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The functional importance of termites across a savanna rainfall gradient

by

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Declaration:

I, …**Andrew Byron Davies**…… declare that the thesis/dissertation, which I hereby submit for the degree ………**PhD Zoology**…………………….… at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE: ..…………………………..

DATE: ………………………………….

i thank You God for most this amazing

day:for the leaping greenly spirits of trees

and a blue true dream of sky; and for everything

which is natural which is infinite which is yes

E. E. Cummings (1894 - 1962)

“Artem natura superat, sine vi, sine cura”

“Nature surpasses art without effort or anxiety”

The functional importance of termites across a savanna rainfall gradient

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Abstract

Termites are ecosystem engineers with well documented functional roles in African savannas. However, how their importance changes across environmental gradients, such as rainfall and nutrition, is less understood. Using LiDAR data from the Carnegie Airborne Observatory, I mapped the distribution of termite mounds across an entire river catchment in the Kruger National Park, South Africa. Abiotic factors shaped mound densities at broader landscape scales, while local hillslope morphology strongly influenced mound distribution at finer scales. Mound distribution exhibited a clustered pattern throughout the landscape, occurring at higher densities on crests, which are nutrient-poor. However, at fine scales mounds exhibited over-dispersion so that evenly spaced aggregations of termite mounds are embedded within a landscape of varying mound densities. The activity status of mounds also varied across the catchment, with a higher proportion of mounds active in drier sites. A key mechanism accounting for the importance of termite mounds is the high concentration of nutrients they hold. Although these nutrient-hotspots are known to enhance savanna biodiversity and attract herbivores, what is less clear is whether they are as important in nutrient-rich compared to dystrophic savannas. Working across a rainfall gradient, I investigated grass communities on and off termite mounds and along transects away from mounds in order to calculate the spatial influence of termite mounds on grass communities and how this changes with landscape context. Although grass species richness was lower on mounds than in the savanna matrix, the assemblage composition varied significantly, with higher nutrient concentrations in grasses located on mounds; this pattern became more distinct with increasing rainfall. The spatial extent of these nutrient-rich grasses also differed across the rainfall gradient, with a larger sphere of influence around mounds in the wetter, nutrient-poor areas, due to patterns in soil nutrients. Using termite mound densities estimated from airborne LiDAR, I upscaled field-based results to determine the percentage of the landscape influenced by termite activity, showing that mounds distinctly altered grass communities over ~2% of the landscape. The impact these altered grass communities have on savanna grazing herbivores was then investigated across the rainfall gradient. Grasses on termite mounds were preferentially grazed at all rainfall sites and in both seasons tested. Importantly, however, mound influence varied in time and space. Mounds were more heavily grazed at wetter savanna sites and influenced more of the landscape here during the wet season. However, during the dry season, when mound utilisation was higher, this pattern was reversed, with more of the landscape (19%) influenced at the driest site. Southern slopes of termite mounds exhibited higher grazing pressure and insects were also shown to prefer mound grasses. Finally, through measuring the decomposition rate of four savanna grass species, I show that grass decomposition in African savannas varies significantly along rainfall gradients, with various factors, including termites, becoming influential in different habitats. Importantly, I demonstrate that fire does not always slow decomposition and that it interacts with other factors to influence the process. Overall, termites are important contributors to savanna heterogeneity, with functional importance varying with landscape context.

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1. General Introduction

Disclaimer

This thesis consists of a series of chapters that have been prepared for submission to, or published in, a range of scientific journals. As a result styles may very between chapters in the thesis and some overlap may occur to secure publication entities.

Chapter 1

General Introduction

Rationale and background

Savanna ecosystems cover an eighth of the global land surface, being particularly widespread on the southern continents where they cover over half of Africa and Australia and 45 % of South America (Scholes and Archer 1997). All savannas around the world are characterised as having a highly seasonal climate consisting of a hot wet season and a warm dry season. They are all landscapes comprising at least a two-layered above ground vegetation structure consisting of a discontinuous tree layer overlying a seemingly continuous grass layer (Scholes 1997). This highly seasonal environment and two-layered vegetation structure make savannas inherently heterogeneous.

Heterogeneity in savanna ecosystems has received considerable attention (see for example du Toit et al. 2003, and individual chapters within) and is considered a key facilitator of biodiversity and ecosystem complexity across the globe (Benton et al. 2003, Pickett et al. 2003, Cromsigt et al. 2009). Heterogeneity in itself provides multiple habitats, providing space and ecological niches that allow different species to exist (Weibull et al. 2000, Tews et al. 2004). Furthermore, heterogeneity enables the coexistence of competing species through influences on competition, thus promoting higher levels of biodiversity (Tilman and Kareiva 1997, Palmer 2003). In savannas, temporal heterogeneity is driven by strong seasonality and long-term fluctuations in rainfall (Fensham and Holman 1999, Venter et al. 2008). Abiotic factors such as landscape topography, including catena sequences (du Toit 2003, Levick et al. 2010a), geologic substrate (Venter et al. 2003) and fire regimes (van Wilgen et al. 2003, Sankaran et al. 2005) have profound effects on spatial heterogeneity at broad scales, while at finer scales biotic agents become important. These include grazing lawns (Archibald 2008), which after an initial, biotic disturbance are maintained by herbivores (Cromsigt and Olff 2008), large trees (Treydte et al. 2007, Treydte et al. 2011) and dung middens (Cromsigt and Olff 2008).

Termites (Blattodea: Termitoidae), which are of considerable ecological importance in savannas, are another biotic agent that creates spatial heterogeneity. They are considered to be ecosystem engineers in that they alter the environment through their activity. Termites modify the mineral and organic composition of soils, affecting soil drainage (Jones et al.

1994, Konaté et al. 1999) by improving infiltration rates and porosity, while decreasing bulk density (Mando et al. 1996). In tropical and sub-tropical systems, termites are considered to be the dominant arthropod decomposer (Collins 1981, Holt 1987, Schuurman 2005) and in African savannas, termites have been shown to have a biomass comparable to ungulates and mega-herbivores (Dangerfield et al. 1998). As decomposers, termites also play an important role in nutrient cycling and distribution (Holt and Coventry 1990, Scholes 1990, Lepage et al. 1993, Konaté et al. 1999).

The distribution of termite species has been well documented in southern Africa through the National Survey of Isoptera. This survey was conducted by W.G.H. Coaton and colleagues during the 1950s and 1960s and consisted of termite sampling in almost every quarter-degree square of southern Africa, with the exception of Botswana and Lesotho. Through this survey and later work, a total of 165 species comprising 54 genera have been described from the region (Uys 2002). Research on termite ecology in southern Africa has demonstrated that termites are abundant (Ferrar 1982) ecosystem engineers, influencing decomposition rates (Schuurman 2005) and soil processes (Dangerfield et al. 1998). More recently, it has been shown that termite diversity changes across environmental gradients and that assemblages are relatively resistant to disturbance (Davies et al. 2012).

The epigeal mounds constructed by some termite genera are characteristic structures of African savannas and act as agents of spatial heterogeneity, affecting savanna ecological dynamics at multiple trophic levels. Through termite activity (the transportation and concentration of soil nutrients and organic material), the soils of these mounds are rich in nutrients (Gosling et al. 2012) and support compositionally distinct, nutrient-enriched plant communities on and around them (Grant and Scholes 2006, Traoré et al. 2008, Moe et al. 2009, Okullo and Moe 2012b, Erpenbach et al. 2013). These vegetation communities result in termite mounds becoming distinct habitats, influencing a host of other organisms including insects (Pringle et al. 2010, Leitner 2012) and small mammals (Fleming and Loveridge 2003, Okullo et al. 2013) which are more abundant on and in close proximity to mounds. Through their nutrient enriched vegetation, mounds also act as foraging hotspots for a wide range of mammalian herbivores (Holdo and McDowell 2004, Loveridge and Moe 2004, Mobæk et al. 2005, Brody et al. 2010, Levick et al. 2010b), with geophagy even documented in some species (Baptista et al. 2013).

Although termite mounds are recognised as important agents of savanna spatial heterogeneity (see Sileshi and Arshad 2012 for a mini-review and synthesis), almost all previous studies have been conducted at single-site locations, with little information available on how patterns may change across environmental gradients. In a first climatic gradient study, Erpenbach et al., (2013) documented an increased difference between mound and savanna matrix vegetation with increasing mean annual precipitation in west Africa. This finding was attributed to increased phytodiversity in wetter habitats. Furthermore, Van der Plas et al., (2013) investigated browsing patterns in relation to termite mound vegetation in South Africa's Hluhluwe-iMfolozi Game Reserve and found higher browsing levels in savanna matrix vegetation. This was the first study that did not document a preference among browsers for mound vegetation (O'Connor 2013). The study was conducted in a relatively nutrient-rich savanna, with matrix vegetation containing higher levels of nutrition than mound vegetation. Herbivores would therefore derive no benefit by browsing on termite mound vegetation relative to the savanna matrix. Similarly, Treydte et al., (2007) measured grass nutritional quality under savanna trees across an African productivity gradient, finding increased grass quality under trees in nutrient-poor savannas, but not at nutrient-rich sites. These studies, although limited in number, suggest that nutrient-hotspots such as termite mounds are not necessarily beneficial or important for spatial heterogeneity in all savannas. There is thus a need for more studies across environmental gradients to elucidate more clearly the role of termite mounds in savanna ecosystems.

Not only have most studies been conducted at single-site locations, but many have only investigated termite mound-induced patterns by measuring responses on and off mounds. Aspects that are not well understood include patterns in the spatial extent of termite influence around mounds and the proportion of landscapes directly affected by them (Levick et al. 2010b, Sileshi and Arshad 2012). This sphere of influence (i.e., the area the mound occupies and has a significant influence on) is likely also to vary with landscape context, being larger in areas of poor nutrition because differences in nutrient concentrations between mounds and the surrounding savanna matrix are larger here, resulting in significant enhancement of nutrients at greater distances from termite mounds.

Objectives and thesis structure

The objective of my study was to enhance scientific knowledge and understanding of the functional roles termites play in savanna ecosystems through the construction of epigeal mounds. The focus was on mounds built by the genus *Macrotermes* because these are the largest termite mounds constructed in African savannas and are known to play important functional roles (see for e.g. Fleming and Loveridge 2003, Levick et al. 2010b, Joseph et al. 2011, Okullo and Moe 2012b, Joseph et al. 2013b). Furthermore, due to their large size, they are readily detected with airborne light detection and ranging (LiDAR) technology from the Carnegie Airborne Observatory (see Asner et al. 2007), a tool extensively used during the course of this study.

Before assessing the functional role of termite mounds, an understanding of how they are distributed across space and the determinants of such distributions is warranted. To this end, Chapter 2 explores the density and spatial patterning of *Macrotermes* mounds using LiDAR terrain data obtained from the Carnegie Airborne Observatory. The study was undertaken across the entire catchment of the N'waswitshaka River in southern Kruger National Park. This enabled a comprehensive investigation of mound distribution patterns at different spatial scales and in response to varying ecological factors. Following this, the functional importance of these mounds is examined in Chapters 3 and 4. Chapter 3 focuses on grass diversity on and around mounds, including the spatial extent of mound influence on grass communities. Grasses were selected over other plant life-forms because they have been less studied in relation to termite mounds, yet are a fundamental component of savanna ecosystems. Using the mound density findings of Chapter 2, I am able to scale my findings up to a landscape level, providing the first estimates of the percentage of the landscape affected by mounds in terms of grass community composition. Chapter 4 builds further on this work, investigating effects these altered grass communities have on grazing savanna herbivores. In this Chapter I investigate grazing patterns around mounds as well as the likely driver of such enhanced grazing, that of increased nutrition of mound grasses. Using LiDAR data, I am again able to provide estimates of the percentage of the landscape influenced by termite mounds. Chapter 5 consists of an additional study carried out to determine the drivers of grass decomposition in African savannas, a process in which termites are intricately involved. This study was performed across four distinct savanna types, varying in the amount of mean annual precipitation received. Within each savanna type, the experiment was carried out on plots that have been burnt on a triennial basis since 1954 and plots that have remained unburnt for the same time period. This enabled me to investigate effects of disturbance regimes, which are likely to undergo future change due to a warming climate, on decomposition. I provide testable hypotheses based on my data for future research which, if conducted, will reveal more clearly the drivers of savanna grass decomposition, including the functional role of termites. Finally, a general discussion to the thesis with suggested future research directions is contained in Chapter 6.

The research was carried out across rainfall and nutrient gradients in South Africa. Most of the study was conducted in the Kruger National Park (KNP, 22° 25' - 25° 32' S and

30° 50' - 32° 02' E) (Fig. 1.1), with Chapters 2 to 4 undertaken in the southern portion of the park, in the N'waswitshaka River catchment (Fig. 1.2). The rainfall gradient for these components of the study ranged from 550 - 750 mm.yr^{-1}. Chapter 5 was across a larger rainfall gradient, ranging from 450 - 900 mm.yr^{-1} and spanning approximately 700 km in distance, including most of the latitudinal range of KNP, and extending south to higher rainfall sites in Hluhluwe-iMfolozi Game Reserve (28° 01' - 28° 25' S and 32° 15' - 32° 26' E), thus extending the rainfall gradient of the study. Working across climatic and productivity gradients allowed an assessment of the functional role termites play in a range of savanna types, enabling quantification of their importance.

Figure 1.1: Location of the Kruger National Park (KNP) and Hluhluwe-iMfolozi Game Reserve (HiP) within South Africa. The position of the N'waswitshaka River catchment, where most of the study was conducted, is also shown within KNP.

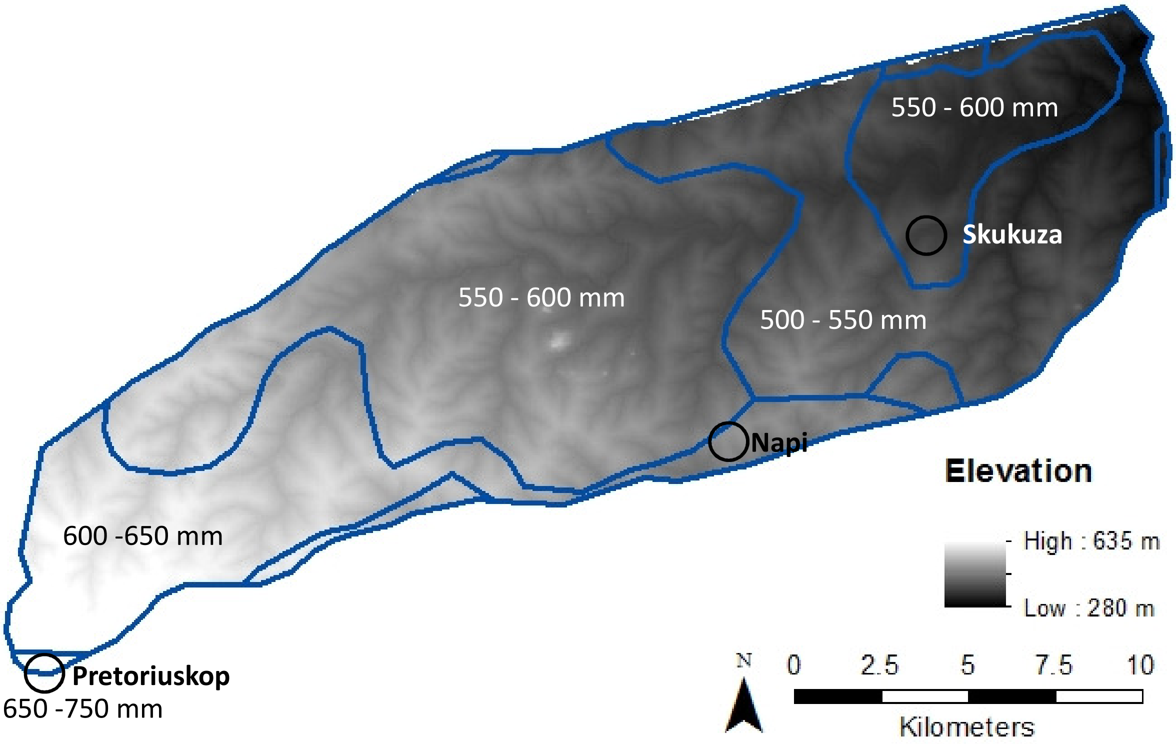

Figure 1.2: Digital elevation model of the N'waswitshaka River catchment in southern Kruger National Park (see Fig. 1.1). Approximate positions of the three savanna study sites sampled in Chapters 3 and 4 are shown as well as the elevation of the catchment and rainfall regimes (boundaries of rainfall regimes outlined with blue lines). Although the study sites are named after KNP rest camps located nearby, their location does not correspond exactly to that of the camps.

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Chapter 2

Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment

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Abstract

Termite mounds contribute to the spatial heterogeneity of ecological processes in many savannas, but the underlying patterns and determinants of mound distributions remain poorly understood. Using the Carnegie Airborne Observatory (CAO), I mapped the distribution of termite mounds across a rainfall gradient within a river catchment (~27 000 ha) of the Kruger National Park, South Africa. I assessed how different factors influenced the distribution and height of termite mounds at three spatial scales: the entire catchment, among three broad vegetation types, and on individual hillslope crests. Abiotic factors such as the underlying geology and mean annual precipitation shaped mound densities at broad scales, while local hillslope morphology strongly influenced mound distribution at finer scales, emphasising the importance of spatial scale when assessing mound densities. Fire return period had no apparent effect on mound densities or height. Mound density averaged 0.46 mounds ha^{-1}, and exhibited a clustered pattern throughout the landscape, occurring at relatively high densities (up to 2 mounds ha^{-1}) on crests, which are nutrient-poor elements of the landscape. Mounds exhibited significant over-dispersion (even spacing) at scales below 60 m so that evenly spaced aggregations of termite mounds are embedded within a landscape of varying mound densities. The tallest mounds were found in dry savanna (500 mm.yr^{-1}) and were positively correlated with mound density, suggesting that dry granitic savannas are ideal habitat for mound-building termites. Mound activity status also varied significantly across the rainfall gradient, with a higher proportion of active (live) mounds in the drier sites. The differential spacing of mounds across landscapes provides essential nutrient hotspots in crest locations, potentially sustaining biodiversity that would otherwise not persist. The contribution to biodiversity and ecosystem functioning that mounds provide is not uniform throughout landscapes, but varies considerably with spatial scale and context.

Introduction

Spatial heterogeneity across landscapes is a key facilitator of biodiversity and ecosystem complexity throughout the world (du Toit and Cumming 1999, Benton et al. 2003, Pickett et al. 2003). Spatial heterogeneity enables the co-existence of competing species, leading to higher species richness and influencing competition between species (Tilman and Kareiva 1997, Palmer 2003).

Among the many drivers of savanna heterogeneity, termites act as ecosystem engineers (Jones et al. 1994, Dangerfield et al. 1998), mostly through their transportation of soil nutrients both vertically and horizontally (Sileshi et al. 2010), as well as by altering soil structure and hydrology (Mando et al. 1996). The large epigeal mounds constructed by the genus *Macrotermes* are a prominent feature of many African savannas and act as agents of spatial heterogeneity creation. Mounds increase the patchiness and heterogeneity of savanna vegetation by forming nutrient hotspots, supporting a significantly higher number of woody plant and forb species compared with the surrounding savanna matrix (Moe et al. 2009, Erpenbach et al. 2013). By concentrating nutrients, termite mounds provide key resource areas with quality forage that is intensely utilized by grazers and browsers (Mobæk et al. 2005, Levick et al. 2010b), enabling the persistence of a wide variety of herbivore species within a landscape that would otherwise offer low forage quality (Grant and Scholes 2006). Indeed termite mounds have recently been shown to be more influential in determining spatial variation in herbaceous savanna vegetation than other, more traditional determinants, such as grazing (Okullo and Moe 2012b).

As well as being agents of ecological heterogeneity through mound construction, the distribution of termite mounds also varies with multiple environmental factors. Variation in the density of termite mounds has been observed at regional scales, with *Macrotermes* preferring sandy, granitic soils to basaltic clay, and undulating topography over concave floodplains (Meyer et al. 1999). Similar patterns have been observed at finer hillslope scales, with these termites avoiding areas with high clay content below seeplines in catena sequences (in order to escape inundation), while at the same time avoiding areas that are too sandy for mound construction (Levick et al. 2010a). Other drivers of heterogeneity, such as fire and rainfall, are poorly understood (but see Benzie (1986)), and competitive interactions between termite colonies also shape mound distributions, evidenced by the over-dispersion exhibited by termites at small spatial scales (Korb and Linsenmair 2001, Pringle et al. 2010). Furthermore, despite the increasingly recognized role played by termite mounds, few studies have examined how mound patterns vary at different ecological scales. Examination over a range of spatial scales is needed to facilitate a better understanding of how the role of termite mounds in structuring savannas varies across space, and providing information on the extent of their influence across different savanna landscapes. However, most studies have focused on small areas, which may poorly represent landscape complexity. In part, this is due to logistical constraints and difficulties with surveying large areas with accuracy.

The Carnegie Airborne Observatory (CAO) (Asner et al. 2007), an integrated LiDAR and hyperspectral system, provided an opportunity to survey large areas of savanna and map termite mound position and height (which relates directly to above-ground volume) across an entire river catchment. Using this remote-sensing technology, I was able to extend the limited coverage of previous studies and provide landscape level insights into termite mound patterns, in order to more fully understand drivers of spatial heterogeneity in African savannas. My aims were to: i) investigate how patterns of termite mound distribution and shape vary across a savanna landscape (an entire river catchment); ii), explore how such patterns differ between broad vegetation types within this landscape; iii) determine the principal factors shaping mound densities across the catchment; and iv) quantify the species diversity of mound-building termites across the catchment. I expected mound density to vary across the landscape in response to topographical features, being located primarily on crests (following Levick et al. 2010a), as well as exhibit variation across vegetation types in response to factors such as rainfall and soil nutrients. Higher densities, with higher species diversity, were expected in wetter savanna areas due to higher levels of primary productivity conducive to increased termite diversity (Davies et al. 2012).

