that bush clump size had a significant positive effect on woody basal area and diameter of largest trees in Cumberland and Uitkomst ($P < 0.001$). (a) The model explained 45.34% of the variation in basal area ($R^2 = 0.453$, $F_{(3, 58)} = 16.04$, $P < 0.001$). (b) The model explained 41.74% of the variation in the diameter of largest trees ($R^2 = 0.42$, $F_{(3, 58)} = 13.85$, $P < 0.001$). (c) The model explained 50.86% of the variation in the diameter of largest *S. pyroides* and *V. sieberiana* ($R^2 = 0.51$, $F_{(3, 58)} = 8.97$, $P < 0.001$). (d) The model explained 49.1% of the variation in the diameter of largest trees excluding *S. pyroides* and *V. sieberiana* ($R^2 = 0.49$, $F_{(3, 58)} = 9.327$, $P < 0.001$).

A beta regression model showed a significant negative effect of bush clump size on the proportion of founder species representatives ($z = 2.17$, $P = 0.03$), indicating that the proportion of founder species representative decreased as bush clumps matured and increased in size (Figure 6.7). The main effect of location, and the interaction between bush clump size and location were not significant ($P > 0.05$), indicating that the observed pattern was similar across Cumberland and Uitkomst. However, the proportion of alien woody species within a bush clump significantly increased with bush clump size.

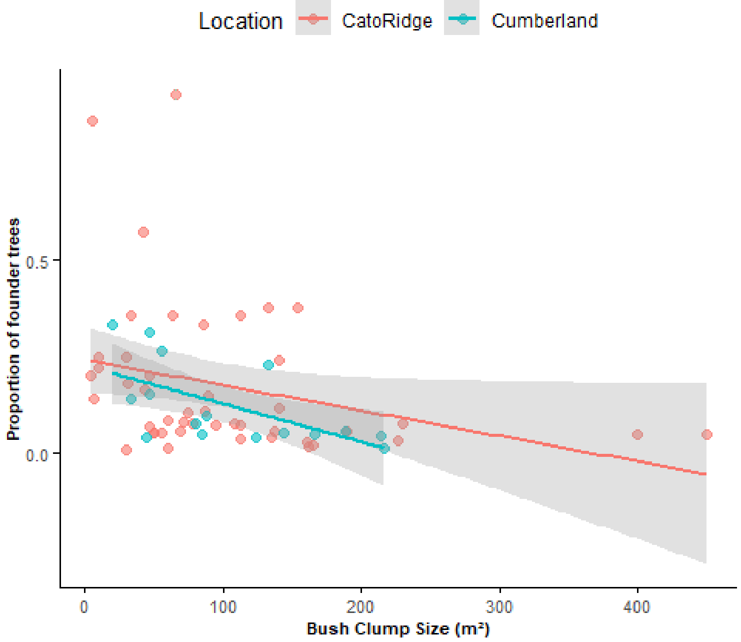

Figure 6.7: A beta regression model revealed a significant negative relationship between bush clump size and the proportion of founder species individuals in a bush clump (pseudo R^2 = 0.17, $z = 5.541$, $P < 0.001$).

A lognormal regression model revealed that the main effect of bush clump size on the community-weighted mean (CWM) of tree forest specialization was not significant ($P > 0.05$), indicating that, on average, tree forest specialization did not increase with bush clumps size. Similarly, the main effect of location was not significant ($P > 0.05$). However, the interaction between bush clump size and location (Cumberland) was significant ($t = 2.38$, $P = 0.021$), indicating that the effect of bush clump size on the CWM of tree forest specialization significantly differed between Cumberland and Uitkomst. The interaction indicates that in Cumberland, bush clump size had a negative effect on the CWM of tree forest specialization (Figure 6.8), whereas in Uitkomst the relationship was not significant. Additionally, the main effect of bush size, location, and the interaction between them had no significant effect on the CMW of woody sapling forest specialization ($P > 0.05$).

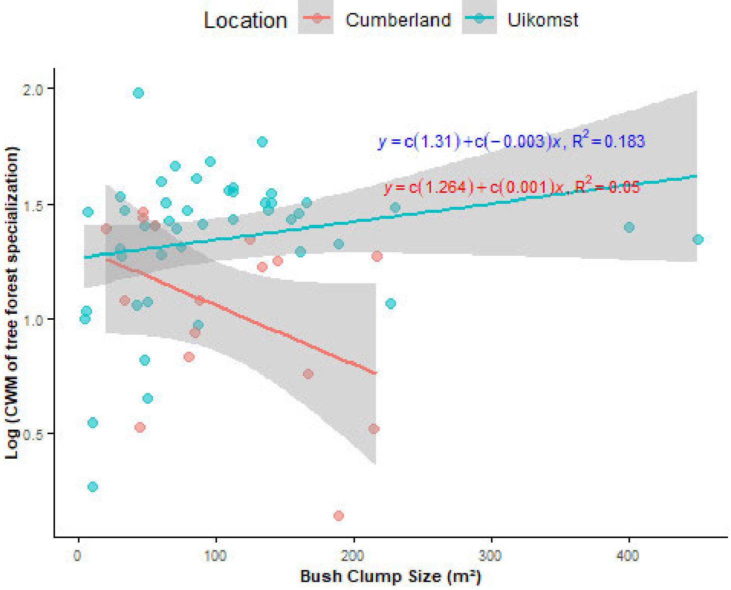

Figure 6.8: The relationship between the bush clump size and the community-weighted mean of tree forest specialization in Cumberland and Uitkomst. A lognormal regression model explained 21.87% of the variance in the community-weighted mean of tree forest specialization ($R^2 = 0.2187$, $F_{(4, 57)} = 3.99$, $P = 0.006$)

Species with narrow habitat breadths were expected to be common in large clumps. However, a lognormal regression model revealed a non-significant relationship between community-weighted mean of tree species habitat breadth and bush clump size ($F_{(1, 58)} = 0.245$, $P = 0.622$). The main effect of location ($F_{(1, 58)} = 0.133$, $P = 0.716$), and the interaction between bush clump size and location ($F_{(1, 58)} = 1.824$, $P = 0.182$) were also not significant, suggesting that the effect of bush clump size on tree species habitat breadth was the same across Cumberland and Uitkomst. Similar results were obtained for woody sapling species habitat breadth.