Methods

Study area

I conducted the study throughout the entire catchment of the N'waswitshaka River, a medium sized non-perennial tributary of the Sabie River in the southern Kruger National Park, South Africa. The catchment covers *ca.* 27 000 ha of gently undulating landscape and varies in altitude from *ca.* 630 m.a.s.l. in the south-west to *ca.* 280 m.a.s.l. in the north-east. The underlying geology consists of granite throughout the catchment except for a narrow gabbro intrusion in the southwest. Mean annual precipitation (MAP) decreases from *ca.* 650 mm.yr^{-1} in the west to *ca.* 500 mm.yr^{-1} in the east of the catchment, with most rainfall occurring during the hot summer months (October – March). The vegetation varies considerably across the catchment; in the wetter west (Pretoriuskop region) it is dominated by nutrient-poor “sour bushveld" consisting of mostly *Terminalia sericea* and *Dichrostachys cinerea* while the drier east (Skukuza region) is relatively nutrient-rich and dominated by an *Acacia nigrescens/Combretum apiculatum* association (Gertenbach 1983). A mosaic of these two vegetation types, with intermediate nutrient levels, occurs as a transition zone in the central region of the catchment (Napi region), with *Combretum zeyheri* and *C. collinum* also becoming prominent. The gabbro intrusion is dominated by open savanna with dense grass cover, and with some areas containing low-standing *Acacia nigrescens* and *Dichrostachys cinerea* shrubs (Gertenbach 1983). Mean annual rainfall also varies across the four regions, being highest (650 $mm.yr^{-1}$) in the west (Pretoriuskop) and lowest (500 $mm.yr^{-1}$) in the east (Skukuza). Mean annual rainfall at Napi and on the gabbro intrusion is between 550 and 600 $mm.yr^{-1}$. Within the catchment there are also distinct vegetation patterns resulting from catena processes with a distinct seepline (where water moving downslope through the soil accumulates against the clay-enriched zone of valley bottoms) being evident. Woody cover is generally higher on hill crests than the lowlands alongside river channels, where, apart from a riparian corridor, the grassy layer dominates (Levick et al. 2010a).

Airborne remote sensing and field data collection

The CAO-Alpha system was operated over the study site in April and May 2010. The CAO-Alpha system used a pushbroom imaging array with 1500 cross-track pixels, sampling across the 367–1058 nm range at up to 2.4 nm spectral resolutions (Asner et al. 2007). The spectrometer sub-system was fully integrated with a LiDAR sub-system having an adjustable laser pulse repetition rate of up to 100 kHz. The CAO-Alpha LiDAR subsystem provided 3-D structural information on vegetation canopies and the underlying terrain surface. The GPS–IMU sub-system provided 3-D position and orientation data for the sensors, allowing for highly precise and accurate projection of LiDAR observations on the ground. Further technical background of the CAO-Alpha is discussed in detail by Asner et al. (2007).

For this study, the CAO LiDAR data were collected from 2000 m above ground level, providing terrain and woody vegetation elevation measurements at 1.12 m spatial resolution. All data collection flights were conducted within 2.5 h of solar noon. Digital terrain models (DTMs) derived from LiDAR were analysed in an object-based manner to extract termite mound spatial locations and size. Image segmentation was weighted towards changes in slope, and the classification hierarchy considered both the relative difference in elevation between neighbouring objects, and image object shape.

In addition to the airborne remote sensing, I collected ground field data on mound structure and activity status during March and April 2011. This also served as ground validation of the LiDAR measurements. Termite mounds are exceptionally long-lasting structures (being up to centuries old) (Watson 1967), and so it is unlikely that the distributions or structure of mounds would have varied much between the time of the airborne measurements and the field checks. The field data consisted of ground validation of 40 termite mounds in each of three of the vegetation types within the catchment (the wet west, dry east and central transition area), although only 10 in the wet west were used for ground validation. Mounds used for field checks were randomly selected prior to detection with LiDAR and later checked against the LiDAR data. At each mound, four height measurements (one at each cardinal direction to account for slope variation) and two diameter measurements (one along a north-south axis and the other along a west-east axis) were measured. The gradient of the mound slope was also recorded using a digital angle gauge. Eight gradient measurements were recorded for each mound (an upper and lower measurement at each cardinal point). Finally, each of the 40 mounds per site were thoroughly searched for termites (with manual searching and excavation) or recent termite activity (evidence of fresh construction) to determine whether the mound was inhabited by termites (i.e., whether it was active or inactive). When present, termites were sampled from the mounds for species identification.

Analysis

I conducted data analysis at three spatial scales: throughout the entire catchment, among broad vegetation types within the catchment, and on individual hillslope crests. First, catchment mound patterns were investigated using Ripley's *K* function, a second-order statistic that utilises information on all inter-point distances to provide information on spatial pattern (Wiegand and Moloney 2004). At this catchment scale I also investigated effects of hydrology (drainage lines) on mound locations. Using flow accumulation tools, drainage lines were mapped in ArcGIS software using DTMs derived from LiDAR, and from these networks, an index of drainage line size was calculated. These drainage lines reflect areas of flow accumulation and their size (order) is calculated in the same manner as traditional stream orders. Since I was interested in the effect of drainage lines (areas of flow accumulation) rather than streams, my index of drainage line size is higher than traditional stream orders. The nearest mound to each segment of a drainage line of a particular size was then calculated and differences between distances were compared with a Kruskal-Wallis test and pairwise Wilcoxon rank sum tests (with a Holm correction for multiple comparisons).

Second, I compared mound distributions (patterning, density and height) using Ripley's *K* function (patterning) and Kruskal-Wallis with pairwise Wilcoxon rank sum tests (densities and heights) across the four broad vegetation types present in the catchment: high rainfall, nutrient-poor savanna in the west (Pretoriuskop), low rainfall nutrient-rich savanna in the east (Skukuza), an intermediate rainfall and nutrient savanna (Napi), and the narrow gabbro intrusion with intermediate to high rainfall in the west. Each region (vegetation type) differed in size, with Skukuza the largest at 17 653 ha, followed by Napi at 5 746 ha and Pretoriuskop at 1 694 ha. The gabbro intrusion covered the smallest area at 1 616 ha. Altogether, the four regions covered the entire catchment. Due to the nature of savanna ecosystems, spatial heterogeneity within the vegetation does exist within regions, but the dominant vegetation is extensive enough to ensure a broadly similar environment throughout each region. The gradient of the mound slope was also assessed in three of the four broad vegetation types (excluding the gabbro intrusion where mound densities are extremely low) using one-way analysis of variance (ANOVA). Slope was compared for the entire mound as well as upper and lower measurements. The activity status and termite species occupying mounds was also investigated across these three sites. Factors that could influence the activity status of these mounds (vegetation type, mound height and mound slope) were compared using generalized linear models with a binomial error family and corrected for overdispersion. The most parsimonious model was selected using Akaike's information criterion (AIC) (Burnham and Anderson 2002).

Because Levick et al. (2010a) found that aggregations of termite mounds are located on crests in the same study region, I further investigated 54 crests across the catchment to determine the principal factors shaping mound distributions. Crests were chosen based on the DTM constructed from the LiDAR and stratified across the catchment, ranging in area from 14.6 ha to 172.6 ha (mean = 61.2 ha and median = 55.5 ha). For each crest, data on the following variables were attained either with the remote sensing or from South African National Parks: crest area (determined from DTMs and defined as the area above the seepline, demarcated by the lowest extent of termite mound occurrence following Levick et al. 2010a), fire return period from 1941 to 2009 (half the crest must have burnt for a fire to be deemed to have occurred in a given year; the vast majority (82%) of fires considered burnt the entire crest when they did occur), mean annual precipitation recorded from 1910 to 2002 (Zambatis 2003), mean percentage woody cover measured with LiDAR at a spatial resolution

1.12 m and dominant geology, following Gertenbach (1983). Some spatial variation across the crests will inevitably be present for each covariate, however, crests were sufficiently small to limit any large variation and the values of each covariate was carefully inspected to minimise variation and ensure consistency across a given crest. Linear models and linear mixed effects models were then fitted to examine relationships between these variables and mound densities and heights respectively. Candidate sets of models (454 and 452 candidate models were constructed for densities and heights, respectively), consisting of the above variables and all ecologically meaningful two-way interactions were ranked according to sample-size-corrected AIC*c* (Burnham and Anderson 2002) and the best model for each response variable (mound density and height) selected. The top regression models for each response variable according to AIC*c* are provided in Appendices 1 and 2, full sets are available from AB Davies on request. A difference in AIC*c* of less than 2 was considered a threshold for determining whether one model performed better than another. All statistical procedures were conducted using R software version 2.15, using the packages spatstat (Ripley's *K*) and lme4 (linear mixed effects models) (R Development Core Team 2012).

Results

Field checks indicated that overall 75% of mounds were detected with the LiDAR survey. Detection rates varied across regions, with an 83% detection rate at the dry site (Skukuza), 64% at the intermediate site (Napi) and 90% at the wet site (Pretoriuskop). Detection was likely lower at Napi because of a relatively high number of very small (<0.5 m) mounds here compared to other sites (7 at Napi compared to 2 at Skukuza and 1 at Pretoriuskop). When mounds of this height class were removed from the ground validation, detection rates improved and were more similar across regions (87% at Skukuza, 78% at Napi and 90% at Pretoriuskop). LiDAR therefore detected medium and large (>0.5 m) mounds (which are likely more ecologically meaningful) with similar, high accuracy at all three sites. Heights of detected mounds at the intermediate site were closely correlated with the LiDAR estimates ($r_s = 0.78$, $P < 0.001$, $n = 25$). However, at the dry and wet sites, LiDAR underestimated mound height with a weaker, but significant, correlation evident at the dry site ($r_s = 0.39$, $P < 0.05$, $n = 34$) and a weak and insignificant correlation at the wet site ($r_s = 0.50$, $P = 0.178$, $n = 9$).

Catchment-level patterns

The overall density of termite mounds across the N'waswitshaka catchment was 0.46 mounds ha^{-1} (a total of 12 505 mounds were detected, Fig. 2.1), with the mean overall termite mound height being 1.21 m (± standard deviation of 0.47 m). Ripley's *K* function showed that mounds exhibit significant over-dispersion (even spacing) at scales below 60 m. At larger scales, however, mounds displayed a clustered pattern, indicating that evenly spaced aggregations of termite mounds are embedded within a landscape of varying mound densities, exhibiting a clustered pattern (Figs. 2.1 and 2.2). Levick et al. (2010a) recorded that such clusters occur on crests within this landscape in response to hillslope hydrological boundaries, resulting from patterns in sand and clay distribution.

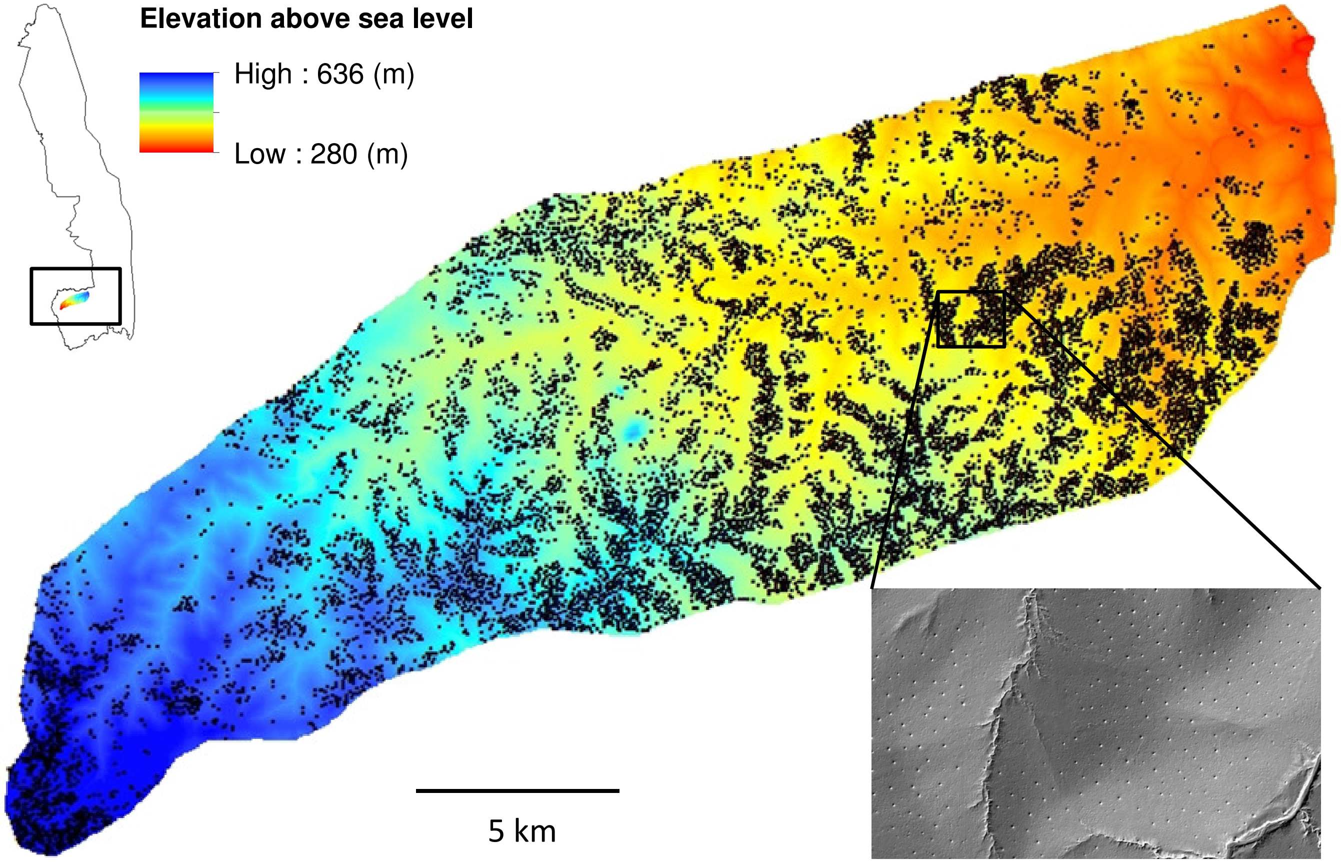


Figure 2.1: Location of the N'waswitshaka catchment (study site) within Kruger National Park. The black dots represent termite mounds which exhibit a clustered distribution at the catchment scale and an over-dispersed one at the hillslope scale (see enlarged area). The catchment is displayed as a digital terrain model (DTM), with red areas representing high elevation and blue areas low elevation.

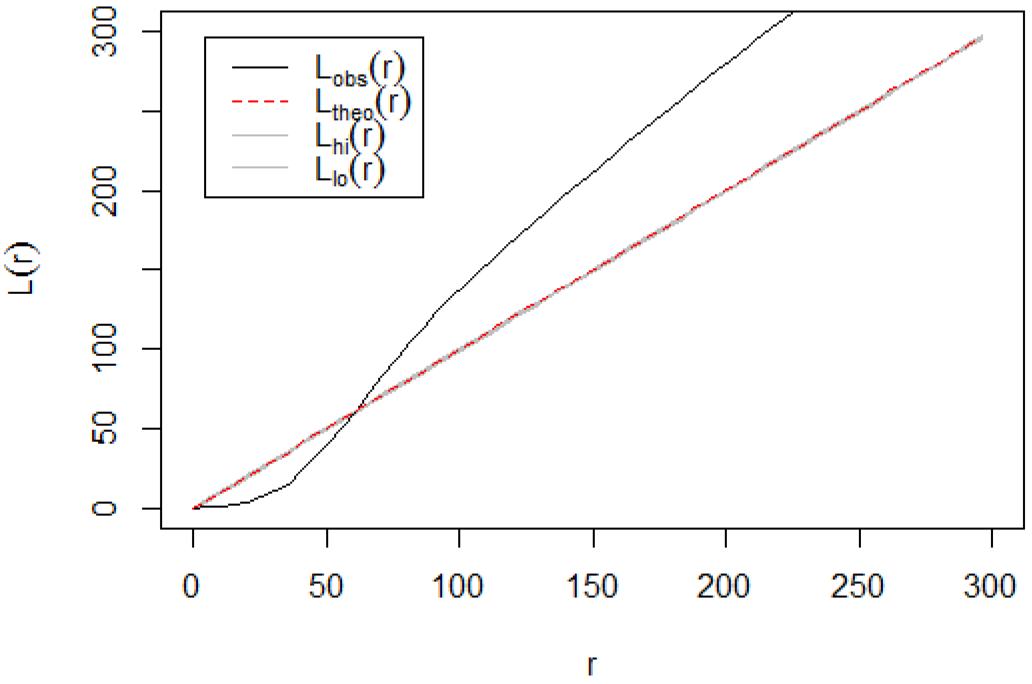


Figure 2.2: Results of Ripley's *K*-function analysis of termite mounds across the entire N'waswitshaka catchment. L(r) values (a transformation of Ripley's *K*) are plotted against distance (r) in meters. The dashed line represents the distribution of mounds under complete spatial randomness, while the solid line represents observed mound distribution. Values below the dashed line indicate over-dispersion (even spacing) while values above the dashed line indicate clustering. 95% confidence intervals expected from a random landscape are plotted as grey lines, but are too close to the theoretical distribution (dashed line) to be noticeable.

Since mounds are clustered on crests, above the seepline of hillslopes, I investigated the effect of drainage line size on the distribution of termite mounds. My results indicate that as drainage line size increases so does the distance to the nearest termite mound (Kruskal-Wallis $X^2 = 565.19$, $p < 0.001$). Pairwise Wilcoxon rank sum tests revealed that these differences were significant between all the different drainage line size classes except for comparisons between 3rd and 5th order drainage lines and between 4th and 6th order drainage lines (Fig. 2.3). Thus, there is a significant increase in the mean distance to the nearest mound when moving from a first order drainage line to a second order drainage line and again to a third order drainage line. However, drainage lines of third to sixth order do not have a major impact on mound distance to drainage line, but an almost two fold jump in mean mound distance to drainage line is observed when moving to a seventh order drainage line, the highest available for my study site. It therefore appears that a threshold is reached at a seventh order drainage line (corresponding to a 5th order stream for this catchment) in terms of mound distance to water.

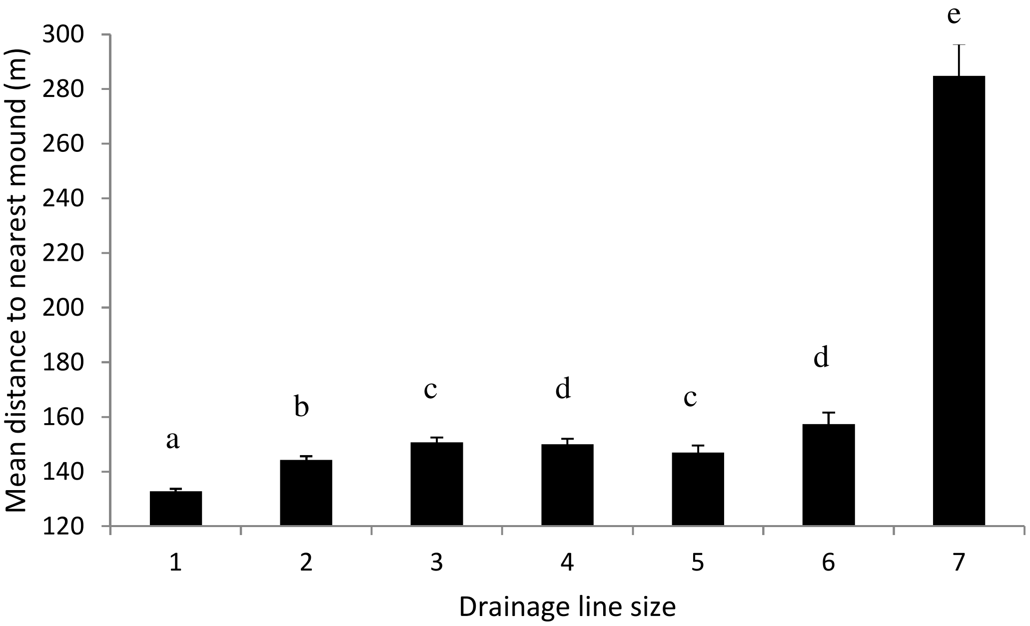


Figure 2.3: Mean (± 1 SE) distance to drainage channel of termite mounds as a function of stream order. Mean distances are calculated as the distance of the nearest termite mound to each segment of the particular stream. Letters indicate significantly different distance classes. Stream orders do not follow traditional classifications and rather incorporate areas of high flow accumulation; thereby first order streams are not streams in the conventional sense, but rather drainage lines where water may accumulate during wet periods.

Mound patterns among vegetation types

Ripley's *K* function demonstrated that mounds were over-dispersed across all vegetation types at small spatial scales (Appendix 2.3). The patterns at the drier sites in particular mirror those of the entire catchment with clustering occurring at spatial scales above 60 m (Appendix 2.3a and b). The wettest site (Pretoriuskop) displayed similar patterns (over-dispersion at small scales and clustering across the landscape), but with the overly-dispersed clusters of termite mounds being smaller in size (occurring below spatial scales of 45 m)

(Appendix 2.3c). Ripley's *K* revealed irregular patterning on the gabbro intrusion, but with the same overall pattern of over-dispersed clusters of mounds (Appendix 2.3d). The irregular patterning could be due to much lower mound densities found here (i.e., small sample sizes) and the shape of the gabbro intrusion (being long and narrow).

Both mound density (Kruskal-Wallis $X^2 = 287.44$, $p < 0.001$) and height (Kruskal-Wallis $X^2 = 1148.49$, $p < 0.001$) varied significantly across the four major vegetation types present in the catchment. Pairwise Wilcoxon rank sum tests showed that all four sites differed significantly from each other in terms of mound density ($p < 0.001$ in all cases) except for Napi and Pretoriuskop ($p = 0.21$). Mound density was highest at the wettest site, Pretoriuskop (0.59 mound ha^{-1}) and decreased with decreasing mean annual precipitation (0.48 mounds ha^{-1} recorded at the driest site, Skukuza). The lowest density was recorded on the gabbro intrusion (0.18 mounds ha^{-1}), suggesting a strong effect of geology on termite mound densities (Fig. 2.4a).

Pairwise Wilcoxon rank sum tests showed that mound height varied significantly between all sites ($p < 0.001$) with taller mounds being located at drier sites (Skukuza and Napi). In contrast to mound densities, an effect of geology on mound height was not apparent (Fig. 2.4b). Mound diameter was significantly correlated with mound height ($r_s = 0.75$, $P < 0.001$, $n = 120$) and so excluded from analysis. Height was selected in preference to diameter because it is more readily obtained from LiDAR, and hence could be used in all analyses. Termite mounds were significantly steeper at drier sites (ANOVA, $F_{2, 117} = 12.25$, $p < 0.001$), with this pattern being consistent for both the upper and lower (pediment) sections of mounds, although differences in steepness were not significant for the pediment, as revealed by Tukey HSD post-hoc tests (Fig. 2.5). Tukey HSD tests also showed that only mounds at the driest site (Skukuza) were significantly steeper than the other two sites, which did not differ significantly from each other. This was the case for the entire mound as well as the upper sections (Fig. 2.5).