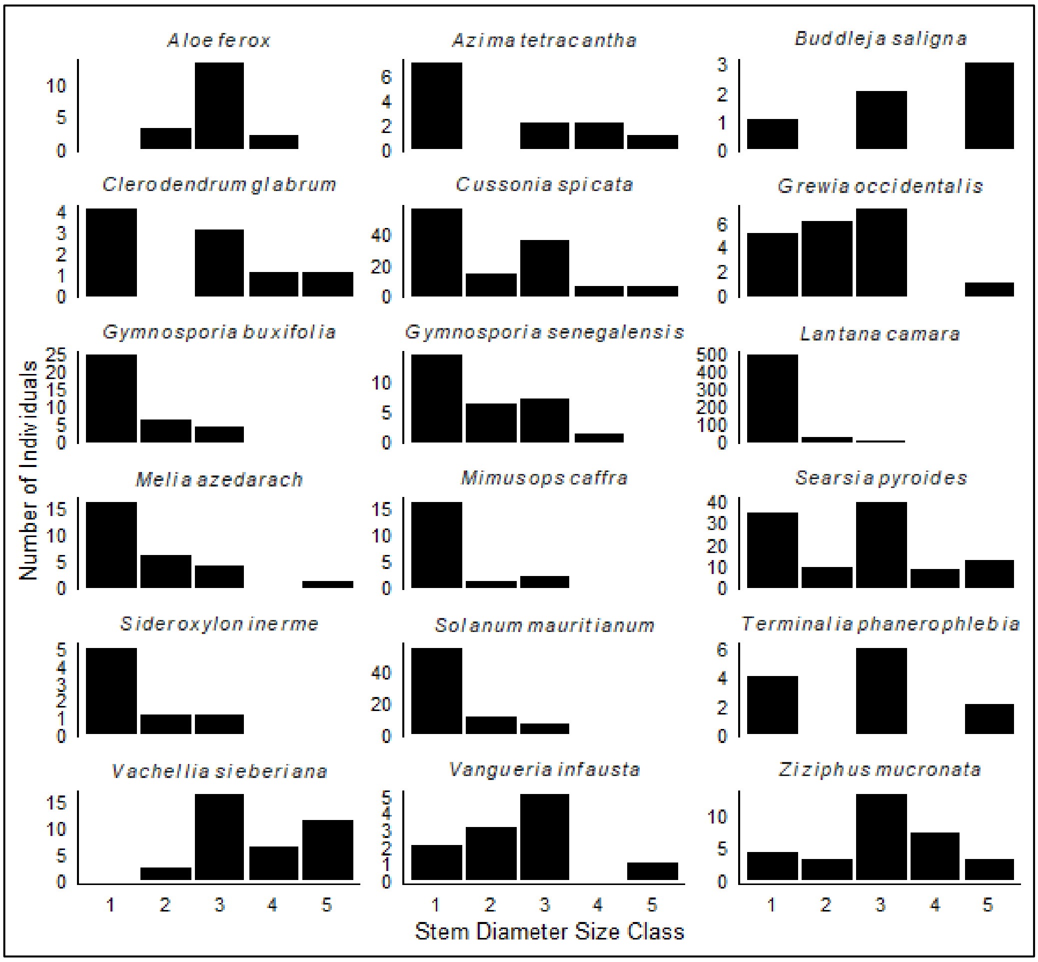

Figure 6.9: Total number of trees per species based on their stem diameter size classes for selected woody species in 62 bush clumps Cumberland and Uitkomst. The stem diameter size class codes were: 1 is < 5 cm, 2 is 5 - 10 cm, 3 is >10- 30 cm, 4 is >30 - 40 cm, and 5 is > 40 cm.

Discussion

Termite mounds facilitate the initiation and development of bush clumps

In grassy ecosystems, bush clumps often develop on fire refugia such as rocky outcrops, under large savanna trees, and on partially abandoned termite mounds (Gower et al., 1992; Bloech, 2008; Carlucci et al., 2011; Joseph et al., 2013; Abreu et al., 2021). Similarly, well developed and developing bush clumps reported in this study occurred on termite mounds. Abandoned mounds, where mound damage is not repaired by the termites, provide a good seed bank, and site for plant establishment (Blösch, 2008). Moreover, woody plants establishing in abandoned mounds are likely to have higher survival changes due to the absence of termites that would otherwise prey on these plants in active mounds. A similar pattern of initial bush clump development has been observed in KwaZulu-Natal, South Africa, where abandoned termite mounds facilitated the establishment of *Vachellia nilotica*, a species commonly associated with woody plant encroachment (Gower et al., 1992). This process, as described by Gower et al. (1992), led to the nucleation of various other species, including *Burchellia bubalina, Cussonia spicata, Dovyalis zeyheri, Ehretia rigida, Grewia occidentalis, Gymnosporia heterophylla*, and *Ziziphus mucronata,* thereby forming bush clumps. However, in the present study, although mound damage was observed in all vegetated mounds (V. Ngcobo, pers. obs., 2023), there was no evidence to suggest that the mounds in the area were abandoned. The absence of data on termite activity limits conclusions regarding the functional status of the mounds. Incorporating pitfall traps to sample for termites on vegetated mounds would have provided valuable insights into the presence of termites and potentially clarified whether the mounds were active or had been abandoned. Shrubs of the invasives *L. camara* and *R. ulmifolium* were the most dominant species in the bush clumps system on termite mounds, occurring at frequencies of up to 30%. This highlights the vulnerability of termite mound vegetation to alien plant invasion, since native species commonly of grassland and savanna origins such as *Lippia javanica, C. spicata*, *V. sieberiana, Ziziphus mucronata, Grewia occidentalis*, and *Searsia pyroides* only occurred at low (< 10%) frequencies. The invasion of native- by alien vegetation, particularly *L. camara,* has been reported many times in southern Africa (e.g. Vardien et al., 2012; Bitani and Downs, 2022; Shiri et al., 2023).

Bush clump initiation

Consistent with Bews (1917), O'Connor and Chamane (2012), and Jemison-Danials et al. (2021), bush clumps reported in this study were simultaneously initiated by several species rather than a single species. *S. pyroides* and *V. sieberiana* were identified as the main founder species responsible for the initiation of ~ 48% of bush clumps in Cumberland and Uitkomst. Trees of these species were the largest individuals in most of the largest bush clumps, with *V. sieberiana* being responsible for the initiation of bush clumps in Cumberland, and also a most common species in the grassland matrix. The successful invasion of *Vachellia* species into grasslands is thought to be linked to characteristics of its seed ecology (O'Connor et al., 2010; O'Connor and Chamane, 2012) and the dynamics of its seedlings in response to changes in fire and grazing regimes (O'Connor, 1994). Additionally, the effects of rising atmospheric CO_2 levels on the growth of C_3 woody plants in C_4 grasslands may also play a role (Bond and Midgley, 2012). *Vachellia* species establish a seedling bank within the grassland (O'Connor, 1994), enabling them to take advantage of rare opportunities for establishment into suitable habitats, like the movement of seeds by small mammals such as rodents and ground-dwelling insects to sites that are conducive for seed germination such as on termite mounds. Although *Vachellia* species offer an unattractive perch to frugivorous birds because they do not produce fleshy fruits (Archer, 1995), they offer shade and forage to mammalian herbivores (O'Connor and Chamane, 2012). As a result, mammalian visitors may enhance seed deposition under the canopy, and the germination and establishment of seedlings is enhanced by modified microclimate and soil conditions on termite mounds under the *Vachellia* species canopy.