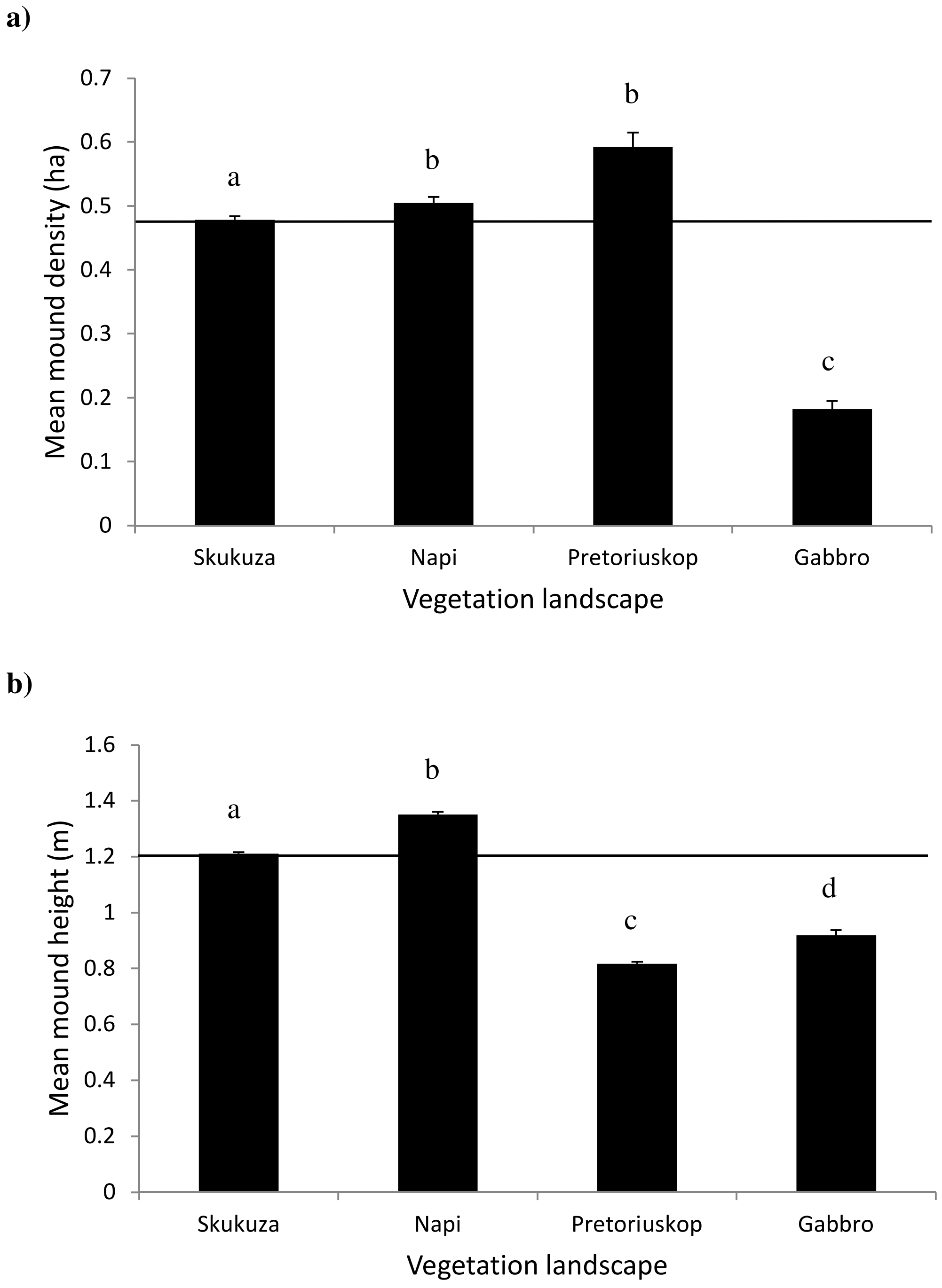


Figure 2.4: Mean (± 1 SE) a) termite mound density and b) height in each of four vegetation landscapes in the Kruger National Park. The solid line on each graph represents the overall density and height for the entire catchment. Letters indicate significantly different distance classes.

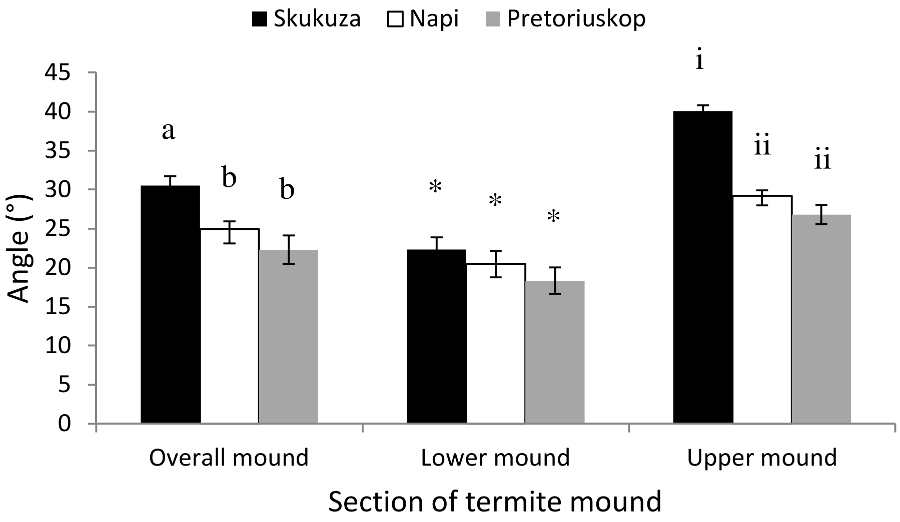
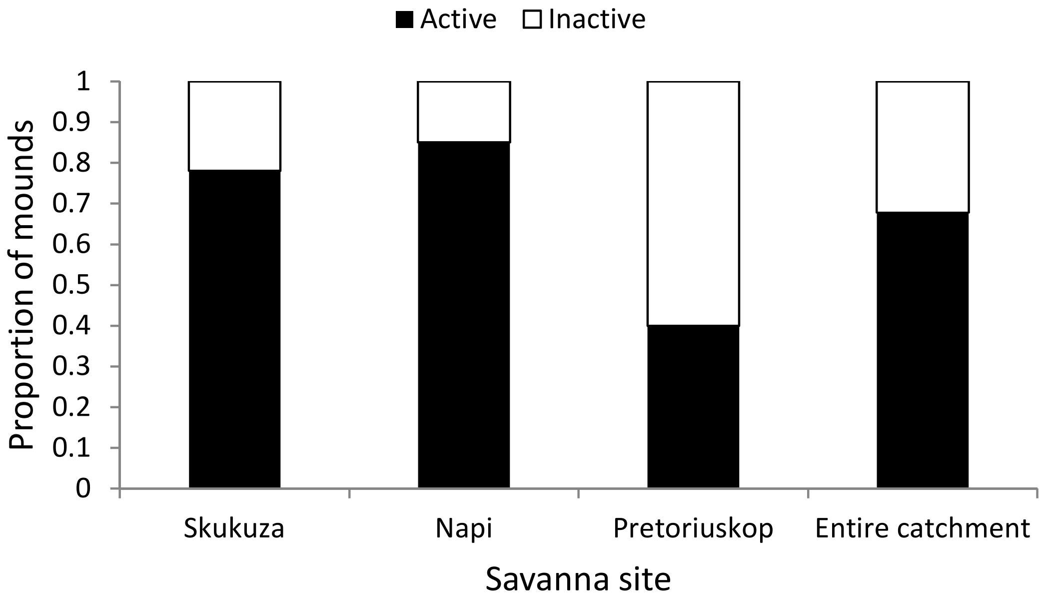


Figure 2.5: Mean (± 1 SE) angle (steepness) of termite mounds in three broad vegetation types, stratified according to the entire mound and the lower and upper sections. Letters and symbols indicate significantly different distance classes.

The activity status (whether mounds are active or not) also displayed significant variation across the rainfall gradient, with a far higher proportion of mounds active in the dry and intermediate sites (Skukuza and Napi, Fig. 6a). There was a significant relationship between both site ($F = 6.87$, $p < 0.01$) and mound height ($F = 7.89$, $p < 0.01$) and the activity status of mounds, but not with the steepness of the mound. The termite species occupying mounds at the time of sampling also varied across the rainfall gradient, with much lower diversity present at the dry site (Skukuza), where *Macrotermes falciger* dominated the landscape (occupying 87% of active mounds). Diversity of termite species peaked at the intermediate site (Napi) with ten termite species sampled here. At the wettest site (Pretoriuskop), six species were sampled (Fig. 6b).

a)



b)

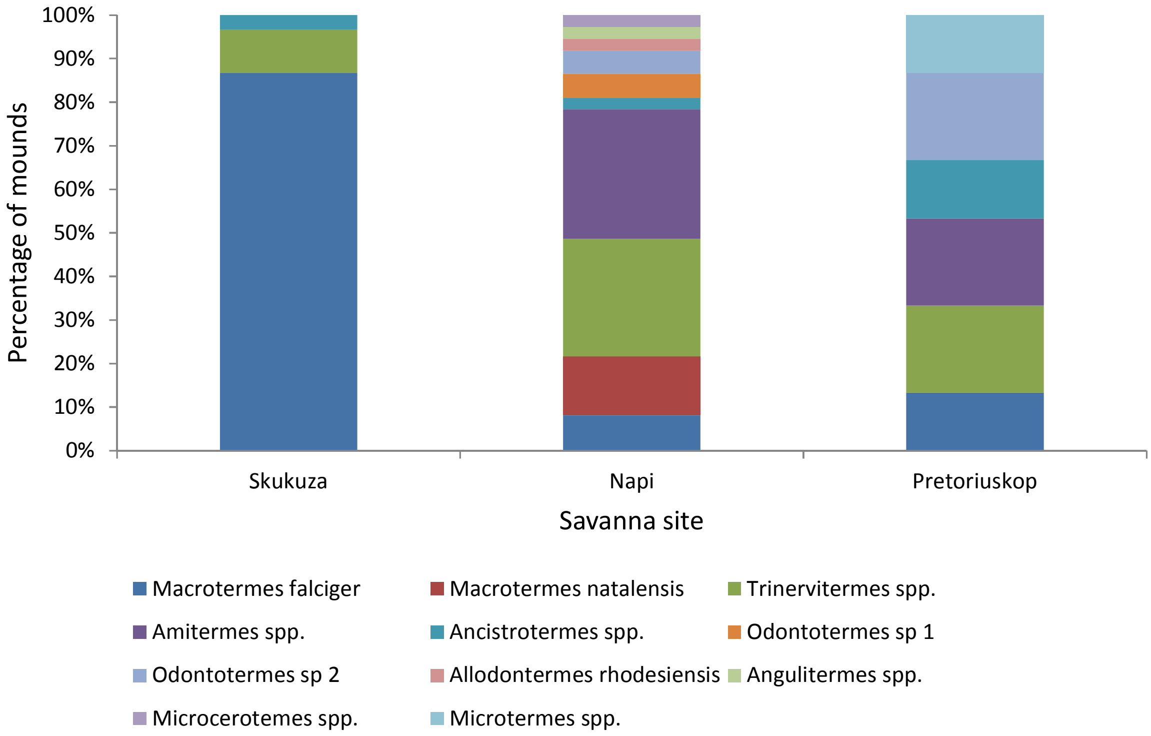


Figure 2.6: a) Proportion of termite mounds (out of a total of 40 per site) that are active in each vegetation landscape and **b)** the relative proportions of termite species sampled from mounds in each vegetation landscape.

Predictors of crest patterns across the catchment

Within the catchment, termite mound density on crests was significantly correlated with mean annual precipitation (MAP, $X^2 = 5.02$, $p < 0.05$), mound height ($X^2 = 12.31$, $p < 0.001$), geology (granite *vs.* gabbro substrate) ($X^2 = 4.24$, $p < 0.05$) and percentage woody cover ($X^2 = 14.41$, $p < 0.001$) (Fig. 7). There was a significant interaction between mound height and mean annual precipitation ($X^2 = 17.17$, $p < 0.001$) and between fire regime and mean annual precipitation ($X^2 = 4.16$, $p < 0.05$), although fire regime itself was not a significant factor ($X^2 = 0.99$, $p = 0.32$) and was not present in the second and third best performing models (Appendix 1). The relationship between mean annual precipitation and mound density had bimodal peaks at the wet and dry ends of the spectrum, with decreased densities at intermediate rainfall (Fig. 7a). There was a significant positive correlation between mound height and density, where mounds were taller, they occurred at higher densities. However, this trend was not evident for shorter mounds (< 1m), where no such correlation was present (Fig. 7b). The significant interaction between mound height and MAP also suggests such a trend and results from high densities of short mounds in the wet western section of the catchment. Mean annual precipitation was also the only variable correlated with mound height ($X^2 = 15.91$, $p < 0.001$; Appendix 2) when height patterns were modelled against environmental variables. A strong positive correlation was observed on crests between percentage woody cover and mound densities (Fig. 7c). Mounds also occurred at significantly higher densities on crests with granitic substrate compared to those on the gabbro intrusion (Fig. 7d). Although overall fire had no effect on mound density, there was a significant interaction between fire regime and MAP; however, these patterns were weak with no clear causality (Appendix 4, Fig. S2). Furthermore, the second best model (with an AIC_c score only 0.05 greater than the top model) did not include fire and this interaction should thus be interpreted with caution (Appendix 1).

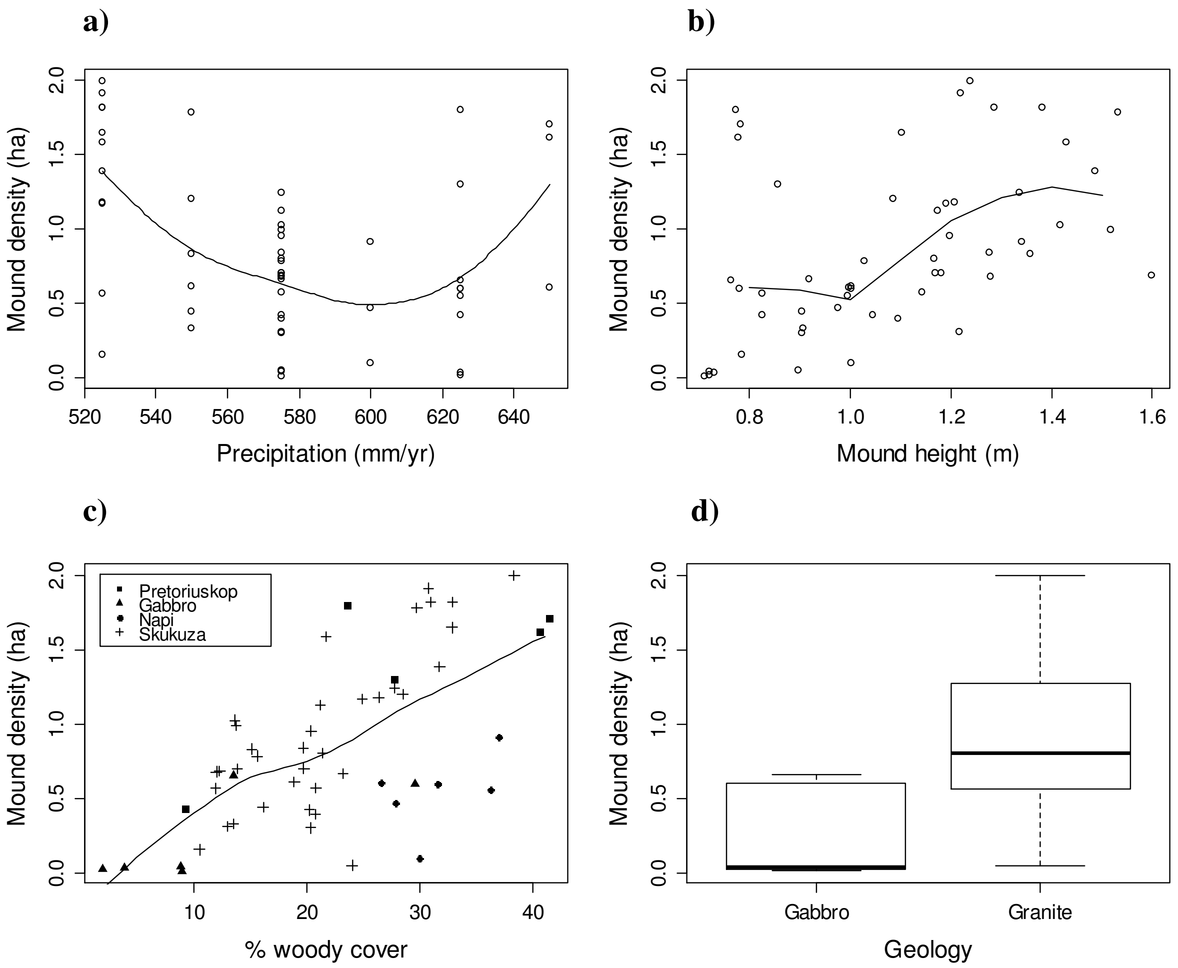


Figure 2.7: Relationships between a) mean annual precipitation, b) mound height, c) percentage woody cover and d) underlying geology on termite mound densities. A LOESS smoother has being added to the scatterplots (a – c) to aid visual interpretation.

Discussion

Spatial patterns of termite mounds across the catchment

The integration of my results across three spatial scales provides novel insights into the spatial structuring of termite mounds, and hence ecological heterogeneity, in African savannas. At the full catchment scale, my recorded mound densities (0.46 ha^{-1}) are relatively low compared to other studies. Meyer et al. (1999) recorded *Macrotermes* mound densities of 0.73 ha^{-1} in northern Kruger National Park (KNP), while Levick et al. (2010a) recorded mound densities of 0.6 – 0.7 ha^{-1} in an area of similar mean annual precipitation (MAP) and vegetation characteristics, also in southern KNP. Elsewhere in Africa, *Macrotermes* mound densities have been recorded as high as 1 – 4 ha^{-1} in Uganda (Pomeroy 1977), 3 – 5 ha^{-1} in Zambia (Trapnell et al. 1976), 4 - 22 ha^{-1} (Lepage 1984) and 11 - 83 ha^{-1} in Ivory Coast

(Korb and Linsenmair 1998). The lower densities recorded for the N'waswitshaka catchment from my study are likely related to the scale at which the study was conducted. Most previous studies, including all those listed above, are field based and consider only one or a few patches in the landscape and infer from them the mound density for the area. In contrast, my measurements are across an entire catchment and hence averaged over different geology and hillslope types. However, there is the possibility that lower densities could be somewhat attributed to the resolution at which the LiDAR was operated, with small mounds escaping detection. Conservatively, patterns presented here are thus more reliably interpreted as those of larger termite mounds, which are likely to be more ecologically meaningful in terms of driving heterogeneity than small ones (see Joseph et al. 2013). Nonetheless, my study as well as Meyer et al. (1999) and Levick et al. (2010a) record consistently lower mound densities for southern Africa than studies conducted in central and east Africa. Termites are restricted to sub-tropical and tropical regions with their diversity decreasing with increasing latitude (Eggleton 2000); lower mound densities are therefore expected for southern Africa where conditions are less optimal, being cooler and with stronger seasonality.

Termite mounds are not evenly distributed across the catchment but display a clustered pattern at spatial scales above 60 m in extent, aggregating on crests above seeplines and being almost entirely absent from lower lying regions. This results in much higher mound densities (up to 2 mounds ha^{-1}) on crests and underscores the importance of spatial scale in ecological studies; where a study is conducted and the spatial extent over which observations are collected has a substantive effect on the results of the study. This supports my reasoning above for the low, but potentially more accurate, mound densities recorded in my study relative to studies cited above from further north in Africa; if only small portions of the landscape where mound densities are high (i.e. crests) were surveyed, extrapolated mound densities would be far higher. Full coverage of large areas is thus necessary to adequately understand patterns in termite mound distributions.

Clustered patterning in termite mound distribution has also been recorded in previous studies and seems to be driven mostly by hydrological controls, with termites avoiding areas with greater risk of inundation (Freymann et al. 2010, Levick et al. 2010a). This is also evident when drainage line effects are considered; termites avoiding even the smallest drainage lines (located approximately 130 m from them) and decreasing in proximity with increasing drainage line size, located up to *ca.* 280 m from high order drainage lines with large floodplains. Such patterning means that mounds will be most important for savanna heterogeneity at localised scales, on crests in landscapes with undulating topography. Although limited to crests, this does not necessarily diminish the importance of mounds for creating landscape heterogeneity because crests are dominant features in these landscapes (accounting for about 35% of the landscape, S.R. Levick *unpublished data*) and the vegetation growing on them (apart from on termite mounds) is generally low in nutrients compared to lower lying regions (Grant and Scholes 2006). My study was conducted in a landscape of undulating topography, how mound distributions are shaped in flatter regions warrants further investigation. In such flatter areas, termites will be unable to build mounds above seeplines to avoid inundation and instead may be influenced by cryptic ecological controls, such as ground water storage (JS Turner, *pers. comm.*). If true, termite mounds may be useful indicators of ground water dynamics, being absent or at lower densities where the water table is close to the surface.

On crests, mounds exhibit significant over-dispersion (even spacing), probably as a result of intra-specific competition (Darlington 1982, Korb and Linsenmair 2001, Pomeroy 2005), suggesting that at these smaller spatial scales, biotic factors (such as competition for resources) are responsible for distribution patterns. Pringle et al. (2010) demonstrated that such even spacing of termite mounds enhances their importance in ecosystems, because the average distance from any given point to the nearest feature in a landscape is minimised in landscapes where the features are evenly spaced. Thus the even spacing of mounds on crests enhances the importance of the spatial heterogeneity induced by them in these otherwise nutrient depauperate areas.

Over broad vegetation types, mounds display variation in their density and height: densities increase with increasing MAP and mounds in wetter areas are significantly smaller (lower in height and diameter which corresponds to volume). Soils in these wet savannas are sandy with low levels of clay (Gertenbach 1983), and since *Macrotermes* require a sufficient amount of clay to construct mounds (Jouquet et al. 2004), it is likely that mound size here is constrained by a lack of clay. Smaller *Macrotermes* mounds support smaller termite colonies (Meyer et al. 2000) which probably forage over smaller areas and is a possible explanation for increased mound densities in the wetter regions of the catchment. If mound spacing is driven by endogenous processes related to competition (Darlington 1982, Korb and Linsenmair 2001, Pomeroy 2005), smaller colonies will therefore be able to persist at higher densities, enabling higher mound densities in wetter savannas where mounds are smaller. Grohmann et al. (2010) demonstrated that larger *Macrotermes* mounds are further apart than smaller mounds, providing direct support for this notion. An alternative explanation could be that higher levels of primary productivity at the wettest site lead to termite home ranges being smaller and consequently higher densities of mounds. However, if higher primary productivity was the driver of higher mound densities, then one would also expect larger colonies (i.e. higher termite abundance) to be supported by this high productivity, resulting in high densities of large termite mounds. However, at the wettest site mounds are smaller, supporting smaller colonies (Meyer et al. 2000), making this an unlikely explanation. Higher mound densities in the wet, upper reaches of the catchment could also be a result of the spatial scale of the study. Smaller drainage lines are present here which result in more crest relative to lowland area. Given the strong relationship between mound location and hydrological features, this may lead to overall higher densities of mounds in the wet, upper reaches of the catchment than in the drier, lower reaches where larger drainage lines result in lower crest: lowland ratios. This means that there is more available area for termite mound construction in the upper catchments (a higher crest: lowland ratio), and therefore higher mound densities when the landscape is considered overall, again emphasising the importance of spatial scale and comprehensive coverage when mapping termite mound distributions.

Mounds in the drier eastern areas of the catchment are steeper, but this is uncorrelated with activity. Hence, mound steepness is likely a function of soil characteristics that allow taller and subsequently steeper mounds, rather than emerging from higher termite activity. Jouquet et al. (2004) found that clay was the most important factor for mound stability and structure and the steeper, taller mounds in my study are all located on soils with higher clay content (on crests in drier savanna). Although crests have lower clay content than lower regions of the catena, the crests in the drier savanna have relatively more clay than crests in the wetter, Pretoriuskop, region.

Termites sampled from the larger mounds in the drier regions consist almost entirely of one species, *Macrotermes falciger*, while diversity increases at wetter sites and peaks at the intermediate region, Napi. Davies et al. (2012) found greater termite diversity in wet savanna habitats and attributed this to higher levels of net primary productivity (NPP). My results indicate a similar trend, but the intermediate peak in diversity suggests that patterns in mound-building savanna termite diversity are not as straight-forward as to follow directly with MAP and hence NPP. I only sampled termites occupying large epigeal mounds in this study, which precludes much of the soil feeding taxa that contribute to the high termite diversity of wet savannas (Davies et al. 2012). A mid-rainfall peak in mound-occupying termites is possibly linked to higher levels of NPP but low enough MAP to prevent leaching of soils, causing them to be dystrophic, thus enabling more termite species to persist here. It should be noted, however, that although different termite genera were occupying mounds, the majority of mounds considered in this study were built by termite species in the genus *Macrotermes*, which is evident by their size and structure (Uys 2002), and were most likely occupied later by other termite species.

Predictors of mound densities on crests

When mound densities on crests (where the majority of mounds occur) were investigated, key correlates were the percentage of woody cover on the crest, the height of the mounds present, mean annual precipitation and the underlying geology. The relationship with mean annual precipitation shows a bimodal pattern instead of a linear response, with densities peaking at the wet and dry ends of the spectrum. As discussed above, the disparity between the overall landscape and crest patterns with relation to mound density is strongly related to scale, and exists because my data were collected across a river catchment, with the low rainfall area being in the lower reaches of the catchment where drainage lines are generally larger, resulting in greater area being unsuitable for mound construction. By examining patterns among crests, such hydrological effects are accounted for and the actual drivers of mound density become apparent. The increase in density at the dry end of the rainfall gradient is likely driven by different factors to those at the wet end (where smaller mounds can be located closer together) since mounds here are much larger and the soils contain more clay (Gertenbach 1983), suggesting that crests in drier savannas can sustain much larger termite populations (high densities of large termite colonies). Furthermore, a far higher proportion of mounds are active in these drier savannas. These drier savannas are higher in nutritional value than wetter ones, and termites are likely responding to higher levels of nutrition, being more abundant in terms of colony densities and numbers of individual termites. Since termites facilitate nutrient cycling (Lavelle et al. 2006), a positive-feedback loop may develop in these drier savannas, with more termites able to persist here which in turn increases nutrient cycling and maintains nutrient-rich savanna.

Moreover, at this hillslope scale, and in contrast to broad catchment patterns, mound height and density are positively correlated, suggesting that where colonies are large they also occur at high densities, with the tallest mounds located in the drier, nutrient-rich, sites where more termites can be sustained. The exception to this pattern is when mounds drop below ~1 m in height; here no pattern exists between height and density. This occurs because in some areas (wetter crests around Pretoriuskop), low mounds occur at high densities, but in most other areas (especially the gabbro intrusion) where mounds are low in height they occur at low densities (although difficulties in detecting small mounds with LiDAR should also be considered here). On such crests, termite colonies are both small and occur at low densities, indicating that such areas (gabbro) are sub-optimal habitat for termites. Although termite mound age may also affect height, age determination is not readily achievable. Furthermore, there is little reason to expect differences in age classes in any one site compared to another.

The effect of geology is pronounced at both the landscape and crest scale, with fewer *Macrotermes* mounds located on the gabbro intrusion. Although still an undulating landscape with crests and lowlands, the soils here are distinct from those on the granitic substrate, with much higher clay content (Gertenbach 1983), making such areas prone to inundation with low permeability and leading to termites avoiding such areas. Meyer et al. (1999) found similar patterns for landscapes with high clay content in northern KNP. However, the few mounds present on the gabbro are taller than the mounds at Pretoriuskop (the wettest landscape with similar MAP to that on the gabbro intrusion). Mound height therefore does not appear to be adversely affected by geology type, where termites can construct mounds on gabbro their construction is not limited in terms of height.

Woody cover on a crest was a strong predictor of mound density, with increased cover coinciding with increased mound density. A large proportion of *Macrotermes* diet consists of dead wood (Donovan et al. 2001) and so where large amounts of dead wood are present, large numbers of termite colonies can survive, with smaller foraging areas needed per colony. Crests with high woody cover will inevitably produce more coarse woody debris and termites respond to this by occurring in higher numbers. Trees respond positively to termites, with higher densities of trees growing on and around mounds (Moe et al. 2009, Erpenbach et al. 2013). Although both mound density and woody cover are strongly linked to topographic position and soil conditions, an interesting positive-feedback loop may strengthen the relationship with higher levels of woody cover creating habitat conducive to *Macrotermes* and higher levels of *Macrotermes* activity creating areas conducive for tree growth, driving strong concomitant patterns in termites and woody cover.

Overall, fire return period had no effect on *Macrotermes* mound densities or height, which is consistent with many other savanna attributes (Parr et al. 2004, Parr and Andersen 2006), including termites (Davies et al. 2012), which have been found to be highly resistant to fire.

Synthesis and ecosystem implications

This is the first study to clearly demonstrate how patterns in termite mound distribution change across a landscape and with respect to the spatial scale at which surveys are conducted. The key factors shaping these distributions also vary with scale; over the entire catchment abiotic factors such as mean annual precipitation, underlying geology and distance to drainage line are essential and lead to clustered patterns in mound distribution. However, when only crests are examined in isolation and topographical effects accounted for, biotic factors including endogenous competition lead to over-dispersed spatial patterning of mounds and factors such as woody cover and mound height become apparent, with the distance between mounds (i.e. higher densities) decreasing in areas that can sustain more termites, such as the nutrient-rich crests in drier savanna. Thus, mound distributions are determined by biotic factors acting on an abiotic template.

Due to the clustered pattern of mound distributions at the landscape scale, termites (through mound construction) are more important as generators of savanna spatial heterogeneity in some areas than others, notably on crests. Crests are otherwise nutrient-poor areas (Grant and Scholes 2006), but the creation of nutrient hotspots by termites will make them more attractive to herbivores and able to sustain higher levels of biodiversity, indeed termite activity has been shown to affect the spatial distribution of savanna vegetation (Sileshi et al. 2010) and mammalian herbivores and their predators (Freymann et al. 2010). Since mounds occur at highest densities in nutrient-rich savanna areas, they are also likely to enhance these already nutrient-rich areas, making such savannas conducive to high levels of biodiversity.

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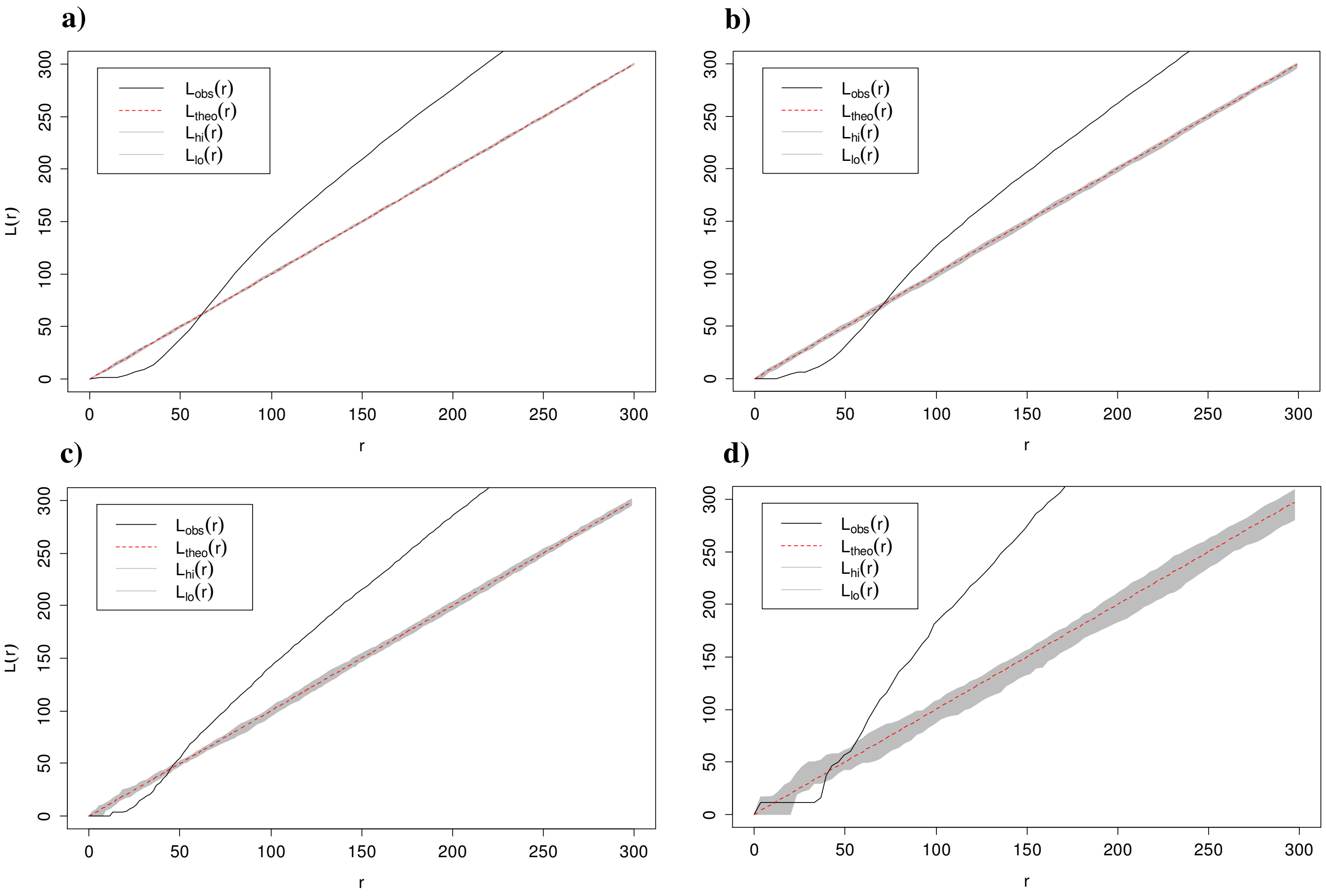
Appendix 2.1: The top eight regression models for mound densities that received considerable empirical support ($\Delta_i < 2$) according to the second order Akaike Information Criterion (AIC*c*). The top selected model I used in the final analysis is in bold. Δ_i is the difference between a model's AIC*c* value and that of the model with the lowest AIC*c*; the Akaike weight w_i is the likelihood of a given model's being the best model in the set. MAP is mean annual precipitation.

Rank	Form of regression model	AIC_c	No. parameters	Δ_i	w_i
1	**% woody cover + Mound height + MAP + Geology + Fire regime + Mound height*MAP + Fire regime*MAP**	**36.8**	**8**	**0.00**	**0.044**
2	% woody cover + Mound height + MAP + Geology + Mound height*MAP	36.9	6	0.05	0.043
3	% woody cover + Mound height + MAP + Mound height*MAP	37.7	5	0.92	0.028
4	% woody cover + Mound height + MAP + Fire regime + Fire regime*Mound height + Fire regime*MAP + Mound height*MAP	37.9	8	1.08	0.026
5	% woody cover + Mound height + MAP + Geology + Fire regime + Mound height*MAP + Fire regime*Mound height + Fire regime*MAP	38.0	9	1.21	0.024
6	% woody cover + Mound height + MAP + % woody cover*Mound height + Mound height*MAP	38.5	6	1.70	0.019
7	% woody cover + Mound height + MAP + Geology + Fire regime + Mound height*MAP	38.6	7	1.78	0.018
8	% woody cover + Mound height + MAP + Fire regime + Mound height*MAP + Fire regime*MAP	38.7	7	1.86	0.017

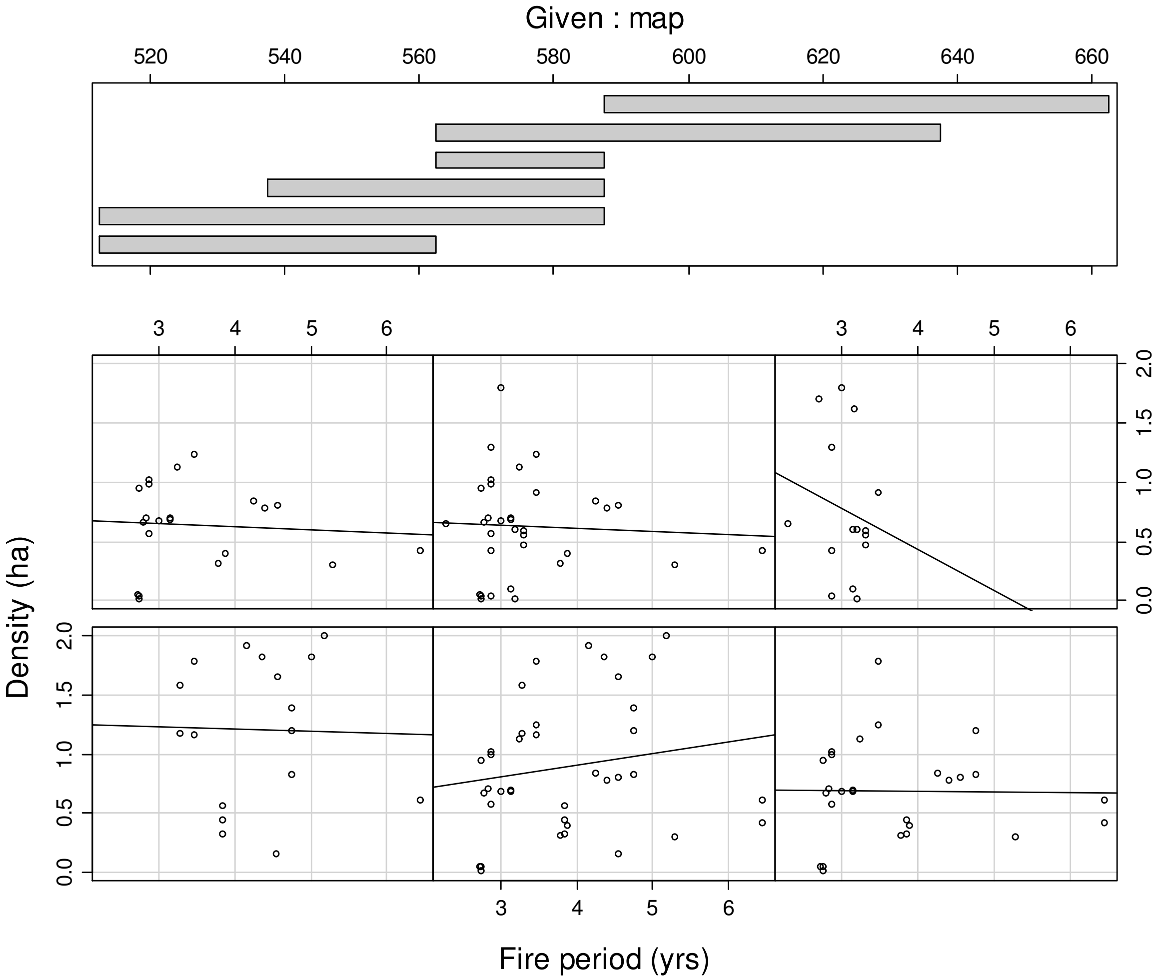
Appendix 2.2: The top regression models for mound height that received considerable empirical support ($\Delta_i < 2$) according to the second order Akaike Information Criterion (AIC*c*), as well as the next best performing models ($\Delta_i < 5$), provided for comparative purposes. The top selected model I used in the final analysis is in bold. Δ_i is the difference between a model's AIC*c* value and that of the model with the lowest AIC*c*; the Akaike weight w_i is the likelihood of a given model's being the best model in the set. MAP is mean annual precipitation. Crest identity (the crest upon which mounds were located) was used as a random effect in all models.

Rank	Form of regression model	AIC_c	No. parameters	Δ_i	w_i
1	**MAP**	**3013.7**	**2**	**0.00**	**0.318**
2	MAP + Geology	3014.8	3	1.12	0.182
3	Geology	3015.7	2	2.02	0.116
4	MAP + Mound density	3016.3	3	2.64	0.085
5	Geology + Mound density	3017.1	3	3.45	0.057
6	Mound density	3017.3	2	3.62	0.052
7	Intercept	3017.4	1	3.73	0.049
8	MAP + Geology + Mound density	3018.1	4	4.42	0.035

Appendix 2.3: Results of Ripley's *K*-function analysis of termite mounds across each of the broad vegetation types, a) Skukuza, b) Napi, c) the gabbro intrusion and d) Pretoriuskop. L(r) values (a transformation of Ripley's *K*) are plotted against distance (r) in meters. The dashed line represents the distribution of mounds under complete spatial randomness, while the solid line represents observed mound distribution. Values below the dashed line indicate over-dispersion (even spacing) while values above the dashed line indicate clustering. 95% confidence intervals expected from a random landscape are plotted as the area shaded grey.



Appendix 2.4: Conditional plot showing how mean annual precipitation (MAP) and fire return period interact to affect termite mound densities. Plots are be read from left to right, bottom to top, starting in the bottom left hand corner and ascending with MAP. On each panel, a linear model is added to aid visual interpretation.



Chapter 3

Variable effects of termite mounds on African savanna grass communities

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Summary

1. Termite mounds are prominent features in African savannas. Termite activity concentrates nutrients in mounds, forming nutrient hotspots that support greater plant diversity, which is of higher nutritional value than the surrounding savanna matrix. However, little is known about grass communities on and around mounds or how the functional importance of mounds varies across environmental gradients.

2. As mean annual rainfall increases, savannas in southern Africa become increasingly dystrophic through leaching of soil nutrients. The functional importance of mounds is concomitantly expected to increase as the difference in nutrient levels between mounds and the savanna matrix increases.

3. I tested this prediction across a rainfall gradient (550 - 750 $mm.yr^{-1}$) in Kruger National Park, South Africa, focusing on grass communities. At three savanna sites differing in annual rainfall, grass diversity and tissue nitrogen concentrations were measured on and off termite mounds and along transects away from mounds in order to calculate the spatial influence of termite mounds on savanna grass communities. Using termite mound densities estimated from airborne LiDAR, I upscaled field-based results to determine the percentage of the landscape influenced by termite activity.

4. Although species richness of grasses was lower on mounds than in the savanna matrix, the assemblage composition varied significantly, with higher nutrient concentrations in grasses located on mounds; this pattern became more distinct with increasing rainfall. The spatial extent of these nutrient-rich grasses also differed across the rainfall gradient, with a larger sphere of influence around mounds in the wetter, nutrient-poor areas, following patterns in soil nutrients induced by termites. Mounds distinctly altered grass communities over ~2% of the entire landscape.

5. *Synthesis.* My results show that termite mounds are important contributors to savanna heterogeneity, and reveal that the functional importance of mounds increases with increasing rainfall.

Keywords: landscape context, LiDAR, *Macrotermes*, nutrients, spatial heterogeneity, rainfall gradient, soil fertility

Introduction

Termites, through the transportation of soil nutrients, act as ecosystem engineers and can have a profound influence on savanna vegetation (Dangerfield *et al.* 1998, Sileshi *et al.* 2010). The epigeal mounds constructed by some genera act as nutrient hotspots and have compositionally distinct plant communities on and around them. Differences are attributed to a range of mechanisms including enhanced nutrient (Jouquet *et al.* 2005, Gosling *et al.* 2012) and moisture availability (Steinke & Nel 1989, Erpenbach *et al.* 2013) as well as increased fire protection (Joseph *et al.* 2013b, Van der Plas *et al.* 2013). Once distinct communities have been established, positive feedback loops resulting from increased shading (Erpenbach *et al.* 2013, Van der Plas *et al.* 2013) and herbivory (Okullo & Moe 2012a) further enhance and maintain differences.

While several studies have documented increased plant diversity on termite mounds (Loveridge & Moe 2004, Traoré *et al.* 2008, Moe *et al.* 2009, Okullo & Moe 2012b, Erpenbach *et al.* 2013), the majority of these have focused on woody plants. Studies explicitly documenting grass patterns have reported a range of responses including no differences between mounds and the savanna matrix in terms of species richness (Moe *et al.* 2009, Okullo & Moe 2012a), a decrease in grass density on mounds (Jouquet *et al.* 2004a) and distinct species assemblages on and off mounds (Spain & McIvor 1988, Jouquet *et al.* 2004a). However, comprehensive studies that consider grass diversity in its entirety (i.e. species richness, abundance (tuft density or cover) and species assemblage composition) are lacking. This despite grasses being a dominant and characteristic plant growth form in savannas, supporting abundant and diverse communities of grazing animals (du Toit & Cumming 1999) and playing an important role in fire dynamics, an important component of savanna ecosystems (Bond & Keeley 2005).

Another shortcoming in our understanding to what extent termite mounds create vegetation heterogeneity is that almost all studies focus on a single site, with only local effects on vegetation considered. How these impacts may change across different savanna types remains unclear. In a first climatic gradient study, Erpenbach *et al.* (2013) investigated vegetation patterns across a climatic gradient in west Africa and considered both woody and herbaceous vegetation. They found that differences between mounds and the savanna matrix became more pronounced with increasing mean annual precipitation, attributing this to increased phytodiversity in wetter habitats. However, when considering herbaceous plants, grass and forb species were pooled, making grass patterns indistinguishable from other herbaceous vegetation (i.e. forbs). Furthermore, a recent study by van der Plas *et al.* (2013) found that browsing herbivores avoided termite mound vegetation in South Africa's Hluhluwe-iMfolozi Game Reserve; this result stands in contrast to previous work recording preferential browsing of mound vegetation (e.g. Holdo & McDowell 2004, Loveridge & Moe 2004, Mobæk *et al.* 2005, Brody *et al.* 2010, Levick *et al.* 2010b). They attribute this unique finding to higher soil nutrients in the savanna matrix of their study site relative to other savanna areas, resulting in little nutritional difference between mound and savanna matrix vegetation. This finding underscores the need for studies across environmental gradients in which nutrient availability differs, possibly resulting in variation in the importance of termite mounds for savanna heterogeneity across such gradients.