Although *S. pyroides* is typically found in various habitats including open grasslands, in Uitkomst it was only found on termite mounds facilitated bush clumps and large trees of this species were also observed in lowlands along the river, but not in the grassland matrix. This suggests the role of endozoochoric dispersal where birds deposit seeds of *S. pyroides* from its large population along the river to termite mounds while perching on termite mounds. Similarly, *C. spicata*, a species typically found in forest margins, bushveld, and on rocky outcrops (Boon, 2010), initiated seven bush clumps, which included five large bush clumps. Trees that produce fleshy fruits may promote a higher rate of initial bush clump development because these trees are mostly preferred by frugivorous birds and mammalian visitors. Other bird-dispersed species such as *Buddleja saligna, Gymnosporia buxifolia, Clerodendrum glabrum,* and *Vangueria infausta* and the invasives *Lantana camara* and *Solanum mauritianum* also initiated 22 bush clumps at Cumberland and Uitkomst.

Lantana camara was the largest tree in two small bush clumps (42 – 47 m^2) and surprisingly in one large bush clump (> 65 m^2) at Uitkomst. Bush clumps initiated by *Lantana camara* were dominated by saplings of *S. mauritamun* and few *S. pyroides* < 2 m tall and stem diameter < 3 cm. This raises questions about using the clump area to approximate its age when dealing with alien species because they are fast growing and can colonize patches in extremely large abundance compared to native species. As a result, bush clumps with these species would expand more rapidly compared to other bush clumps. Similar patterns may be true for bush clumps where *Melia azedarach* was the largest individual; an observation that was made on the largest bush clump at Uitkomst, which was dominated by a dense stand of *L. camara* and *S. mauritamun* > 2 m in height. As a result, knowledge of growth rates of these species would improve the strength of the assumption about large individuals being founder individuals (O'Connor and Chamane, 2012).

Bush clump development

This study found that as bush clump size increased, there was a corresponding increase in tree abundance, woody basal area, species richness, and overall diversity; however, species evenness did not show a similar trend. The results reported in this study are consistent with those reported in O'Connor and Chamane (2012) for bush clumps in the Kei Road region of the Eastern Cape and Jamison-Daniels et al. (2021) for bush clumps in Buffelskloof Nature Reserve, South Africa. Studies have linked these patterns to changes in soil conditions, microclimate, and light availability as bush clumps mature and increase in size (Schönbeck et al., 2015; Jamison-Daniels et al., 2021; Nell et al., 2024). For example, Jamison-Daniels et al. (2021) reported that minimum temperature increased with bush clump size. High temperature increases the growth rates of tree seedlings thereby allowing them to escape the fire trap and grow into mature trees, resulting in a higher number of trees in large bush clumps. Bush clumps have been also reported to improve soil fertility (Jarvel and O'Connor, 1999; Bloesch, 2008; Zuwanza and Shackleton, 2016). Improved soil fertility promotes plant growth, enhance plant productivity, and allow different species to coexist.

Consistent with the results reported in O'Connor and Chamane (2012), the results of the present study indicate that woody plant species composition changes with bush clump maturation, resulting in distinct assemblages between small and large bush clumps. In this study, differences in species composition between large and small bush clumps may have resulted from the decreasing in proportion of founder species representatives as clumps increased in size. Low irradiance (Jarvel and O'Connor, 1999), reduced evapotranspiration rate (Jemison-Danials et al., 2021), low light intensity (Abreu et al., 2021; Adie et al., 2023), and increase soil moisture content under the canopy of large bush clumps can favour the late entry of species that are shade-intolerant, have high water requirements, or both, such as*, Ekebergia capensis, Searsia natalensis,* and *Mystroxylon aethiopicum* which were found in bush clumps in Cumberland and Uitkomst. Only *L. camara* maintained its representation across the bush clump size gradient because it was found in very early stages of bush clump initiation in Uitkomst and also found in accruing in very high abundances in large bush clumps across Cumberland and Uitkomst.

Although species typically found in riparian habitats, forest margins and true forest species were present in the bush clumps, evidence of a directional change towards forest-like species in large bush clumps was lacking. In particular, the results on this study showed no evidence of a relationship between species forest specialization and bush clump size or maturity in

Uitkomst, while in Cumberland tree forest specialization showed a decreasing trend as bush clumps increased in size. Instead, alien invasive plants, particularly *L. camara* as were more abundant in large bush clumps across Cumberland and Uikomst (V. Ngcobo per. Obs. 2023), suggesting termite mound facilitated bush clumps were susceptible to an invasion by alien plants as they matured. Alien invasive plants with as *L. camara* and *R. ulmifolium* being the most abundant among these may have suppressed the establishment forest-type species in large bush clumps. Consistent with these results, Pandey and Chauchan (2012) stated that the allelopathic aggression of alien vegetation, particularly the invasive *L. camara* can reduce germination, growth, and vigour of nearby plants, thereby competitively excluding them. Moreover, invasive shrubs can be dominant understorey species in disturbed systems, which can disrupt succession and decrease local diversity (Pandey and Chauchan, 2012). This may also explain why the species habitat breadth showed no relationship with succession. Another explanation can lie within browsing intensity across the studied locations. For example, browsing intensity appeared to very high Cumberland which can be attributed to high number of browsing animals in the area. These animals may have utilized saplings of forest species in large bush clump, thereby suppressing them.

The species composition of saplings in small bush clumps was found to be similar to that of mature trees in large bush clumps (Morisita-Horn index > 0.7), consistent with patterns expected under deterministic succession. This suggests that the composition of mature trees in larger clumps is closely related to that of saplings in smaller clumps, reflecting a predictable trajectory in species turnover as clumps develop (Jamison-Danials et al., 2021). This would indicate that saplings establishing from the seed bank of small bush clumps grow to become the large trees in large bush clumps, consistent with findings made by Jamison-Danials et al. (2021). According to Cramer (2007) and Norden et al. (2009), the direction of a successional pathway can be affected by factors such as site condition and dispersal limitation. Dispersal barriers can result in spatial clustering and increased species dissimilarity between nearby sites (Dent et al., 2013), which was the case in this study, where patches of similar size may have similar conditions, and consequently, similar species composition. Moreover, the majority of bush clump species bear drupe-type fruits, which indicates the role of animal seed dispersal (Sinnott-Armstrong et al., 2018). As a result, seed dispersal from the nearby lowland to communities on termite mounds, which provide perches and shade for bird and mammal dispersers, was not restricted. However, seeds of more woody species were captured on large bush clumps, and the altered microclimatic and soil conditions may have allowed the establishment of new species that are rare and may not be supported in small bush clumps. Seeds that germinate beneath the canopy of these founder trees, likely facilitated by the increased resource availability on termite mounds, contribute to the further expansion of the bush clumps (Bews, 1917; O'Connor and Chamane, 2012).

Conclusions

This study highlights the role of founder species in the initiation and development of bush clumps on fire refugia such as termite mounds. I found that in Cumberland and Uitkomst bush clumps were simultaneously initiated by more than one species, with *V. sieberiana* and *S. pyroides* accounting for the initiation of nearly 50% of the bush clumps recorded. The dissimilarities in species composition between small and large bush clumps, increase in species richness, diversity, and woody plants productivity with bush clump size suggests deterministic succession, which may be influenced by changes in soil properties and microclimatic conditions as bush clumps mature. However, the introduction of alien woody species into the system may have resulted in changes to succession patterns leading to an increase in abundance and frequency of these species, while limiting the entry of forest specialist species in later successional stages as reported by many studies. In the context of woody plant encroachment, such patterns could be skewed towards alien woody species at the expense of native herbaceous and woody vegetation, leading to significant changes in the landscape. As bush clumps expand and mature, they could eventually merge with nearby clumps and dominate large areas, leading to a more homogenized closed canopy system typical of encroached landscapes or formation of forests.

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CHAPTER 7

Synthesis and directions for future studies

General discussion

Land degradation in grassy ecosystems is commonly demonstrated by a decrease in herbaceous vegetation cover with its associated changes in plant species composition, particularly towards the increase of woody vegetation cover and density (woody plant encroachment). Although large scale factors such as the global increase of atmospheric CO_2, climate change, and changes in land use and land management practices are commonly cited to be the leading factors driving grasslands transition to woody plants dominated landscapes (Kgosikoma and Mogotsi, 2013; O'Connor et al., 2014). However, processes occurring at a local scale such as the presence of termite mounds and associated termite activities, depending on their density and spatial distribution may be some of the important factors influencing vegetation assemblages in landscapes in which they occur.

This study aimed to investigate the role of termite mounds in shaping woody vegetation patterns within grassy ecosystems, with a particular emphasis on how termite mounds facilitate the formation and expansion of bush clumps, ultimately contributing to woody plant encroachment. The objectives were: 1) to review relevant literature in order to identity the mechanisms in which termites generate spatial heterogeneity, thereby influencing woody vegetation assemblages in African grassy ecosystems, 2) investigate the development pattern of bush clumps in Uitkomst, 3) to assess the influence of termite mounds on woody species richness, diversity, composition, and examine the role of termite mounds to the formation of bush clumps, 4) to explore how the species richness, diversity, and composition of woody plants changes in relation to termite mound size, and assess the relationship between spatial distribution of termite mounds and woody vegetation cover, and 5) to investigate the pattern and processes of woody plant succession linked to the formation and evolution of bush clumps in systems facilitated by termite mounds.

A review of literature highlighted that termites generate spatial heterogeneity in resource distribution through several ways. For example, their mound-building and associated activities improve soil fertility and increase soil moisture retention by redistributing mineral rich clay particles from deep soil layers. Increased soil fertility and moisture on termite mounds promote high seed germination probability, seedling establishment, and rapid woody plant growth.

Reduced competition from grasses due to high consumption of grass biomass by termites, and protection from frequent fires due to reduced grass fuel biomass on termite mounds and elevated topography of mounds may further amplify this process, leading to a formation of bush clumps which are an initial indicator of woody plant encroachment. Woody plant encroachment is a threat to grassland management due to the suppression herbaceous vegetation by woody species (Inman et al., 2020). This can have negative impacts on the ecosystem functioning and the provision of ecosystem services. For example, the increase of cover and density associated with woody plant encroachment can reduce the extent of high-quality rangeland and livestock carrying capacity (Archer, 2010).

In chapter 3, the results provided evidence that bush clumps in Uitkomst initiated on termite mounds. The earliest reported bush clumps in this area were observed in prior 1964, and all the bush clump that were observed in in 1964 were present in 2024. Bush area increased over the 60-year period, with the increase being more prevent in the grassland at an overall expansion rate of 4.7 m^2. $year^{-1}$ compared to 0.15 m^2.$year^{-1}$ in the cropland area (now abandoned) between 1964 and 2003. However, post 2003 (when the cropland was abandoned) the expansion rate of bush clumps was higher in the cropland area.

In chapter 4, the results showed that the occurrence of termite mounds had an effect on woody vegetation species richness, diversity and composition in Cumberland and Uitkomst. The results showed that termite mounds supported more woody species, and termite mound assemblages had higher Shannon-Wiener index and species evenness values than in the matrix. Density of woody plant was also high on termite mounds. The results showed that tree height was influenced by whether the tree was on the mound or in the matrix. Termite vegetation was dominated by mature trees ($\geq$ 1.5 m), while saplings (< 1.5 m) dominated the matrix. This suggest that due to the commonly reported improved soil fertility and moisture on termite mounds (e.g., Konaté et al. 1999; Joseph et al., 2013; Muvengwi et al., 2017), they provide suitable microhabitats for rapid seed germination, woody plants establishment, and increase the growth rate of trees.

Increased resource availability can also allow species with different nutrient, water, or even habitat requirements to co-exist on termite mounds, as a result, producing woody vegetation species composition different from the matrix. For example, 39 (of 54) woody species were restricted to termite mounds, including species that are typically fire sensitive such as *Cussonia spicata, Clerodendrum glabrum, Celtis africana*, and *Euclea natalensis*, thereby supporting the idea that termite mounds may act as refugia for woody plants from frequent savanna fires. Termite mounds vegetation assemblages were characterized by bird-dispersed woody species that produces drupe-type fruits, i.e., *Lantana camara*, *Searsia pyroides*, and *C. spicata*, suggesting that birds perching on termite mounds bring seeds, and when those seed germinate, they may form clumps of woody recruits that provide more perching sites for birds, which may create a feed-back loop of seed deposition and tree seedling establishment. Therefore, as this processes progress, bush clumps within the area simultaneously expand in size creating large woodland patches.