In addition to variation in the degree of difference between mound and savanna matrix vegetation across an environmental (nutritional) gradient, it is also likely that the sphere of influence around termite mounds (i.e., the area the mound dominates and has significant influence on) will vary across such gradients. Most studies have only assessed patterns on and off mounds, with limited information available on the extent of mound influence. As a result, impacts of termite mounds and the spatial extent of such impacts at landscape scales are poorly quantified (Levick *et al.* 2010b, Sileshi & Arshad 2012).

Here I investigate effects of termite mounds on grass assemblages across an African savanna rainfall gradient. Importantly, I investigate the sphere of influence around mounds and scale these findings up to the landscape level, thus uncovering how the overall influence of mounds on ecological processes varies across savanna types. The aims of the study were to i) determine the degree to which grass assemblages (species richness, grass cover (abundance) and community assemblages) differ between termite mounds and the savanna matrix, ii) determine the spatial extent (sphere of influence) to which mounds influence grass communities, both locally around mounds and at a landscape scale, including whether there is a gradual change in grass assemblages from mound to savanna matrix or if clear thresholds of change can be detected, and iii) to investigate whether these patterns differ across a rainfall gradient from relatively dry (550 mm.yr^{-1}) and nutrient-rich savanna to relatively wet (750 mm.yr^{-1}) and nutrient-poor savanna. I predicted that effects of mounds, including both the degree of difference in grass communities and the spatial extent of their influence, would be strongest in wetter, nutrient-poor savannas where plant-available nutrients were expected to differ most between mounds and the savanna matrix.

Materials and methods

Study site

I undertook my study in three savanna vegetation types along a rainfall gradient in southern Kruger National Park (KNP), South Africa (Fig. 3.1). The three savanna sites occur in a summer rainfall region and vary in mean annual precipitation and vegetation characteristics; the driest site (Skukuza) is nutrient-rich savanna (sweet veld) characterised by an *Acacia nigrescens/Combretum apiculatum* association and receives a mean rainfall of 550 $mm.yr^{-1}$. The wettest site (Pretoriuskop) is dominated by *Terminalia sericea* and *Dichrostachys cinerea* and is comparatively nutrient-poor (sour veld); mean annual rainfall here is 750 $mm.yr^{-1}$. An intermediate site (Napi) is located between these two distinct regions and contains a mosaic of the two vegetation types, with *Combretum zeyheri* and *C. collinum* being dominant tree species, rainfall here is also intermediate, *ca.* 625 $mm.yr^{-1}$ (Gertenbach 1983). Herbivore biomass varied across the three sites, with the highest levels recorded at the intermediate site (Napi, 3490.36 kg/km^2), followed by the driest site (Skukuza, 1568.24 kg/km^2) and finally the wettest site (Pretoriuskop, 838.20 kg/km^2). More detailed information on herbivore biomass is contained in Chapter 4. All three sites occur within an undulating landscape on granitic substrate; termite mounds occur predominantly on crests and upper sections of hillslopes (Levick *et al.* 2010a, Chapter 2).

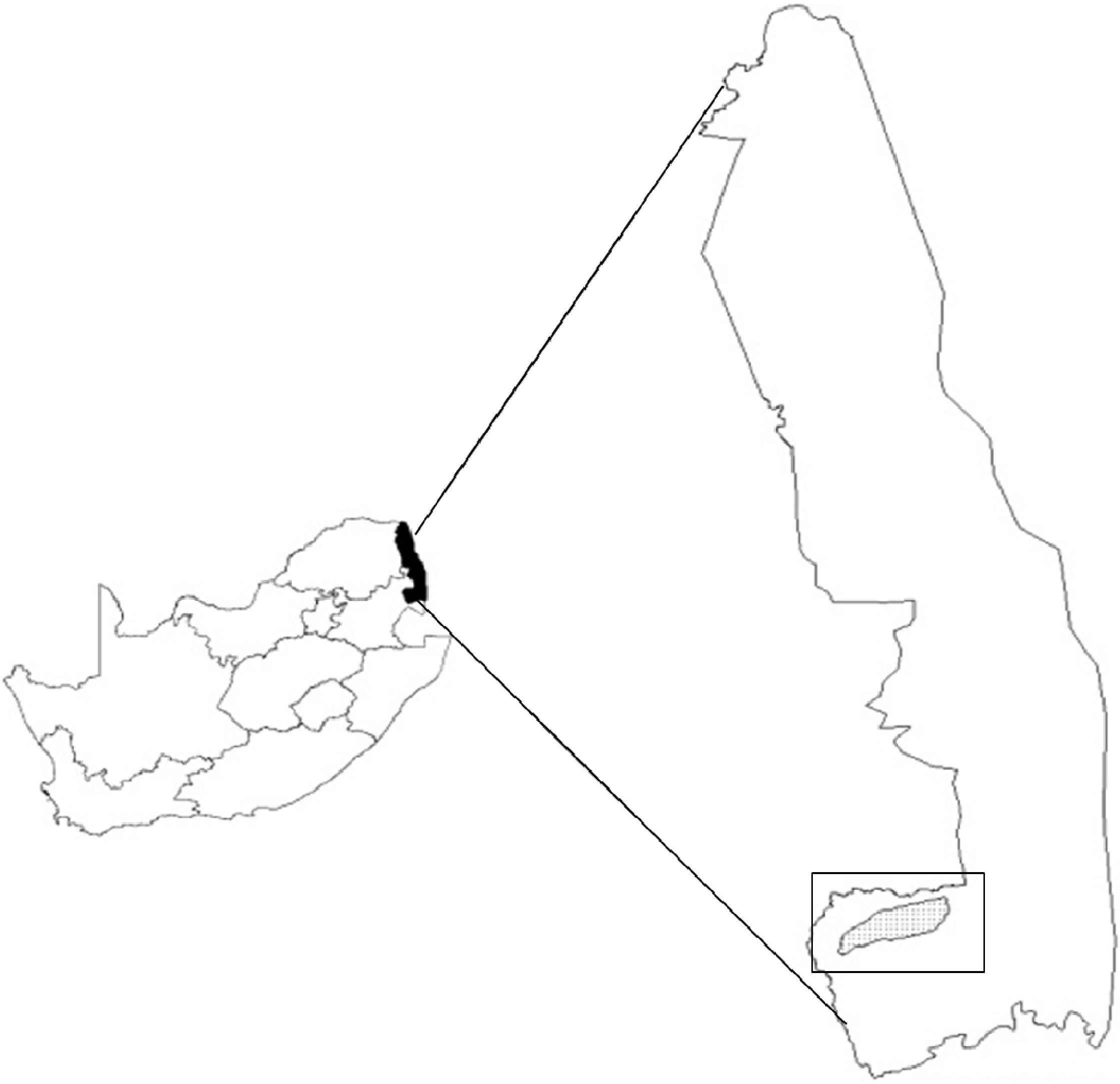


Figure 3.1: Location of the study site within southern Kruger National Park, South Africa. The three study sites where located within or just outside of the N'waswitshaka River catchment (hatched area within the rectangle).

Survey design

Within each savanna site, areas of high termite mound densities were selected using Light Detection and Ranging (LiDAR) data from the Carnegie Airborne Observatory Alpha sensor package (CAO-Alpha; Asner *et al.* 2007). Ten termite mounds were then selected within three sites across the rainfall gradient and surveyed during January 2012, the peak summer month when grasses are abundant and identifiable. All surveyed termite mounds were built by *Macrotermes*, with the dominant species in the area being *M. falciger* and *M. natalensis* (Chapter 2). Both active and inactive mounds are vegetated in this region so I did not discriminate between these two classes. Mound diameter was measured for each mound along the north-south and east-west axes and the average diameter calculated from these measurements.

The grass communities on and around each mound were surveyed using 1 m^2 quadrats. Sixteen quadrats were placed on the termite mound, six on the upper sections and ten on the lower sections, where more surface area was available. Each grass species present in the quadrat was identified and the percentage of the quadrat that it occupied (basal cover) was visually estimated. Sampling quadrats were also stratified according to aspect, with half (eight) on the northern section of the mound and the other half on the southern section. For each termite mound, a paired savanna plot situated 30 m from the mound was also sampled. A random direction for the placement of the savanna plot was chosen each time and this plot was placed at least 30 m away from any neighbouring mounds. At this savanna plot, 16 quadrats were placed in a grid formation of 4 by 4, spaced one meter apart. Finally, transects were laid out from each mound in the four cardinal directions. A total of six quadrats were placed at the following distance intervals from the base of the mound along each transect: 1 m, 2 m, 4 m, 8 m, 16 m and 32 m (Supplementary material, Appendix 3.1). Changes in vegetation composition were expected to be most pronounced closer to mounds; hence a geometric progression with the common ratio of 2 was selected. In each quadrat (on the mounds, savanna plots and transects) standing biomass readings were recorded using a disc pasture meter. The disc pasture meter has been calibrated for this vegetation type and biomass was calculated with the following formula from Trollope (1990):

$$(\sqrt{X} \text{ x } 2260) - 3019 = \text{kg ha}^{-1}$$

where X is the disc height reading in cm obtained from the disc pasture meter.

Nutrient samples

Grass samples from the termite mounds and each quadrat along the transects were harvested for analysis of nitrogen and carbon content. Grass samples were representative of all species present in each quadrat, and the amount of each species harvested was in proportion to its abundance in the quadrat. All samples consisted of above-ground plant material. Samples were dried at 60° C for 48 hr immediately after collection, following which they were homogenised. Total C and N concentrations of ground grass material were analysed using an elemental analyser "Vario EL" (Elementar Analysensysteme GmbH, Hanau, Germany) at the Max Planck Institute for Biogeochemistry, Jena, Germany.

Data analysis

Sampling adequacy of the grass surveyed on termite mounds and savanna plots was assessed using sample-based rarefaction curves and appropriate richness estimators (Gotelli & Colwell 2001) using EstimateS software version 8.2 (http://viceroy.eeb.uconn.edu/estimates). If the observed rarefaction curve approaches an asymptote or converges closely with appropriate richness estimators at the highest observed species richness, sampling is considered to be adequate and representative of the studied assemblage (Gotelli & Colwell 2001, Longino *et al.* 2002). In most cases, sampling was adequate and so observed data were used in subsequent analyses. The sampling at the wettest site, Pretoriuskop, was the least complete, but not considered to be grossly under sampled. Moreover, sampling adequacy on termite mounds and savanna plots was relatively similar here (Appendix 3.2).

Grass species richness, basal grass cover (percentage of the quadrat occupied by grass) and standing biomass on and off termite mounds was compared using two-way analysis of variance (ANOVA), after data were assessed for normality and homogeneity of variance. An arc sine square root transformation was applied to all percentage (basal grass cover) data before analysis. Tukey Honest Significant Difference (Tukey HSD) tests were applied to conduct pair-wise comparisons of the data. For multivariate community assemblage analyses, data were fourth root transformed to weight common and rare species more equally (Clarke & Warwick 2001), following which a Bray-Curtis dissimilarity matrix was constructed. Overall differences in grass community assemblages on and off mounds were compared using a two-way analysis of similarity (ANOSIM) with pair-wise comparisons made between sites. One-way ANOSIMs were used to compare treatment (mound *vs*. savanna) assemblages at each site separately. The *R*-value obtained from ANOSIM is a measure of dissimilarity and can take a value between -1 and 1, the closer this value is to 1 the more dissimilar the assemblages are (Clarke & Warwick 2001). Non-metric multi-dimensional scaling (nMDS) ordinations for each savanna site were constructed to visually display patterns.

Individual grass species indicative of termite mounds were identified for each savanna habitat using the Indicator Value (IndVal) method (Dufrêne & Legendre 1997). This method uses a combination of site specificity (uniqueness to a particular habitat) and fidelity (frequency of occurrence within that habitat) to assess the extent to which a species is indicative of that site. A high indicator value, expressed as a percentage, signifies that a species is characteristic of a specific site (Dufrêne & Legendre 1997). Species that scored significant IndVal values greater than 60% were subjectively considered characteristic of that habitat (modified from McGeoch *et al.* 2002). Although the method was originally designed to detect species indicative of specific habitats, in this context it was used to test if there are specific grass species associated with termite mounds and if such characteristic species change across the rainfall gradient.

Data collected from the distance transects were pooled across the four directions and grass species richness, grass basal cover (arc sine square root transformed) and standing biomass were compared using two-way ANOVAs after assessment of normality and homogeneity of variance. Tukey HSD tests were used to detect where pair-wise differences occurred. Grass assemblages were analysed in a similar fashion to those on and off mounds, with the use of ANOSIMs and nMDS ordinations. In order to detect changes in assemblages with distance relative to mounds and to identify where such changes become apparent, ANOSIM was used to compare grass assemblages at each distance category (pooled across directions) to assemblages on the mound. Further, I used Mantel's test to construct Mantel correlograms to calculate patterns of spatial autocorrelation. The Mantel test can be used to examine relationships between multivariate dissimilarity matrices and a matrix of their geographic positions and determines spatial dependence at different distance classes (Borcard *et al.* 2011). The correlogram produces r coefficients between -1 and 1, where 1 is completely spatially dependent and -1 spatially independent. Mantel correlograms conduct pair-wise tests with a Holm correction for multiple comparisons for each distance class. A Bray-Cutis dissimilarity matrix was constructed from the assemblage data (after an arc sine transformation was applied) and detrended by regression on the site coordinates before Mantel correlograms were constructed (Borcard *et al.* 2011). For these correlograms, data were pooled across the ten mounds per site, but directional data were not pooled in order to increase statistical power.

The C: N ratio was calculated from the tissue samples. The data were log transformed to meet assumptions of normality and homogeneity of variance and changes in the C: N ratio along the transects assessed with two-way ANOVA. Tukey HSD tests were used to investigate pair-wise differences between sites and distance classes. The ANOSIM and nMDS analyses were performed using Primer software version 5.2 (Clarke & Warwick 2001), while all other analyses were conducted with R software version 2.15.1 (R Development Core Team 2012), the R package vegan was used for the Mantel correlograms.

To determine the sphere of influence of mounds on grass assemblage composition in each study site, the mean mound diameter was calculated and added to the extent of direct influence determined from the distance transects to obtain a radius of influence from the centre of a termite mound. This sphere of influence was assumed to be circular, and the area under direct influence of a termite mound calculated. For these calculations, the influence on grass community composition was used instead of species richness, basal cover or standing biomass because these patterns were the clearest and are more meaningful for savanna heterogeneity as mounds have more effect on grass assemblages than the other variables measured (see Results). Using LiDAR terrain data from the Carnegie Airborne Observatory (CAO, http:cao.ciw.edu), mound densities on crests in each study area were estimated and a correction factor applied to account for variation in detection rates across the study site (see Chapter 2). The area that is directly influenced by mounds was then calculated for each study site. Crests were chosen instead of the entire landscape because *Macrotermes* mounds occur predominantly on them (Levick *et al.* 2010a, Chapter 2) and therefore will be influential in these areas. Due to the nature of the remote sensing technique used, some small mounds (< 1m height) escaped detection and these estimations can thus be considered minimum values.

Results

Grass assemblages on and off termite mounds

Grass species richness varied significantly across the rainfall gradient (two-way ANOVA, F = 6.988, $p < 0.01$, Fig. 3.2a) and there were significantly more species off mounds than on mounds (two-way ANOVA, F = 72.123, $p < 0.001$, Fig. 3.2a). The interaction between these two factors was not significant (two-way ANOVA, F = 0.239, p = 0.788), indicating that the effect was similar across all three sites. A Tukey Honest Significant Difference (Tukey HSD) test showed that between sites, Skukuza had significantly more species than both Napi and Pretoriuskop ($p < 0.01$ and < 0.05 respectively), which did not differ from each other (p = 0.644). Across the rainfall gradient, grass species richness on mounds did not differ, i.e. mounds in all three areas had similar species richness (Fig. 3.2a). Among the savanna matrix plots, only Skukuza had significantly more species than Napi ($p < 0.05$), but a similar number to Pretoriuskop (Fig. 3.2a). When comparing species richness on and off termite mounds, savanna matrix plots contained more species at every site ($p < 0.001$ for all three sites, Fig. 3.2a).

Grass cover did not differ significantly between sites (two-way ANOVA, F = 0.218, p = 0.805) nor between mound and savanna plots, although this comparison did approach significance: two-way ANOVA, F = 3.982, p = 0.051, most notably at Skukuza where more cover was found on mounds than in the savanna matrix (Fig. 3.2b). The interaction between site and treatment was not significant (two-way ANOVA, F = 2.306, p = 0.109). Standing biomass varied significantly across sites (being highest at Napi, two-way ANOVA, F = 5.817, $p < 0.01$). Biomass was significantly higher at Napi than Pretoriuskop ($p < 0.01$), but not among other sites. No biomass differences were recorded between mound and savanna plots (two-way ANOVA, F = 0.045, p = 0.834, Fig. 3.2c).

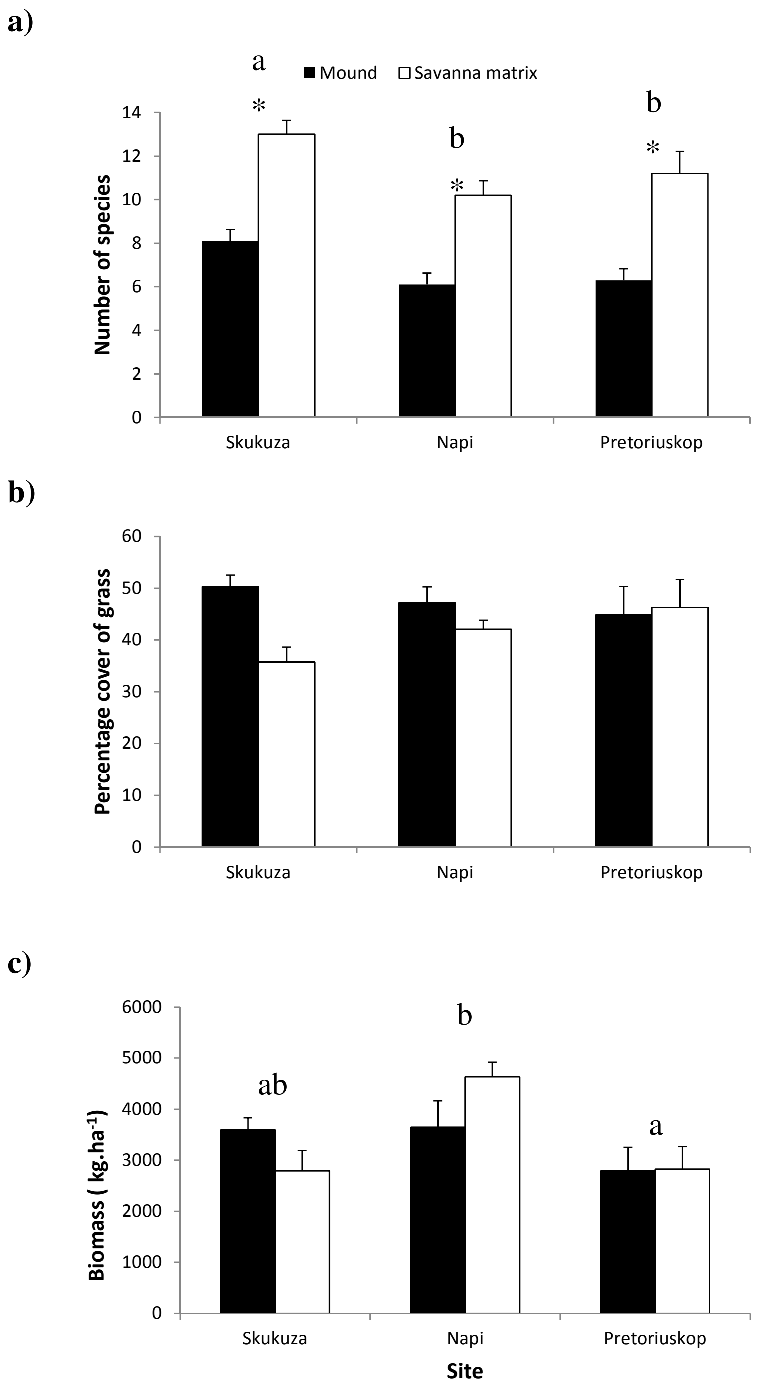
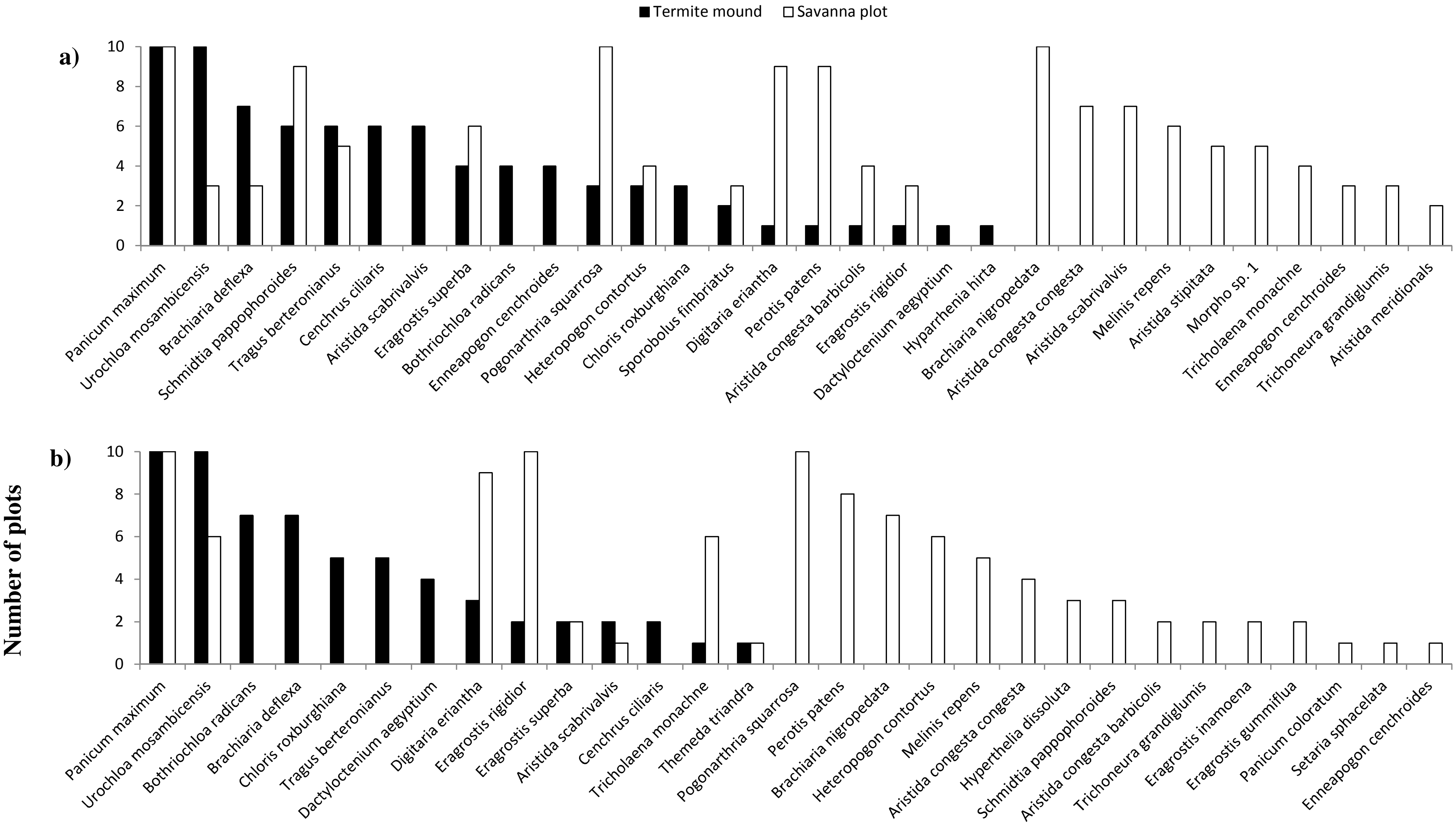


Figure 3.2: Grass species richness (a), percentage basal grass cover (b), and standing biomass of grass (c) on and off termite mounds at three savanna sites situated across a rainfall gradient. Sites are arranged in order of increasing mean annual rainfall. Letters indicate differences between savanna sites while asterisks denote significant differences between treatments (mounds *vs*. savanna).