In chapter 5, the results revealed that the density of bush clumps was positively related to the density of termite mounds in the area. These results suggest that in areas with high termite mound densities, the recruitment of woody plants on termite mounds may lead to the formation closed canopy woodlands or forests. A trend towards forest-type woody vegetation composition on bush clumps as they mature have been reported in literature (e.g. Jamison-Daniels et al., 2021; Nell et al., 2024), similarly with forests that have savanna bush clumps origin (e.g., Adie et al., 2023). The results reported termite mound densities of up to 5.4 mounds ha^{-1} for both Cumberland and Uitkomst, with the density of vegetated mounds (3 – 3.4 ha^{-1}) being generally higher than the density of bare mounds (1.2 – 2.4 ha^{-1}), highlighting that most termite mounds were colonized by woody plants in the landscapes.

The reason why some termite mounds were not vegetated remains unknown. One assumption is that the mounds that were not colonized by woody plants were active mounds. Studies showed that bush clumps often initiate on abandoned mounds (e.g. Gower et al., 1992; Bloech, 2008). Another assumption is that they were of recent origin, and they may have not yet reached the soil resource status and habitat stability sufficient to support woody vegetation community compared to other older termite mounds with the landscape. For example, studies have shown that the concentrated decomposition of organic materials and relocation of soil over extended time periods increase the mound size, and it soil nutrient and water status (Jouquet et al., 2004; Joseph et al., 2013; Seymour et al., 2014; Lima et al., 2018). Increased soil nutrient concentrations and moisture status results in increased woody plant recruitment, while the size of the mound may determine the amount of space available to be colonized and how much protection from frequent fire they can provide to saplings (habitat stability).

The species richness of woody plants increased with the increase in termite mound surface area. Shannon-Wiener index was high in large termite mounds compared to small and medium-size mounds, but the species evenness remained constant among termite size classes. Furthermore, the species composition remained to constant across different termite mound size classes. This suggest that while large termite mounds captured more species, woody plant assemblages of termite mounds were similar across the landscape which may indicate a trend towards habitat homogenization. Studies have reported that constant species composition among patches in a landscape may be a result of a limited shared regional species pool (e.g. Tatsumi et al., 2020; He et al., 2023), or reduction of the local species richness by the introduction of alien invasive vegetation. Mature tree density was higher on lager termite mounds, while the density of saplings was not affected by tree size which suggest that whether saplings grow into mature trees depended on the mound size. Earlier I highlighted the importance of mound size to soil nutrient composition, space availability and habitat stability.

In chapter 6, I reported the role of a founder species during the initiation of bush clumps on termite mounds. I found that bush clumps appeared to be simultaneously initiated by more than one species. *Vachellia sieberiana* and *S. pyroides* had the largest individual representatives in ~ 50% of the bush clumps, suggesting trees of these species initiated and facilitated the development of approximately half of the bush clump reported in this study. After initiation these bush clump appeared to be dominated by the shrubs of the invasives *L. camara* and *Rubus ulmifolium*, occurring at frequencies of up to 30%. This highlights the vulnerability of termite mound vegetation to alien plant invasion, since native species commonly of grassland and savanna origins such as *Lippia javanica, C. spicata*, *V. sieberiana, Ziziphus mucronata, Grewia occidentalis*, and *S. pyroides* only occurred at low (< 10%) frequencies The invasion of native by alien vegetation, particularly *L. camara,* has been reported many times in southern Africa (e.g. Vardien et al., 2012; Bitani and Downs, 2022; Shiri et al., 2023).

The development of bush clumps on termite mounds followed a deterministic successional pattern through facilitation by the combined effort of termite mounds and the first arriving trees. For example, studies have reported that nutrient rich patches develop under isolated trees following increased animal activity as animals use these trees for shade while simultaneously bringing seeds (Abreu et al., 2021). Birds perching on these trees also bring more seeds, and the resource rich microhabitats on termite mound may also promote mass seed germination and seedling recruitment. The species richness, number of mature trees, and woody basal area increased as the bush clump increase in size, further indicating deterministic succession. Furthermore, the species composition of saplings in an early successional stage (small) resembled the species composition of mature trees in bush clumps in late successional stage (large). This suggests that saplings establishing from the seed bank of small bush clumps grow to become the large trees in large bush clumps, which is another indication of a deterministic succession pattern as described by Jamison-Daniels et al. (2021).

Directions for future studies

1. Future studies could examine the effects of termite mounds on the formation and development of bush clumps across a land use and land management practice gradient. For example, we can compare trends where large herbivores are present and in localities where there are absent. We can also analysis and compare the effects of termite mounds on woody vegetation assemblages in localities that have different fire management practices. Furthermore, we could analyse woody vegetation trends facilitated by termite mounds in undisturbed grasslands and abandoned croplands.
2. The use of historical remote sensing data and climate data can be used to study spatiotemporal patterns of bush clump initiation and development along a climate change gradient.
3. Analyses of soil data on termite mounds in different land use and land management practices in order to identify differences in soil mineral composition, nutrient fluxes, and soil water status, and how these differences may in turn influence the species composition of woody plants, woody plant successional patterns, and the rate of bush clump development on termite mounds.

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APPENDICES

Appendix 4.1: Functional traits of selected woody species associated with seed dispersal, nutrient availability and response to herbivory on and off termite mounds in Cumberland Nature Reserve and Uitkomst Conservation Area. The upper letter T in brackets indicates indicator species of termitaria, while the upper letter M indicates a matrix indicator species. In growth form and leaf phenology column the traits are code as: T – tree, Sh – shrub, C – climber, S – succulent, E- evergreen, and D – deciduous. Data about traits was retrieved from multiple tree guides and tree databases. Y and N represents the presence and absence, respectively of a species in matrix or termitaria habitats.

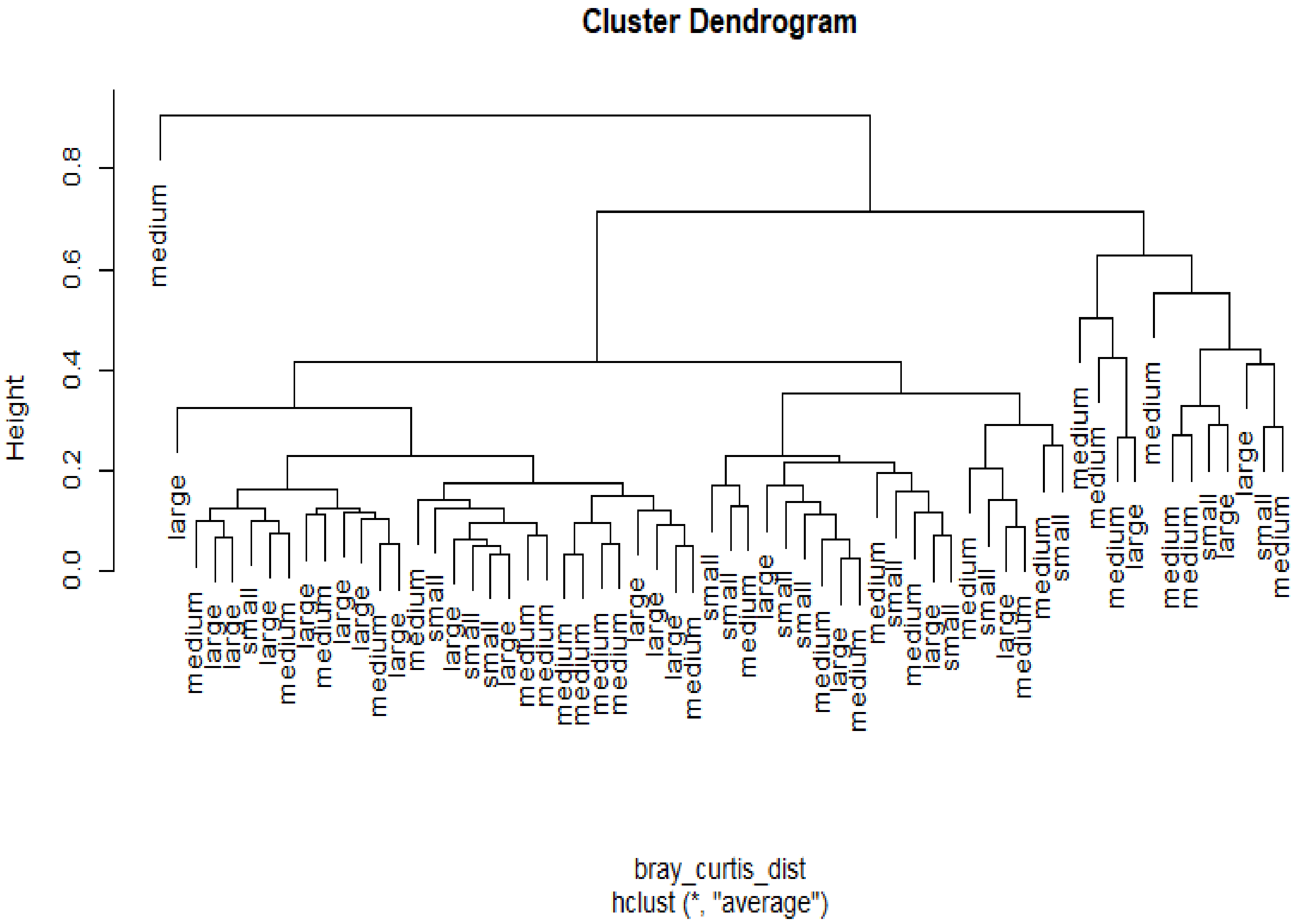
Species (indicator)	**Family**	**Matrix**	**Termitaria**	**Dispersal Mode**	**Fruit type**	**N-fixing**	**Growth form and leaf phenology**	**Source**
Acacia mearnsii De Wild. (M)	Fabaceae	Y	Y	Endozoochory	Pod	Yes	T,D	https://invasives.org.za/fact-sheet/black-wattle/
Afrocanthium mundianum (Cham. & Schltdl.) Lantz	Rubiaceae	N	Y	Birds, Endozoochory	Drupe	No	Sh, E	https://wildflowernursery.co.za/indigenous-plant-database/afrocanthium-mundianum/
Aloe ferox Mill.	Asphodelaceae	Y	Y	Wind	Capsule	No	S, E	https://wildflowernursery.co.za/indigenous-plant-database/aloe-ferox/; https://treesa.org/aloe-ferox/
Aloe marlothii A.Berger	Asphodelaceae	Y	Y	Wind	Capsule	No	T/Sh/S, E	https://pza.sanbi.org/aloe-marlothii; https://treesa.org/aloe-marlothii/
Asparagus falcatus L. (T)	Asparagaceae	N	Y	Birds	Berry	No	C/Sh, E	https://wildflowernursery.co.za/indigenous-plant-database/asparagus-falcatus/; https://pza.sanbi.org/asparagus-falcatus
Azaima tetracantha Lam.	Salvadoraceae	N	Y	Birds, endozoochory	Drupe	No	Sh, D	https://pza.sanbi.org/azima-tetracantha;
Buddleja saligna Willd. (T)	Scrophulariaceae	N	Y	Wind	Capsule	No	T, E	https://treesa.org/buddleja-saligna/; https://pza.sanbi.org/buddleja-saligna
Canthium inerme (L.f.) Kuntze	Rubiaceae	N	Y	Birds	Drupe	No	T/Sh, E	https://treesa.org/canthium-inerme/; https://pza.sanbi.org/canthium-inerme
Capparis sepiaria L.	Brassicaceae	N	Y	Birds	Drupe	No	Sh/C, D	https://www.zimbabweflora.co.zw/speciesdata/species.php?species_id=124450; http://redlist.sanbi.org/species.php?species=1133-15
Celtis africana Burm.f.	Cannabaceae	N	Y	Birds	Drupe	No	T, D	https://pza.sanbi.org/celtis-africana; https://treesa.org/celtis-africana/
Clerodendrum glabrum E.Mey. var. *glabrum*	Lamiaceae	N	Y	Birds	Drupe	No	Sh/T, D	https://pza.sanbi.org/clerodendron-glabrum; https://treesa.org/volkameria-glabra/
Coddia rudis (E.Mey. ex Harv.) Verdc.	Rubiaceae	N	Y	Birds	Drupe	No	Sh/T, E	https://pza.sanbi.org/coddia-rudis; https://treesa.org/coddia-rudis-4/