Grass community assemblages differed significantly between mounds and savanna plots at all three sites along the rainfall gradient with little overlap of species (Table 3.1, Figs. 3.3 and 3.4). Between sites, Skukuza and Napi had the most similar assemblages, while Pretoriuskop had a markedly different assemblage from Napi and Skukuza (Table 3.1, Fig. 3.4).

Table 3.1: Results from an analysis of similarity (ANOSIM) of grass assemblages between termite mounds and savanna plots as well as between the three research sites. A two-way crossed ANOSIM was performed for overall treatment differences (averaged across all sites) and site differences (including pair-wise comparisons), while a one-way ANOSIM was performed for treatment effects at each savanna site separately. The R-statistic is a measure of similarity of assemblages, the closer this value is to 1, the more dissimilar assemblages are. Sites are arranged in order of increasing rainfall.

Factor	R statistic	P value
Treatment (overall)	0.900	0.001
Skukuza	0.823	0.001
Napi	0.982	0.001
Pretoriuskop	0.886	0.001
Site	0.710	0.001
Skukuza vs. Napi	0.313	0.001
Skukuza vs. Pretoriuskop	0.905	0.001
Napi vs. Pretoriuskop	0.894	0.001


■ Termite mound
☐ Savanna plot
a)
10
8
6
4
2
0
Panicum maximum
Urochloa mosambicensis
Brachiaria deflexa
Schmidtia pappophoroides
Tragus berteronianus
Cenchrus ciliaris
Aristida scabrivalvis
Eragrostis superba
Bothriochloa radicans
Enneapogon cenchroides
Pogonarthria squarrosa
Heteropogon contortus
Chloris roxburghiana
Sporobolus fimbriatus
Digitaria eriantha
Perotis patens
Aristida congesta barbicolis
Eragrostis rigidior
Dactyloctenium aegyptium
Hyparrhenia hirta
Brachiaria nigropedata
Aristida congesta congesta
Aristida scabrivalvis
Melinis repens
Aristida stipitata
Morpho sp. 1
Tricholaena monachne
Enneapogon cenchroides
Trichoneura grandiglumis
Aristida meridionals
Number of plots
b)
10
8
6
4
2
0
Panicum maximum
Urochloa mosambicensis
Bothriochloa radicans
Brachiaria deflexa
Chloris roxburghiana
Tragus berteronianus
Dactyloctenium aegyptium
Digitaria eriantha
Eragrostis rigidior
Eragrostis superba
Aristida scabrivalvis
Cenchrus ciliaris
Tricholaena monachne
Themeda triandra
Pogonarthria squarrosa
Perotis patens
Brachiaria nigropedata
Heteropogon contortus
Melinis repens
Aristida congesta congesta
Hyperthelia dissoluta
Schmidtia pappophoroides
Aristida congesta barbicolis
Trichoneura grandiglumis
Eragrostis inamoena
Eragrostis gummiflua
Panicum coloratum
Setaria sphacelata
Enneapogon cenchroides

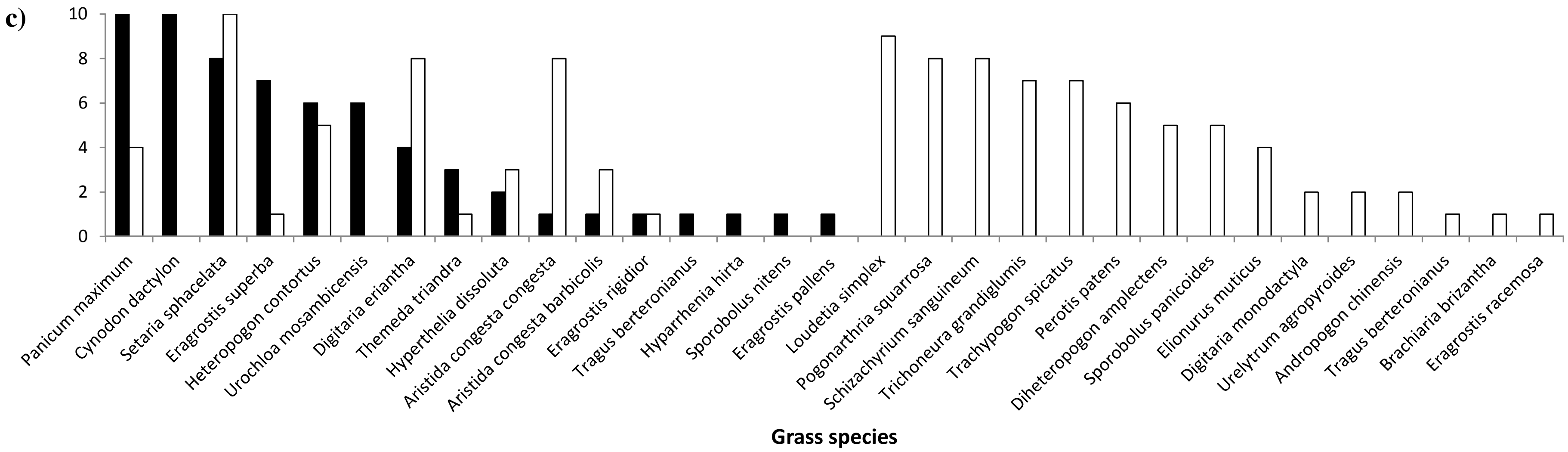
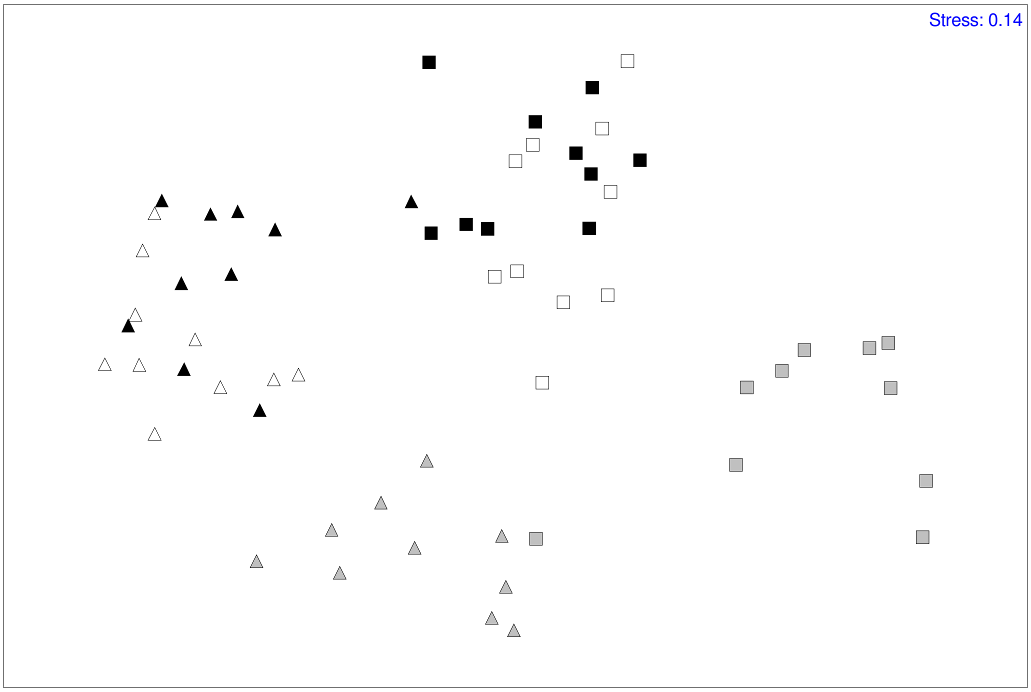


Figure 3.3: Number of mounds or savanna matrix plots (n = 10 for both) where a particular grass species was recorded at each of three savanna sites arranged in order of increasing mean annual rainfall, (a) Skukuza, (b) Napi and (c) Pretoriuskop. Species are ranked according to the frequency of their presence on mounds, i.e. the frequency of grass species on mounds decreases along the x-axis.



Legend: ▲ = termite mounds at Skukuza; △ = termite mounds at Napi; ◭ = termite mounds at Pretoriuskop; ■ = savanna plots at Skukuza; □ = savanna plots at Napi; ▨ = savanna plots at Pretoriuskop

Figure 3.4: Non-metric multi-dimensional scaling (nMDS) ordination of grass assemblages occurring on and off termite mounds at three savanna sites.

Seven grass species were identified as characteristic of termite mounds (Table 3.2). More indicator species were identified with increasing site precipitation (four species at Pretoriuskop, three at Napi and two at Skukuza) with a perfect indicator (*Cynodon dactylon*) identified at Pretoriuskop. One species (*Urochloa mosambicensis*) was characteristic of termite mounds at all three sites.

Table 3.2: Species identified as characteristic of termite mounds for each research site arranged along a climatic gradient from dry to wet. Significant indicator values above 60% are shown (100% being a perfect indicator, $P < 0.05$, 1000 iterations). * denotes a significant indicator but with an IndVal value <60%; n.s. is present but not significant; – denotes that the species is absent from the site.

Species	**Site**		
	Skukuza	Napi	Pretoriuskop
Cynodon dactylon	–	–	100.0
Urochloa mosambicensis	89.48	77.66	60.00
Panicum maximum	n.s.	n.s.	87.26
Bothriochloa radicans	*	70.00	–
Brachiaria deflexa	*	70.00	–
Eragrostis superba	n.s.	n.s.	65.97
Cenchrus ciliaris	60.00	n.s.	–

Grass assemblages across distance transects

Species richness differed significantly along the transects (two-way ANOVA, $F = 5.454$, $p < 0.001$), with a Tukey HSD test revealing that mounds had significantly fewer species than the 4 m ($p < 0.01$), 8 m ($p < 0.05$), 16 m ($p < 0.01$) and 32 m ($p < 0.001$) distance categories. Furthermore, there were significantly more species at 32 m than at 1 m ($p < 0.01$) distance from mounds. Neither site nor an interaction between site and distance were significant at the 95% confidence limit, indicating that patterns were consistent across savanna sites (Appendix 3.3a).

Grass cover differed significantly between both site and distance category (two-way ANOVA, site: $F = 8.344$, $p < 0.001$; distance: $F = 3.101$, $p < 0.01$), but the interaction between the two variables was not significant (two-way ANOVA, $F = 0.856$, $p = 0.593$). Tukey HSD tests showed that Pretoriuskop had significantly greater grass cover than Skukuza ($p < 0.001$), and there was a trend of more grass at Pretoriuskop compared to Napi ($p = 0.09$). No pairwise comparisons were significant between distance classes, but there was a trend toward less grass cover at intermediate distance classes (8 and 16 m) compared to the edge of the mound (1 and 2 m) where more cover was recorded: 8 m compared to 1 m, $p = 0.056$; 8 m compared to 2 m, $p = 0.066$; 16 m compared to 1 m, $p = 0.069$; 16 m compared to 2 m, $p = 0.080$ (Appendix 3.3b).

For standing biomass, site, distance class and the interaction between the two differed significantly (two-way ANOVA, site: F = 5.929, $p < 0.01$; distance: F = 2.325, $p < 0.05$; interaction: F = 1.806, $p < 0.05$). Napi had a significantly higher biomass than the other two sites ($p < 0.05$ for Pretoriuskop and $p < 0.01$ for Skukuza). Across distance classes, less biomass occurred at the 1 m distance category compared to the 4 m ($p = 0.078$), 8 m ($p < 0.05$) and 32 m ($p = 0.086$) distances, these effects were most pronounced at Napi, with considerably lower biomass at the 1 m distance class (Appendix 3.3c).

Differences in grass assemblage composition along transects varied across the rainfall gradient. At the driest site, Skukuza, a gradual change in grass composition from mound to matrix was observed, with no clear threshold at any one point. As mean annual rainfall increased, a clearer transition in grass composition was evident among distance categories, most notably from 2-4 m. This change was most pronounced at the wettest site, Pretoriuskop. Spatial turnover in grass communities was clear from both the nMDS ordinations and the R statistics from an ANOSIM, which depict the magnitude of change in assemblages between the mound and particular distance category (Fig. 3.5). Spatial autocorrelation analyses (Mantel correlograms) confirm the thresholds in grass composition across the rainfall gradient with a more gradual response at Skukuza, where no significant spatial dependence was detected (Fig. 3.6a). Spatial dependence persists further from mounds with increasing mean annual rainfall: grass community assemblages are significantly spatially dependent at 1 m distances at Napi (Fig. 3.6b) and up to 2 m at Pretoriuskop where they are also spatially independent at distances over 25 m (Fig. 3.6c). At both Napi and Pretoriuskop, assemblages are spatially independent and no longer positively correlated at 4 m distances.

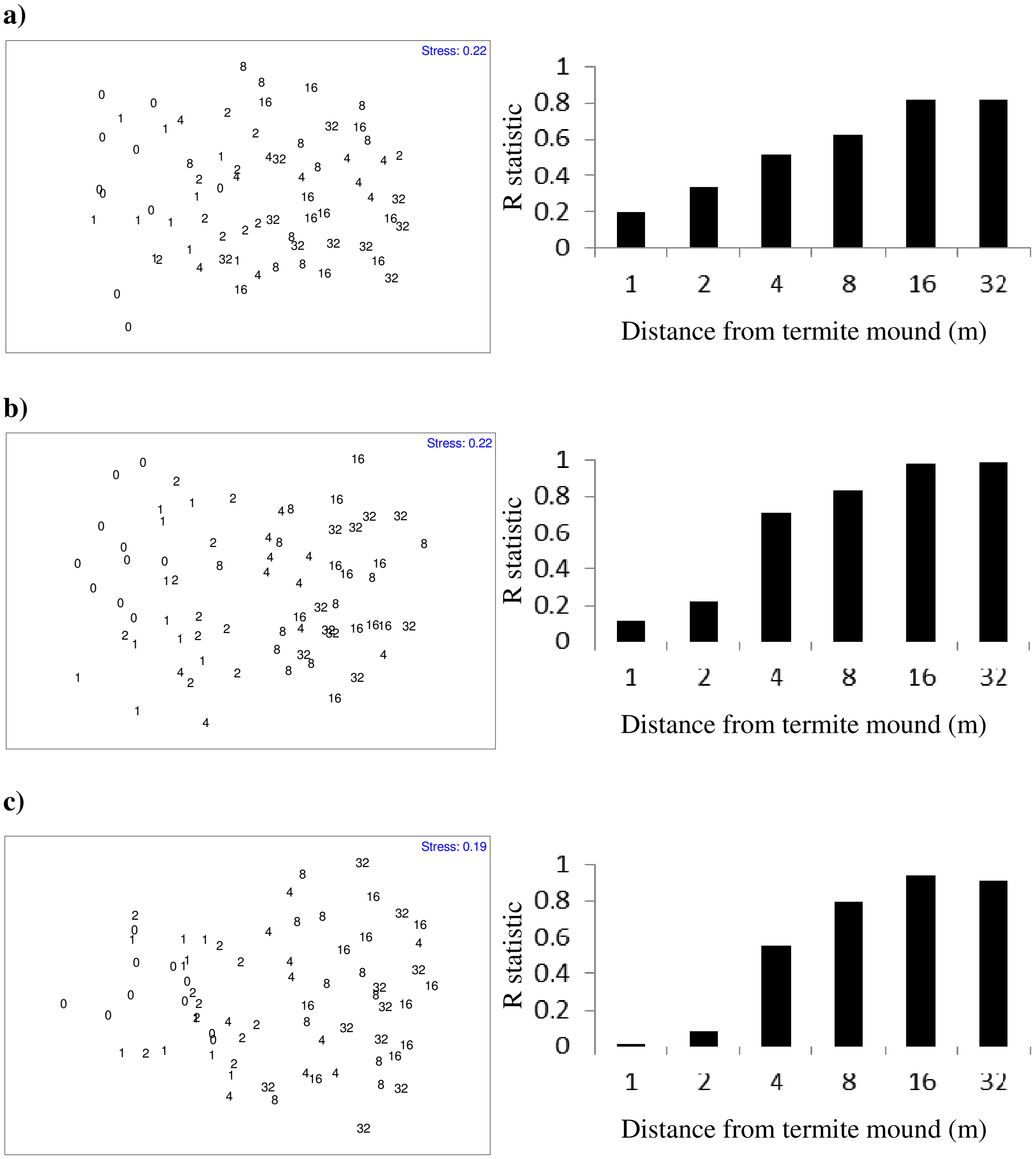


Figure 3.5: Non-metric multi-dimensional scaling (nMDS) ordinations of grass assemblages along transects of increasing distance from termite mounds at three savanna sites differing in mean annual rainfall, Skukuza (a), Napi (b) and Pretoriuskop (c). Ordinations are displayed on the left panel (numbers represent distances (in meters) of sampling quadrats) while the bar graphs in the right panel represent the size of the R statistic from an ANOSIM between assemblages on termite mounds and at various distances away. All R statistics were significant ($p < 0.05$) at Skukuza, from 2 m upwards at Napi and from 4 m upwards at Pretoriuskop.

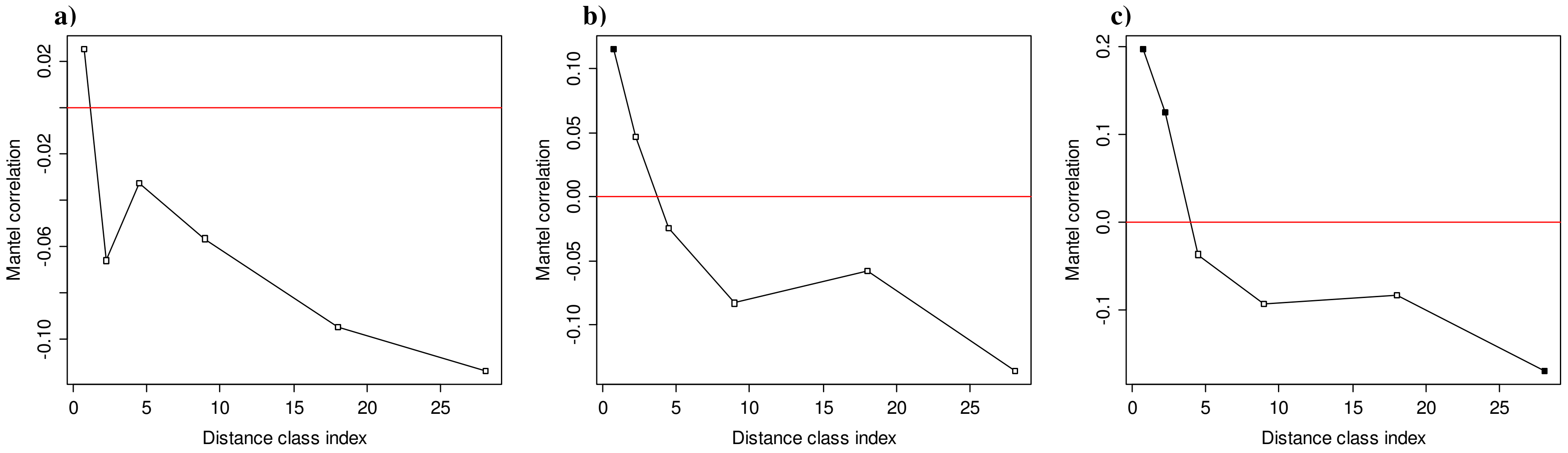


Figure 3.6: Spatial dependence of grass communities (Mantel Correlograms) surveyed around termite mounds at three savanna site across a rainfall gradient, the three site arranged in order of increasing mean annual precipitation are: a) Skukuza, b) Napi and c) Pretoriuskop. Black squares represent significant spatial auto-correlation (α = 0.05); the line through zero indicates the transition from spatial dependence (above zero) to spatial independence (below zero); distance class index is measured in meters.

Foliar nutrients

Results from the C: N ratio of the grass sampled at each distance category mirror these assemblage changes, with a clear increase recorded from the mound up until 2 m from the mound, followed by a levelling off at Skukuza. At both Napi and Pretoriuskop a steep increase is evident up until 4 m from the mound, with the C: N ratio only levelling off 16 m into the savanna matrix (Fig. 3.7). Two-way ANOVA confirmed that the C: N ratio differed with site and distance as well as the interaction between the two factors (site: $F = 33.348$, $p < 0.001$; distance: $F = 37.967$, $p < 0.001$; interaction: $F = 2.565$, $p < 0.01$). Tukey HSD tests revealed that Skukuza had a significantly lower C: N ratio than both Napi ($p < 0.001$) and Pretoriuskop ($p < 0.001$), Napi and Pretoriuskop did not differ from each other ($p = 0.081$). The C: N ratio increased significantly with distance from mounds, with all distance classes having a higher C: N ratio than the mound ($p < 0.001$ for all pair-wise comparisons). Off the mound, the 1 m and 2 m distance categories did not differ from one another ($p = 0.220$), but all other classes (4 m upwards) had a higher C: N ratio than 1 m from the mound ($p < 0.001$ for all comparisons). Between 2 m and 4 m, C: N ratio did not differ ($p = 0.304$), but all other classes (8 m upwards) had a significantly higher C: N ratio than 2 m ($p < 0.01$ for 8 m and $p < 0.001$ for both other comparisons). Comparisons between the other classes (4 m, 8 m, 16 m and 32 m) did not differ significantly from each other, apart from the comparison between 4 m and 32 m ($p < 0.05$). Thus, the C: N ratio significantly increases up until 4 m from mounds, after which it increases only slightly to be higher at 32 m compared to 4 m. The interaction term was significant, with stronger (steeper increases in C: N ratio) responses observed with increasing rainfall, being highest at Pretoriuskop (Fig. 3.7).