Combretum erythrophylum (Burch.) Sond.	Combretaceae	N	Y	Wind, water	Winged	No	T, D	https://pza.sanbi.org/combretum-erythrophyllum;
Cussonia spicata Thunb. (T)	Araliaceae	Y	Y	Birds	Drupe	No	T, D	https://pza.sanbi.org/cussonia-spicata; https://treesa.org/cussonia-spicata/
Ehretia rigida (Thunb.) Druce	Boraginaceae	N	Y	Birds, endozoochory	Drupe	No	Sh/T, E	https://pza.sanbi.org/ehretia-rigida; https://treesa.org/ehretia-rigida/
Ekebergia capensis Sparrm.	Meliaceae	N	Y	Birds, endozoochory	Drupe	No	T, E	https://pza.sanbi.org/ekebergia-capensi; https://treesa.org/ekebergia-capensis/
Euclea divinorum Hiern	Ebenaceae	N	Y	Birds, Endozoochory	Drupe	No	Sh/T, E	https://pza.sanbi.org/euclea-divinorum; https://www.zimbabweflora.co.zw/speciesdata/species.php?species_id=143880
Euclea natalensis A.DC.	Ebenaceae	N	Y	Birds, Endozoochory	Berry	No	Sh/T, E	https://pza.sanbi.org/euclea-natalensis; https://treesa.org/euclea-natalensis/
Euclea undulata Thunb.	Ebenaceae	N	Y	Birds, Endozoochory	Drupe	No	Sh/T, E	https://pza.sanbi.org/euclea-undulata; https://wildflowernursery.co.za/indigenous-plant-database/euclea-undulata/
Euphorbia trigona Mill.	Euphorbiaceae	N	Y	Wind	Capsule	No	S, E	
Grewia caffra Meisn.	Malvaceae	N	Y	Birds, endozoochory	Drupe	No	Sh/C/T, D	https://pza.sanbi.org/grewia-caffra; https://www.zimbabweflora.co.zw/speciesdata/species.php?species_id=138400;
Grewia occidentalis L. (T)	Malvaceae	N	Y	Birds, Endozoochory	Drupe	No	Sh/T, D	https://pza.sanbi.org/grewia-occidentalis; Pooley (1993)
Gymnosporia buxifolia (L.) Szyszyl. (T)	Celastraceae	N	Y	Birds	Capsule	No	Sh/T, E	https://pza.sanbi.org/gymnosporia-buxifolia
Gymnosporia senegalensis (Lam.) Loes	Celastraceae	Y	Y	Birds	Drupe	No	Sh/T, E	https://pza.sanbi.org/gymnosporia-senegalensis
Halleria lucida L.	Stilbaceae	N	Y	Birds	Capsule/ berry	No	Sh/T, E	https://pza.sanbi.org/halleria-lucida; https://treesa.org/halleria-lucida/;
Indigofera natalensis Bolus	Fabaceae	N	Y	Wind	Pod	Yes	Sh/T, D	https://pza.sanbi.org/indigofera-natalensis
Jacaranda mimosifolia D.Don	Bignoniaceae	Y	Y	Wind	Winged	No	T, D	https://invasives.org.za/fact-sheet/jacaranda/
Kirkia acuminate Oliv.	Kirkiaceae	N	Y	Endozoochory	Capsule	No	T, D	https://treesa.org/kirkia-acuminata/; https://pza.sanbi.org/kirkia-acuminata
Lantana camara L. (T)	Verbenaceae	Y	Y	Birds	Drupe	No	Sh, E	https://invasives.org.za/fact-sheet/lantana/; https://www.arc.agric.za/arc-;ppri/Pages/Lantana-camara.aspx; Bitani and Downs (2022)
Lippia javanica (Burm.f.) Spreng	Verbenaceae	Y	Y	Wind	Capsule	No	Sh, E	https://treesa.org/lippia-javanica/
Melia azedarach L. (T)	Meliaceae	Y	Y	Birds	Berry	No	T, D	https://invasives.org.za/fact-sheet/syringa/;
Mimusops caffra E.Mey. ex. A.DC	Sapotaceae	Y	Y	Birds, endozoochory	Drupe	No	T, E	https://pza.sanbi.org/mimusops-caffra
Morus indica L.	Moraceae	Y	N	Birds, endozoochory	Berry	No	T, D	https://invasives.org.za/fact-sheet/white-mulberry/

Mystroxylon aethiopicum Thunb. Loes.	Celastraceae	N	Y	Birds, endozoochory	Drupe	No	Sh/T, E	https://pza.sanbi.org/mystroxylon-aethiopicum
Ochna serrulate (Hochst.) Walp.	Ochnaceae	N	Y	Birds	Drupe	No	Sh/T, E	https://pza.sanbi.org/ochna-serrulata
Opuntia littoralis (Engelm.) Cockerell	Cactaceae	Y	Y	Birds, endozoochory	Berry	No	S, E	https://www.arc.agric.za/arc-ppri/Pages/Prickly-pear.aspx; https://www.arc.agric.za/arc-ppri/Pages/Prickly-pear.aspx
Podocarpus latifolius (Thunb.) R.Br. ex Mirb.	Podocarpaceae	N	Y	Birds, endozoochory	Drupe	No	T, E	https://pza.sanbi.org/podocarpus-latifolius
Rothmannia capensis Thunb	Rubiaceae	N	Y	Birds, endozoochory	Berry	No	Sh/T, E	https://pza.sanbi.org/rothmannia-capensis
Rubus cuneifolius Pursh	Rosaceae	Y	Y	Birds	Berry	No	Sh, D	https://invasives.org.za/fact-sheet/american-bramble/)
Rubus niveus Thunb. (T)	Rosaceae	N	Y	Birds	Berry	No	Sh, D	https://invasives.org.za/fact-sheet/mysore-raspberry/
Rubus ulmifolium Schott 1818	Rosaceae	N	Y	Birds, endozoochory	Berry	No	Sh, D	https://datazone.darwinfoundation.org/en/checklist/?species=1669; https://www.inaturalist.org/taxa/78895-Rubus-ulmifolius
Schinus terebinthifolius G. Raddi	Anacardiaceae	N	Y	Birds, endozoochory	Drupe	No	Sh/T, E	https://invasives.org.za/fact-sheet/brazilian-pepper-tree/
Searsia natalensis (Bernh.ex C.Krauss) F.A.Barkley	Anacardiaceae	N	Y	Birds	Drupe	No	Sh/T, E	https://pza.sanbi.org/searsia-natalensis;
Searsia pyroides (Burch.) Moffett (T)	Anacardiaceae	N	Y	Birds	Drupe	No	Sh/T, E	https://pza.sanbi.org/searsia-pyroides
Sideroxylon inerme L. subsp. *inerme*	Sapotaceae	N	Y	Birds, endozoochory	Drupe	No	T, E	https://pza.sanbi.org/sideroxylon-inerme; https://treesa.org/sideroxylon-inerme/
Solanum mauritianum Scop.	Solanaceae	Y	Y	Birds	Berry	No	Sh/T, E	https://invasives.org.za/fact-sheet/bugweed/; https://www.arc.agric.za/arc-ppri/Pages/Solanum-mauritianum-(bugweed).aspx
Spirostachys africana Sond.	Euphorbiaceae	N	Y	Birds	Capsule	No	T, D	https://pza.sanbi.org/spirostachys-africana; https://treesa.org/spirostachys-africana/
Tecoma stans (L.) Juss. ex Kunth	Bignoniaceae	N	Y	Wind	Capsule	No	Sh/T, E	https://invasives.org.za/fact-sheet/yellow-bells/
Terminalia phanerophlebia Engl. & Diels (T)	Combretaceae	N	Y	Wind,	Winged	No	Sh/T, E	https://pza.sanbi.org/terminalia-phanerophlebia; https://treesa.org/terminalia-phanerophlebia/
Trema orientalis (L.) Blume	Cannabaceae	N	Y	Birds	Drupe	No	T, D/E	https://pza.sanbi.org/trema-orientalis; https://www.zimbabweflora.co.zw/speciesdata/species.php?species_id=120090
Vachellia sieberiana (DC.) Kyal. & Boatwr. var. *woodii* (Burtt Davy) Kyal. & Boatwr.	Fabaceae	Y	Y	Endozoochory	Pod	Yes	T, D	https://pza.sanbi.org/vachellia-sieberiana-var-woodii; https://treesa.org/vachellia-sieberiana/
Vangueria infausta Burch. subsp. Infausta (T)	Rubiaceae	N	Y	Birds, endozoochory	Drupe	No	Sh/T, D	https://pza.sanbi.org/vangueria-infausta; https://treesa.org/vangueria-infausta/
Zanthoxylum capense (Thunb.) Harv.	Rutaceae	N	Y	Endozoochory	Capsule	No	Sh/T, E	https://pza.sanbi.org/zanthoxylum-capense; https://treesa.org/zanthoxylum-capense/