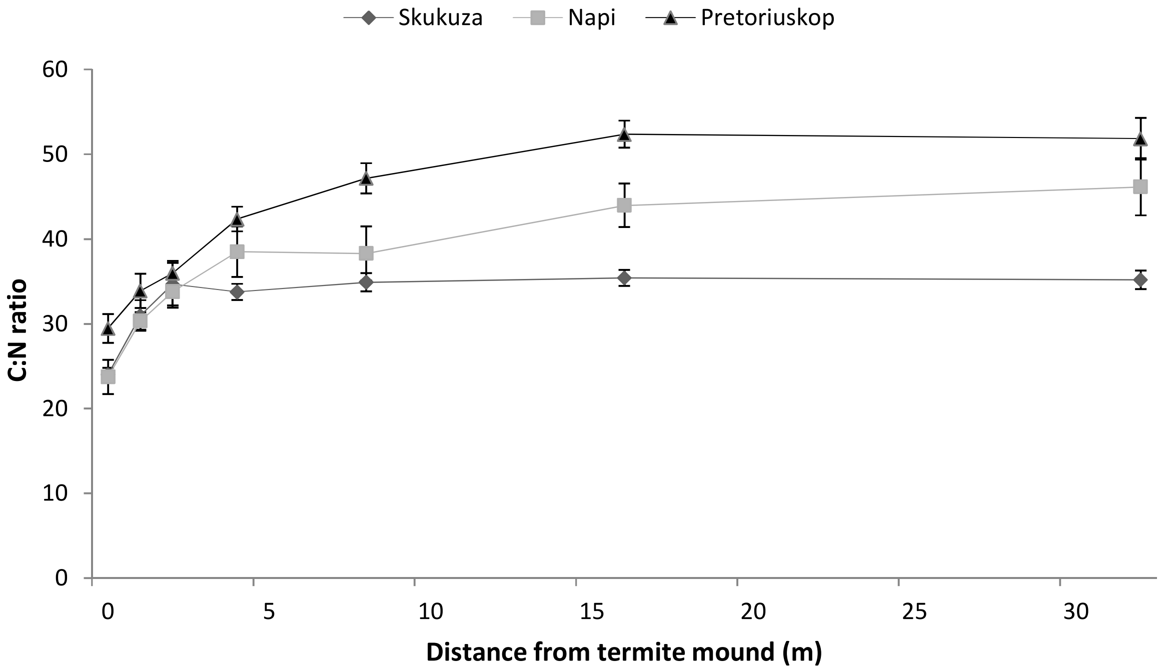


Figure 3.7: Carbon to Nitrogen (C: N) ratio for grass samples across distance transects from termite mounds. Samples were taken from the four cardinal directions around mounds.

Sphere of influence around termite mounds

The sphere of direct influence around mounds was determined for each study site using the magnitude of grass assemblage changes at various distance intervals from ANOSIM and nMDS results (Fig. 3.5), as well as results from the Mantel correlograms (Fig. 3.6). Considering these assemblage changes, a gradual compositional change was observed at Skukuza where, according to the ANOSIM, grass assemblage composition continues to change relative to the mound as far as 16 m into the savanna matrix. However, community differences beyond 2 m are not enough to garner support from the Mantel correlograms, suggesting a gradual rather than abrupt change. Mound influence was therefore conservatively considered to extend to 2 m, following which differences in assemblages are less pronounced (Fig. 3.5a) and spatially independent (Fig. 3.6a). At Napi and especially Pretoriuskop, thresholds in community compositional change are easier to detect, with grass communities being distinctly different at a distance of 4 m into the savanna matrix at both sites (Fig. 3.5b and c and Fig. 3.6b and c). Based on the Mantel correlograms, mound influence at these sites was considered to extend to 4 m, following which communities are spatially independent of the mound. The sphere of influence around termite mounds was therefore considered to be greater than at Skukuza, extending to 4 m into the savanna matrix. When the sphere of direct influence of mounds was then calculated at each site (using average mound diameter at each site and magnitude of grass assemblage changes: 2 m at Skukuza and 4 m at both Napi and Pretoriuskop), mounds have a larger direct effect at the wettest site, Pretoriuskop, where 2.37% of crest landscapes are directly affected. Although mounds had the largest sphere of influence at Napi, the overall landscape effect is smallest here due to lower mound densities, being 1.89% of the crest landscape. Skukuza had intermediate landscape effects (2.16%) because although mounds here are larger and occur at higher densities, the sphere of influence extends only to 2 m from mounds compared to 4 m at the wetter sites (Table 3.3).

Table 3.3: The area under direct influence (sphere of influence) around termite mounds with respect to change in grass communities. The mound densities from which the percentage figures are drawn are attained from LiDAR terrain data and reflect densities on crests within the landscape, the landscape percentage under direct influence subsequently refers to percentages of crests under direct influence.

Savanna site	Sphere of influence around mounds	Mound density	Percentage of landscape under direct influence
Skukuza	115.33 m^2	1.87 ha^{-1}	2.16%
Napi	192.71 m^2	0.98 ha^{-1}	1.89%
Pretoriuskop	156.10 m^2	1.52 ha^{-1}	2.37%

Discussion

My findings reveal that the importance of termite mounds for grass communities is not uniform across landscapes, but varies with context. Mounds are more important in wetter, nutrient-poor landscapes where differences between mounds and savanna are more pronounced, leading to a larger proportion of the landscape being affected. Nonetheless, across all savanna types investigated, termite mounds remain important agents for savanna grass heterogeneity, acting as keystone structures that provide nutrient-rich patches of distinct grass species to those found in the savanna matrix.

Differences between mound and savanna matrix grasses

Grass communities on termite mounds were markedly different to those in the savanna matrix across the rainfall gradient. At all three sites, grass species richness was greater in the savanna matrix, in contrast to documented patterns for woody plants and forbs (Loveridge & Moe 2004, Traoré *et al.* 2008, Moe *et al.* 2009, Erpenbach *et al.* 2013). This finding concurs with Arshad (1982), while Moe *et al.* (2009) recorded no difference in grass species richness between mounds and the savanna matrix. It is well established that plant species richness follows a hump-shaped relationship along productivity gradients, with a peak at intermediate levels of productivity (Grime 1973, Mittelbach *et al.* 2001). My findings suggest that for African savanna grasses, termite mounds represent areas of high productivity with species richness peaking at productivity levels lower than that of mounds. In temperate systems, grass species richness has been shown to peak in relatively nutrient-poor soils (Cornwell & Grubb 2003), particularly where nitrogen and phosphorous levels are low (Crawley *et al.* 2005) and my results, along with those from east Africa (Arshad 1982, Moe *et al.* 2009), indicate that savanna grasses follow similar patterns. This pattern is consistent across the rainfall gradient, suggesting that the nutrient levels of termite mounds are consistently higher than optimal for grass species richness, possibly as a result of competitive exclusion leading to the dominance of a few species which monopolise the resource (Grime 1973). Moreover, many savannas are nitrogen limited environments due to their frequent burning (Asner *et al.* 1997); most grass species are therefore likely adapted to nutrient levels lower than that of termite mounds.

Although the majority of studies that record plant biomass as a measure of productivity report a hump-shaped relationship between species richness and biomass, richness peaking at intermediate biomass levels (Mittelbach *et al.* 2001), neither standing biomass nor grass cover on and off termite mounds differed in my study at any site. Termite mounds act as focal feeding sites for both mammalian (Mobæk *et al.* 2005) and insect (Leitner 2012) grazers in savanna systems, which likely leads to lower standing biomass and grass cover than would be expected in the absence of herbivores. Potential biomass (biomass in the absence of grazers) is therefore likely to be much higher than observed standing biomass on mounds.

The grass communities on termite mounds differed significantly from the savanna matrix vegetation, with very little overlap of species. Thus, although supporting fewer species than the savanna matrix, the species composition on mounds was almost entirely different, providing a distinct habitat to that of the more expansive savanna matrix. Similar high levels of dissimilarity between mounds and savanna matrix were recorded at all three sites, despite the grass communities at the wettest site being very different to those at the other two sites. Termite mounds therefore appear to play a consistent keystone role across ecosystem types by supporting different grass assemblages. Indeed, similar differences in grass assemblages have been recorded in various African (Arshad 1982, Jouquet *et al.* 2004a) and Australian (Spain & McIvor 1988) savannas.

Grass species growing on mounds are highly nutritious with significantly lower C: N ratios than savanna matrix grasses, making assemblages distinct both taxonomically and functionally. Moreover, all species identified as characteristic of termite mounds (except *Bothriochloa radicans*) are highly nutritious and palatable to grazing animals (van Oudtshoorn 1999), and several are stoloniferous, forming grazing lawns under high grazing pressure (notably *Cynodon dactylon* and *Urochloa mosambicensis*). Grazing lawns are important forage patches for herbivore populations (Archibald 2008, Cromsigt & Olff 2008). It is likely *Bothriochloa radicans* occurs on mounds because termite activity concentrates clay particles here (Jouquet *et al.* 2004a), providing an ideal habitat for this species which grows in soils with high clay content (van Oudtshoorn 1999); savanna matrix soils in this system are generally sandy with low clay content.

The heterogeneity induced by termites through mound construction thus plays a critical functional role in savannas through the provision of nutrient-rich grass patches which are favoured by herbivores (Mobæk *et al.* 2005, Leitner 2012). Furthermore, termite mounds are predominantly located on nutrient-poor crests within this landscape (Levick *et al.* 2010b, Chapter 2) and their presence here is likely to facilitate the persistence of herbivores in areas that are more marginal habitat and would be otherwise less suitable (Grant & Scholes 2006).

Spatial extent of termite influence

In line with my reported patterns on and off termite mounds, grass species richness increased with distance from termite mounds, while cover and standing biomass exhibited mixed patterns with no clear threshold detected. Across the three sites, grass species richness was significantly higher at a distance of 4 m than on the mounds. However, the threshold for change in grass composition varies among sites. At the driest and most nutrient-rich site, Skukuza, the sphere of influence is smaller, extending only to 2 m from mounds, with grass community assemblages changing gradually with distance from termite mounds. As mean annual precipitation increases (and both grass and soil C: N ratio also increases), differences become more pronounced and the sphere of influence around mounds increases to 4 m. These findings support my predictions: mounds in wetter areas have a stronger effect on grass communities and clearer thresholds are detected; this is likely due to stronger differences in nutritional content between mounds and the savanna matrix.

The more distinct differences in grass assemblages detected at the wetter sites mirror the changes in the C: N ratio recorded from the grass samples. At these wetter sites there is a consistent, steep increase in C: N up to 4 m from mounds, after which the increase is more gradual to 16 m, and then levels off beyond 16m from the mound. In contrast, at the driest site near Skukuza, the C: N ratio levels off after only about 2 m. The lower C: N ratio sustained in the drier, relatively nutrient-rich savanna mitigates the effect termite mounds have on grass assemblages, and enables the persistence of nutrient-rich grasses away from mounds. Indeed even some of the dominant grasses in the savanna matrix (e.g. *Digitaria eriantha* and *Brachiaria nigropedata*) not found on termite mounds are also nutritious and considered palatable (van Oudtshoorn 1999). *Macrotermes* mound soil provides an ideal environment for grazing lawn species such as those growing on the mounds themselves, and enhances their spread through erosion of mound soil to the matrix (Gosling *et al.* 2012). However the already relatively high nutrient content in the drier savanna site lessens this effect, causing changes to be gradual and the sphere of influence here to be smaller compared to that of the wetter sites, where this eroded material is more important for maintaining high nutrient availability for lawn grasses. Working in a relatively nutrient-rich savanna, van der Plas *et al.* (2013) found that trees off mounds are more favoured by browsers than those on mounds, in contrast to all previous studies relating browsing activity to termite mounds. They attribute this finding to the high nutrient value of the savanna matrix, which results in differences on and off mounds being reduced, and suggests that the importance of mounds as nutrient hotspots varies with landscape nutritional value. The smaller spheres of influence around termite mounds in the drier, relatively nutrient-rich savanna in my study indicate that similar processes are likely operating for grass communities in southern Africa.

The sphere of influence around termite mounds in relation to savanna grasses constitutes around 2% of crest landscapes. In Uganda, Moe *et al.* (2009) report that termite mounds themselves occupy about 5% of the landscape, while Levick *et al.* (2010b) calculated the sphere of influence mounds have on browsing patterns to be as high as 20%. The lower values that I found compared to east Africa may be attributed to lower mound densities recorded in southern Africa, but are also potentially more accurate due to the possibility of surveying larger areas with LiDAR compared to field-based studies, which could be focused on small areas with high mound densities (Chapter 2). Although browsing extent around mounds is an order of magnitude greater (Levick *et al.* 2010b) than the influence mounds have on grasses, the effect on woody species assemblages is so far unknown, and here I do not report grazing influences of mounds (which would be more closely related to browsing) but rather grass species patterns. However, woody plants have deeper, more extensive root systems than grasses with their roots extending well beyond their own canopy (Scholes & Archer 1997). It is likely that the larger rooting systems enable woody plants to access the nutrient and moisture enriched soil around termite mounds at greater distances than grasses, enlarging the sphere of influence that mounds have on browsing patterns and likely woody plants.

The sphere of influence measured in this study reflects the direct influence *Macrotermes* mounds have on grass communities; indirect ecosystem effects are likely to be larger. For example, grazing herbivores are attracted to mounds (Mobæk *et al.* 2005, Grant & Scholes 2006) and such cascading effects induced by mounds are likely to be extensive. Furthermore, although only directly affecting around 2% of the landscape, 18% of the grass species recorded during this study occurred exclusively on or within the sphere of influence of termite mounds. These compositionally distinct grass assemblages increase overall savanna biodiversity and also differ functionally, providing hotspots of enhanced nutrition in otherwise nutrient-poor regions. Therefore, although termite mounds constitute a relatively small proportion of the savanna landscape, they are keystone structures that have a much greater influence on savanna structure and function than mound size alone would suggest.

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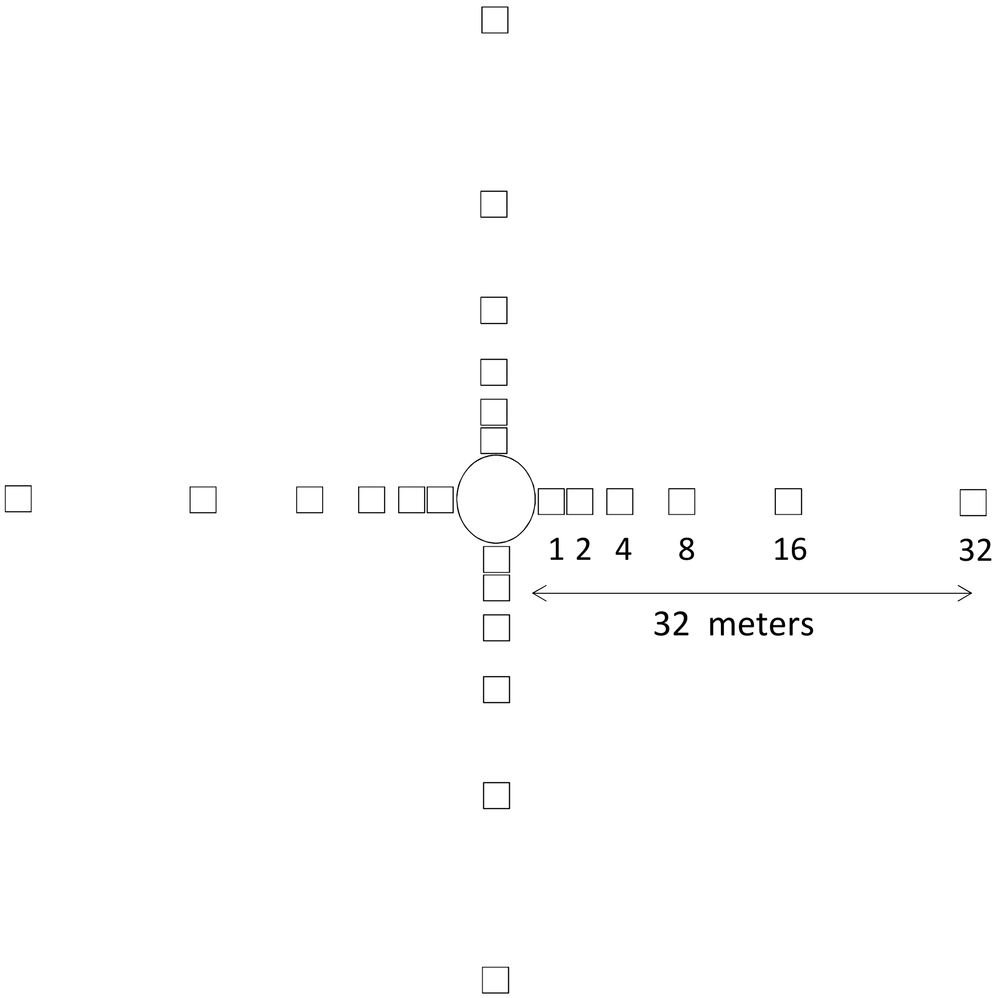
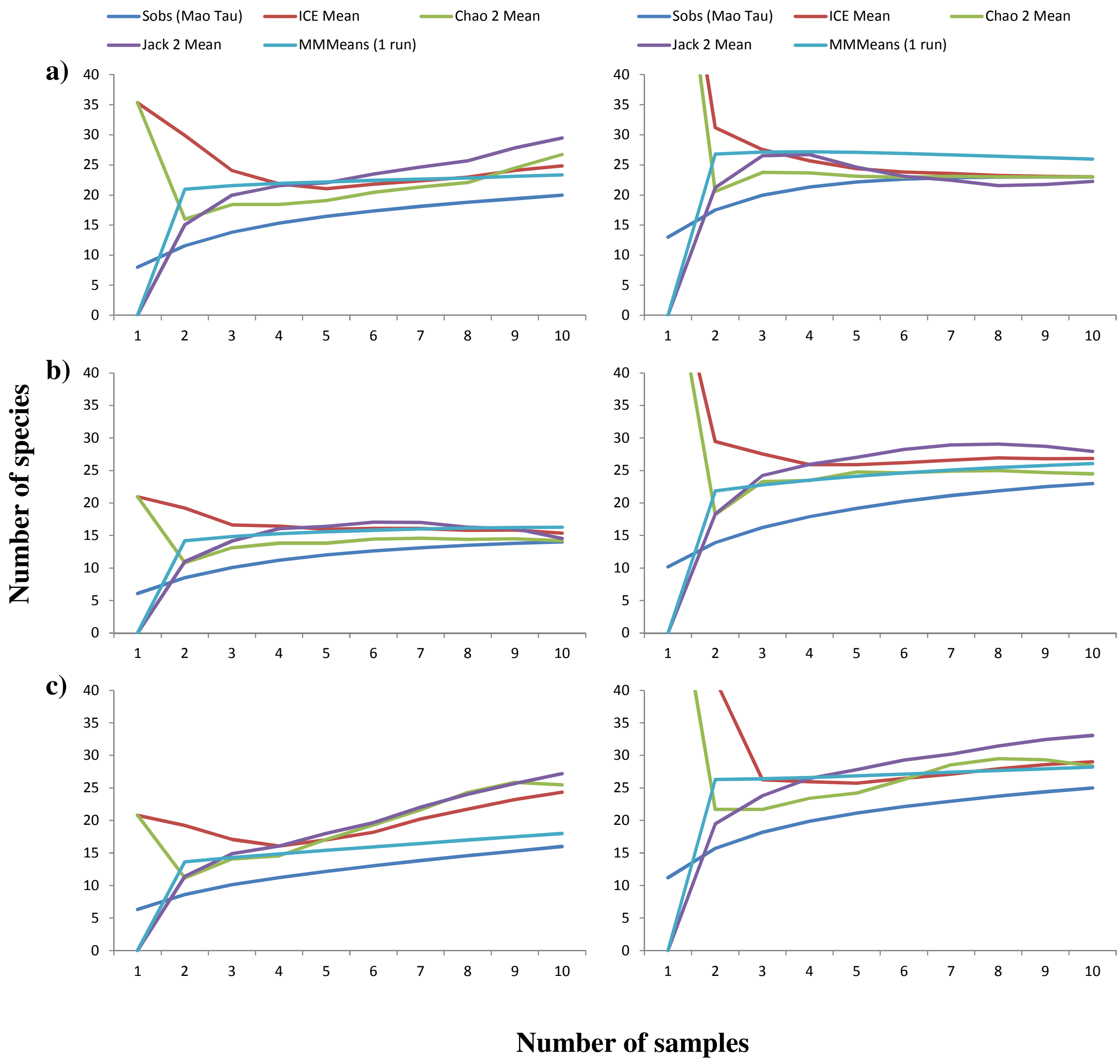
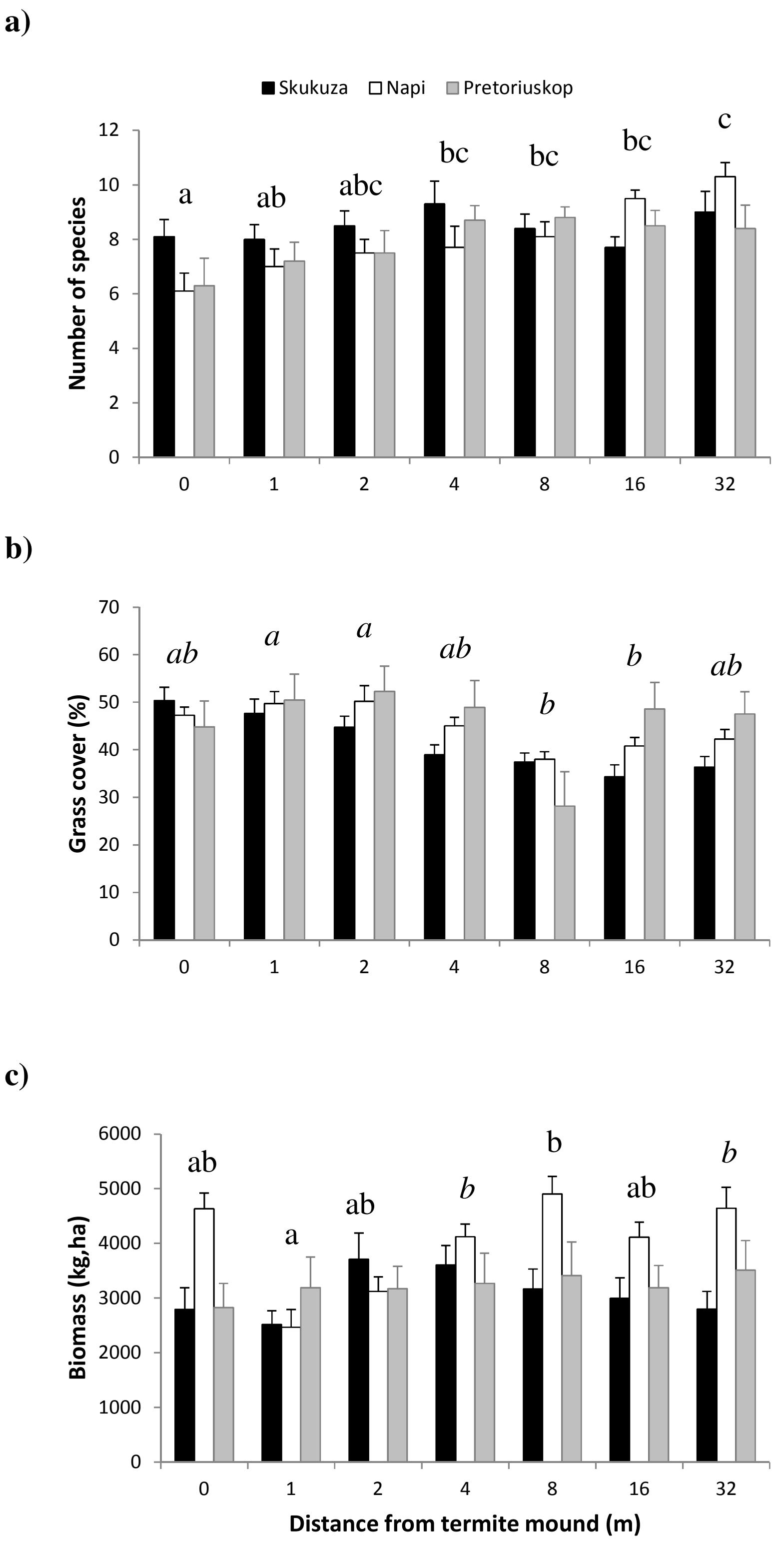


Appendix 3.1: Schematic representation of the sampling employed for the grass survey transects. Four transects consisting of 1 x 1 m quadrats placed at set distance intervals (1, 2, 4, 8, 16 and 32 m) were laid out from termite mounds in the four cardinal directions and the grasses occupying them surveyed. Grass and soil samples were also collected from each quadrat for nutrient analyses.