Ziziphus mucronata Willd. (T)	Rhamnaceae	N	Y	Birds, Endozoochory,	Drupe	No	Sh/T, D	https://treesa.org/ziziphus-mucronata/

Appendix 4.2: Cluster analysis dendrogram demonstrating the differences in woody plant assemblages of small, medium and large termite mounds.



Appendix 6.1: List of tree species and their habitat preferences in Cumberland Nature Reserve and Uitkomst Conservation Area, South Africa. The table shows the forest specialization values, and habitat breadths calculated for each of the species (compare with Appendix 6.2). Founder species were identified as those species that initiated a bush clump. Forest species were classified according to field guides as those species that only occurred in forest-type habitats. The table was constructed using data from Jamison-Daniels et al. (2021) and numerus tree guides and databases

Species	**Forest specialization**	**Habitat breadth**	**Native species**	**Founder species**
Acacia mearnsii	2.33	2	N	Y
Afrocathium mundianum	4	3	Y	N
Aloe ferox	3	2	Y	Y
Aloe marlothii	3	2	Y	N
Asparagus falcatus	7.5	3	Y	N
Azima tetracantha	6.8	4	Y	N
Buddleja saligna	6	3	Y	Y
Canthium inerme	4	4	Y	N
Capparis sepiaria	5.5	4	Y	N
Celtis africana	3.86	1	Y	Y
Clerodendrum glabrum	4	3	Y	Y
Coddia rudis	3.5	3	Y	N
Combretum erythrophylum	3.5	6	Y	N
Cussonia spicata	3.75	4	Y	Y
Ehretia rigida	2.67	5	Y	N
Ekebergia capensis	5	3	Y	Y
Euclea divinorum	4	3	Y	N
Euclea natalensis	4	1	Y	N
Euclea undulata	3.75	3	Y	N
Euphorbia trigona	5	3	Y	N
Grewia caffra	6	3	Y	N
Grewia occidentalis	5	3	Y	Y
Gymnosporia senegalensis	4.25	3	Y	N
Gymnosporia buxifolia	3	1	Y	Y
Halleria lucida	4.2	5	Y	N
Indigofera natalensis	8	1	Y	N
Jacaranda mimosifolia	4.5	2	N	Y
Lantana camara	4.5	5	N	Y
Lippia javanica	5.3	3	Y	N
Melia azedarach	4	3	N	Y
Mimusops caffra	8	1	Y	N
Mystroxylon aethiopicum	6,.6	2	Y	N
Nuxia floribunda	7	2	Y	N
Opuntia littoralis	5.8	2	Y	N
Podocarpus latifolius	5.5	2	Y	N
Rothmannia capensis	5	5	Y	Y
Rubus cuneifolius	3.3	4	N	N

Rubus niveus	4.5	8	N	N
Rubus ulmifolium	6	3	N	N
Schinus terebinthifolius	5	2	N	N
Searsia natalensis	6.5	2	Y	N
Searsia pyroides	3.6	3	Y	Y
Sideroxylon inerme	7	2	Y	N
Solanum mauritianum	7	2	N	Y
Spirostachys africana	6	1	Y	N
Tecoma stans	4.5	2	N	Y
Terminalia phanerophlebia	4.7	3	Y	Y
Trema orientalis	5.3	3	Y	N
Vachellia sieberiana	2.33	5	Y	Y
Vangueria infausta	3	3	Y	Y
Zanthoxylum capense	4	2	Y	N
Ziziphus mucronata	4	3	Y	Y
Ochna serrulata	4.25	4	Y	N

Appendix 6.2: An eight-class habitat gradient classification ranging from closed habitats (values close to 8) to open habitats (values close to 1). Each tree species (compare with Appendix 6.1) was scored on the habitat class/es they were reported in the literature. For species occurring in a number of different habitat classes, an average forest specialization score was calculated as the mean class for which the species was described (Appendix 5.1). The table was adopted from Jamison-Danials et al. (2021), https://doi.org/10.1111/btp.12890.

Habitat	**Ordered gradient**	**Field guide descriptions**
Forest	8	Mist-belt forest, evergreen forest, Afromontane forest, coastal forest, riverine forest, montane forest
Wooded crevices	7	Forest margins, wooded gullies/ kloofs/ ravines
Thicket	6	Riverine fringe thicket, coastal thicket/ dune bush, sand dunes/ coastal scrub, valley bushveld, Albany thicket, coastal bush
Closed woodland (mesic)	5	Thornveld, moist bushveld, bushveld, Jesse bush, low altitude woodlands

Open woodland (arid)	4	Grassy woodlands, wooded grassland, open woodland/bushveld, dry woodlands, wooded grasslands, high altitude woodlands
Rocky areas in otherwise shrubland, woodland or grassland	3	Rocky ridges, including termite mounds, mountain slopes and hillsides
Open shrubland	2	Low scrub (taller forms to be placed under thicket), karroid scrub
Grasslands	1	Montane grasslands, high-altitude grasslands, grassy hillsides/mountain slopes, highveld grassland, plateau, coastal grasslands

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