Appendix 3.2: Sampled-based species rarefaction curves based on the observed number of species (S Obs) and richness estimators: ICE Mean, Chao 2 Mean, Jack 2 Mean and MM Means. The first column represents termite mounds while the second column represents savanna areas, for a) Skukuza, b) Napi and c) Pretoriuskop.



Appendix 3.3: Grass species richness (a), percentage of cover (b) and standing biomass (c) along transects of increasing distance from termite mounds at three savanna sites situated across a rainfall gradient. Sites are arranged in order of increasing mean annual rainfall. Letters denote significant differences between distance classes (α = 0.05), letters in italics denote differences at the alpha level of 0.1 and are included to show trends.

Chapter 4

Spatial and temporal variation in the use of termite mounds by African savanna grazers

Prepared for submission to *Ecology* as: Davies, A.B., Levick, S.R., Robertson, M.P., van Rensburg, B.J., Asner, G.P., & Parr, C.L. Spatial and temporal variation in the use of termite mounds by African savanna grazers.

Abstract

African savanna herbivores do not forage uniformly across landscapes, but select for patches of higher nutrition and lower predation risk. *Macrotermes* mounds contain higher concentrations of soil nutrients and support higher nutritional grasses than the surrounding savanna matrix. These grasses attract grazers which preferentially forage on termite mound vegetation. However, little is known about how such termite influence on grazers differs in time and space, and whether mounds are attractive to a wide range of savanna herbivores, including insects. As mean annual rainfall increases, savannas in southern Africa become increasingly dystrophic through leaching of soil nutrients. The functional importance of mounds for grazing herbivores is concomitantly expected to increase as the difference in nutrient levels between mounds and the savanna matrix increases. Furthermore, mounds are expected to be more important for grazers during the dry season when grass nutrient levels are lower in the savanna matrix. I tested these predictions across a savanna rainfall gradient in South Africa during two seasons. Moreover, I investigated if mounds are preferred foraging patches to insect as well as mammalian herbivores. Tuft utilisation and grass nutrient content were measured along transects away from mounds, enabling me to calculate the spatial influence of termite mounds on savanna grazing. Using termite mound densities estimated from airborne LiDAR, I upscaled field-based results to determine the percentage of the landscape influenced by termite activity. Grazing lawn extent was also measured around termite mounds and exclosures were constructed to compare insect and mammalian herbivory. Grasses on termite mounds were preferentially grazed at all rainfall sites and in both seasons. Importantly, however, mound influence varied in time and space. Mounds were more heavily grazed at wetter savanna sites and influenced more of the landscape here during the wet season. However, during the dry season, when mound utilisation was higher, this pattern was reversed, with more of the landscape (19%) influenced at the driest site. Southern slopes of termite mounds exhibited higher grazing pressure and insects were also shown to prefer mound grasses and added to grass biomass depletion on mounds. My results show that termite mounds enhance the value of savanna landscapes for grazers and reveal that the functional importance of mounds varies spatially and temporally.

Keywords: anisotropy, Kruger National Park, landscape context, LiDAR, *Macrotermes*, nutrients, spatial heterogeneity, rainfall gradient, soil fertility

Introduction

Foraging patterns of African savanna herbivores are not uniform across landscapes, but respond to spatial and temporal heterogeneity, selecting patches with enhanced nutrition and lower predation risk (Turner et al. 1997, Owen-Smith 2002, Anderson et al. 2010, Hopcraft et al. 2010). Some nutrient-rich sites, such as grazing lawns are maintained by the herbivores themselves (Archibald 2008), while for others, e.g., sodic sites, abiotic processes are more important in their establishment and persistence (Grant and Scholes 2006), although grazing does play a role in maintaining them. At fine spatial scales, biotic structures such as large trees (Treydte et al. 2011) and dung middens (Cromsigt and Olff 2008) create nutrient-enriched sites that are attractive to herbivores. Through termite activity (the concentration of soil nutrients and organic material), the epigeal mounds constructed by some genera (including *Macrotermes*) are rich in nutrients and support compositionally distinct, nutrient-enriched plant communities on and around them (Traoré et al. 2008, Moe et al. 2009, Okullo and Moe 2012b, Erpenbach et al. 2013). These vegetation communities result in termite mounds becoming foraging hotspots, favoured by a diverse range of browsing and grazing herbivores (Holdo and McDowell 2004, Loveridge and Moe 2004, Mobæk et al. 2005, Brody et al. 2010, Levick et al. 2010b).

However, in a recent study conducted in South Africa's Hluhluwe-iMfolozi Game Reserve, van der Plas et al., (2013) documented higher browsing pressure on savanna matrix vegetation than termite mound vegetation, providing evidence for the first exception to the generally accepted rule of enhanced browsing on termite mounds (O'Connor 2013). This unique finding is attributed to the context of their study site: a relatively nutrient-rich savanna system, with higher soil nutrients relative to other savanna areas, which results in little nutritional difference between mound and savanna matrix vegetation and herbivores derive limited benefit from feeding on mound vegetation. The role of termite mounds in driving savanna heterogeneity and their importance as foraging hotspots may therefore depend on landscape context, with mounds being less important to herbivores in nutrient-rich savannas. Indeed, two recent studies from west (Erpenbach et al. 2013) and southern (Chapter 3) Africa show that differences in vegetation communities between termite mounds and the savanna matrix become increasingly pronounced with increasing mean annual precipitation. Due to processes such as increased denitrification and soil leaching, wetter savannas are generally nutrient-poor compared to drier ones (Scholes 1997), with nutritional differences between mounds and the savanna matrix being less pronounced and concomitantly weaker differences in vegetation composition and nutrition are present in these wet savannas (Chapter 3). These findings highlight the need for studies across environmental gradients if we are to understand the role of termite driven heterogeneity in shaping herbivore feeding patterns; currently, to my knowledge, all studies concerning herbivory on mounds have been conducted at single site locations.

Differences in the importance of mounds for savanna herbivores are likely to be reflected in the size of the sphere of influence around termite mounds (i.e. the area around the mound influenced by the mound). Where mounds are predicted to be of less consequence to herbivores (i.e. high-nutrient savannas), a smaller area of intense herbivory around them is expected. The majority of studies have, however, only compared herbivory on and off mounds, with limited information available on the extent of mound influences. Loveridge and Moe (2004) demonstrated that browsing intensity displayed a negative relationship with distance from termite mound centres while Levick et al., (2010b) measured this spatial extent to be as large as 20 m, influencing as much as 20% of the landscape. The spatial extent of grazing patterns has yet to be investigated.

On a temporal scale, Grant and Scholes (2006) suggested that mounds sustain mammalian herbivore populations through the dry season in southern African savannas because their vegetation contains essential nutrients throughout the year, as opposed to the savanna matrix vegetation which is only nutritious enough during the wetter months. Mounds are therefore predicted to experience higher utilization during the dry season, but whether this pattern is consistent across nutritionally different savanna types has not been adequately tested (but see Grant and Scholes (2006)). Utilization of termite mound vegetation is expected to increase in the dry season, but such increases are likely to be less pronounced in nutrient-rich savannas because the savanna matrix contains enough nutrients to sustain herbivore populations here. In contrast, wetter, nutrient-poor savannas may not be able to provide enough nutrition during the dry season when savanna vegetation deteriorates in both quantity and quality, with mounds becoming essential nutrient hotspots for herbivore populations.

Further shortcomings in our knowledge of how termite mounds influence herbivory relate to anisotropic effects (differences in properties along different directional axes) as well as the type of herbivory. Whether any termite induced patterns exhibit anisotropy has been poorly quantified (Sileshi and Arshad 2012), but could have implications for management and monitoring if termite mounds are used to detect early signs of environmental degradation in ecosystems due to increased herbivory of vegetation growing on them (Grant and Scholes

2006). The importance of mounds for various groups of taxa has been investigated in relation to browsers *vs.* grazers, large *vs.* small mammal species and between sexes; with mounds been consistently attractive to all groups (Mobæk et al. 2005). However, attention has focused on mammalian herbivores despite the large biomass and diversity of insect herbivores in savanna systems. Pringle et al., (2010) and Leitner (2012) demonstrated that mounds harbour higher abundances of insects, but their contribution to herbivory compared to that of mammalian herbivores, as well as whether they respond in similar ways to mammals with increased herbivory on mounds compared to the savanna matrix has not been quantified.

Here, I investigate the effects of *Macrotermes* mounds on grazing patterns across a savanna rainfall gradient. Importantly, I investigate the sphere of influence in relation to grazing around mounds and scale these findings up to the landscape scale, demonstrating how the overall influence of mounds on grazing varies across savanna types and providing the first estimates of the percentage of landscapes influenced by mound-induced grazing. The aims of the study were to i) determine whether termite mounds are preferentially grazed across markedly different savanna types, ii) determine the spatial extent into the savanna matrix of such grazing, iii) determine whether grazing on and around termite mounds exhibits anisotropy, iv) determine whether the spatial extent of grazing and anisotropic effects differ across a rainfall gradient from relatively dry, nutrient-rich savanna to relatively wet, nutrient-poor savanna, and v) quantify the relative contribution of mammalian and insect herbivory on termite mounds and in the savanna matrix. All of these aims were further investigated across seasons (wet and dry). I predicted that the importance of mounds for grazers (including both the degree of difference in mound and savanna grazing and the spatial extent of their influences) would be higher in nutrient-poor, wetter savannas and during the dry season following patterns of plant available nutrients, which were expected to differ most between mounds and the savanna matrix in nutrient-poor landscapes and during the dry season. Furthermore, I expected insect herbivory to be greater on mounds compared to the savanna matrix and differences between insect and mammalian herbivory to be stronger on mounds because of higher herbivore pressure from both groups.

Methods

Study site

The study took place in three savanna vegetation types across a rainfall gradient in southern Kruger National Park (KNP), South Africa. The three savanna sites occur in a summer rainfall region and vary in mean annual precipitation and vegetation characteristics; the driest site (Skukuza, 25°02' S, 31°30' E) is considered to be a nutrient-rich savanna (sweet veld) characterised by an *Acacia nigrescens/ Combretum apiculatum* association and receives a mean rainfall of 550 mm.yr^{-1} (Gertenbach 1983). The dominant grasses on termite mounds are *Panicum maximum* and *Urochloa mosambicensis*, while in the savanna matrix *P. maximum*, *Pogonarthria squarrosa*, *Digitaria eriantha* and *Brachiaria nigropedata* are common (Chapter 3). The wettest site (Pretoriuskop, 25°12' S, 31°16' E) is dominated by *Terminalia sericea* and *Dichrostachys cinerea* and is considered to be nutrient-poor (sour veld) (Gertenbach 1983); grasses on mounds are dominated by *Cynodon dactylon* and *P. maximum*, while the savanna matrix is characterised by *Setaria sphacelata*, *Loudetia simplex*, *P. squarrosa* and *Schizachyrium sanguineum* (Chapter 3). Mean annual rainfall here is 750 mm.yr^{-1}. An intermediate site (Napi, 25°06' S, 31°27' E) is located between these two distinct regions and contains a mosaic of the two vegetation types, with *Combretum zeyheri* and *C. collinum* being dominant tree species. Rainfall here is also intermediate, *ca.* 625 mm.yr^{-1} (Gertenbach 1983). Common grasses on mounds are *P. maximum* and *U. mosambicensis* while in the savanna matrix *D. eriantha*, *Eragrostis rigidior* and *P. squarrosa* dominate (Chapter 3). All three sites occur within an undulating landscape on granitic substrate; *Macrotermes* mounds occur predominantly on crests and upper sections of hillslopes (Levick et al. 2010a, Chapter 2).

Primary grazers and mixed-feeders in the study area include white rhinoceros (*Ceratotherium simum*), Cape buffalo (*Syncerus caffer*), plains zebra (*Equus quagga burchellii*), blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), elephant (*Loxondonta africana*), waterbuck (*Kobus elipsiprimnus*), tsessebe (*Damaliscus lunatus*), eland (*Taurotragus oryx*) and sable antelope (*Hippotragus niger*). Herbivore biomass in each savanna study site was calculated from KNP aerial census data collected between 1987 and 1993. During this time period, total area counts were conducted during the dry season at a spatial resolution of 800 m with a fixed-wing aircraft flying at 65-70 m at a speed of 95-100 knots. Location and herd size of the key mammalian herbivores were recorded on a one decimal degree resolution grid. After 1993, the aerial census technique changed in KNP to a sample-based, distance sampling approach with the resultant resolution too coarse for use in this study (see Smit et al., (2007) for more information on how these data were collected). For this study, biomass values for grazers and mixed-feeders were obtained from the six grid cells closest to the termite mound locations (covering the area and immediate surrounds of the ten termite mounds surveyed in each savanna site) and a mean value for each savanna site calculated (Table 4.1).

Table 4.1: Biomass (kg/km^2) of primary grazers (buffalo, sable antelope, tsessebe, waterbuck, white rhino, blue wildebeest and zebra) and mixed-feeders (impala, elephant and eland), as well as their total biomass at each savanna site surveyed. Sites are arranged in ascending order of mean annual rainfall and nutrition.

Savanna site	Grazer biomass	Mixed-feeders biomass	Total biomass
Skukuza	653.24	915.00	1568.24
Napi	1352.83	2137.53	3490.36
Pretoriuskop	654.49	183.72	838.20

Experimental design

Within each savanna site, areas of high termite mound densities were selected using LiDAR imagery from the Carnegie Airborne Observatory (CAO, see Asner et al. 2007, Levick et al. 2010a). Forty termite mounds were then selected at each site across the rainfall gradient; all mounds surveyed were built by *Macrotermes*, with the dominant species in the area being *M. falciger* and *M. natalensis* (Chapter 2). Within the study region, both active and inactive mounds are vegetated so I did not discriminate between these two classes. Mound diameter was measured for each mound along the north-south and east-west axes and the average diameter calculated from these measurements. Grass communities were surveyed as part of the broader project (see Chapter 3). In addition, the abundance of dominant mound grasses (occurring on at least half the termite mounds surveyed in each savanna site) on northern and southern slopes was recorded to explore potential effects of aspect on grazing patterns. This was achieved using sixteen 1 m^2 quadrats stratified across the mound (covering the upper and lower slopes), with the percentage of basal grass cover visually estimated for each species in each quadrat during January 2012.

Grazing on and around termite mounds was quantified using three methods. First, grass tuft utilization was estimated at ten of the forty termite mounds at each site during early April 2012 (the end of the growing season when forage is in abundance) and September 2012 (the end of the dry season when food for grazers is most limited). However, due to a natural fire at the intermediate site in August 2012, September surveying was only conducted for the driest and wettest site; all vegetation at the intermediate site was burnt. Tuft utilization was estimated by laying out distance transects in the four cardinal directions around termite mounds. On each distance transect, 4 m line transects (parallel to each other and perpendicular to the distance line transect) were placed at seven distance categories starting on the mound, and then at a distance of 1 m, 2 m, 4 m, 8 m, 16 m and 32 m from the mound. Grazing pressure was expected to be higher closer to mounds; hence a geometric progression with the common ratio of 2 was selected for the distance transects. Along each 4 m line transect, the tuft of grass located closest to each 40 cm mark was identified and scored according to grazing intensity, thus 11 tufts per 4 m line transect were assessed, 308 tufts per mound. Scoring was according to the following scale: 0 = no grazing evident, 1 = very light grazing, 2 = light to moderate grazing, 3 = moderate to heavy grazing, 4 = heavy grazing and 5 = tuft completely grazed, only roots remaining. In order to avoid any observer bias, the same observer ranked each tuft of grass throughout the study.

Second, the extent of heavy grazing leading to grazing lawn establishment was measured around termite mounds. For this aspect of the study, 30 mounds in each savanna site were surveyed. Beginning in May 2012, grazing lawns were measured in the four cardinal directions from termite mounds. Measurements were then taken approximately bimonthly until April 2013, however, due to the accidental fire in August 2012, measurements at the intermediate site (Napi) were not recorded during September and December 2012. Lawns were defined as the area where the biomass of the grass layer was noticeably reduced due to grazing (distinguished by careful examination of tufts, see Appendix 4.7).

Finally, grazing exclosures were constructed on and off ten termite mounds at the intermediate site, Napi. This site was selected because grazing pressure here is higher than the other two sites (Table 4.1). Two types of exclosures (full and partial) were constructed and measured a cubic meter. The full exclosures consisted of a metal frame covered with 2 x 2 mm aluminium gauze mesh, pegged at ground level and designed to exclude mammalian and insect herbivores, whereas the partial exclosure consisted only of the metal frame to exclude mammalian herbivores, but allow access by insect herbivores. A control site was also established one meter adjacent to each exclosure. This design was set-up on the pediment of the ten termite mounds and at a distance of 30 m into the savanna matrix, in a random direction from the mounds.

Thermochron iButtons® (Maxim/Dallas Semiconductor Corp., USA) recording temperature and relative humidity were placed approximately 2 cm below the soil surface in eight exclosures (four full and four partial paired ones) to record any potential alterations in micro-climate caused by the mesh of the full exclosure. At approximately bimonthly intervals beginning in January 2012, grass biomass readings were recorded in each exclosure and control site using a disc pasture meter. The disc pasture meter has been calibrated for this vegetation type and standing biomass was calculated with the following formula from Trollope (1990):

$(\sqrt{X} \text{ x } 2260) - 3019 = \text{kg ha}^{-1}$

where X is the disc height reading in cm obtained from the disc pasture meter.

Nutrient samples

Grass samples from the termite mounds and at each distance category along the distance transect used for tuft utilization were collected for nutritional analysis. Grass samples were representative of all species present in a 1 m by 1 m quadrat at each distance category with the amount of each species harvested in proportion to its abundance in the quadrat; all samples consisted of above-ground plant material and were collected in January 2012, the peak summer month. Grass samples were homogenised and analysed for nutrient content (N, C, P, K, Na, Mg, Ca, Zn, Al, Cu, Fe, Mn and S) at the Max Planck Institute for Biogeochemistry, Jena, Germany.

Data analysis

All statistical procedures were conducted using R software version 2.15.1 (R Development Core Team 2012). For each of the grazing response variables (tuft utilization, grazing lawn extent and herbivore exclusion), a candidate set of generalised linear mixed-effects models with Poisson error distributions was constructed to examine relationships between the response variable and the distance from termite mounds in relation to savanna site, season and direction from mounds. Models were applied using the *lme4* package in R (Bates et al. 2007) and ranked according to sample-size-corrected AIC*c* (Burnham and Anderson 2002) using the R package *MuMIn* (Barton 2010) and the best model for each response variable selected for further data analysis. The top models for each response variable ranked according to AIC*c* are provided in Appendices 4.1, 4.2, 4.3 and 4.4. For the tuft utilization dataset, the 4 m line transect with which each tuft was associated was considered a random effect and nested within the relevant termite mound. For both grazing lawn extent and herbivore exclusion, termite mound identity was considered a random effect. After application of the best model, multiple comparisons of means *post-hoc* testing for mixed-effects models, using

Tukey contrasts averaged across interaction terms when present, was used to examine pairwise comparisons with the R packages *multcomp* (Hothorn et al. 2008) and *mvtnorm* (Genz et al. 2011).

Differences in temperature and relative humidity between full and partial exclosures were assessed with paired Wilcoxon Rank Sum Tests. Differences in abundance (percentage cover) of dominant grass species between northern and southern termite mound slopes were similarly assessed with paired Wilcoxon Rank Sum Tests when data were non-parametric and paired Student's t-Tests when data were normally distributed. Percentage cover data were arc sine transformed before analysis.

For the nutrient data, C: N ratio was calculated and after an arc sine transformation, linear mixed-effects models were fitted to the data to examine changes in C: N with distance from termite mounds and between savanna sites. Termite mound identity was considered a random effect. Similarly, linear mixed-effects models were fitted to the other nutrient data to examine how nutrient quantity ($mg.kg^{-1}$) differed with distance from mounds and between sites, with termite mound identity used as the random effect. After model selection using AIC*c*, the top performing model was used for further analysis and multiple comparisons of means *post-hoc* testing conducted on the fixed effects using Tukey contrasts averaged across interaction terms when present (all cases apart from Cu).

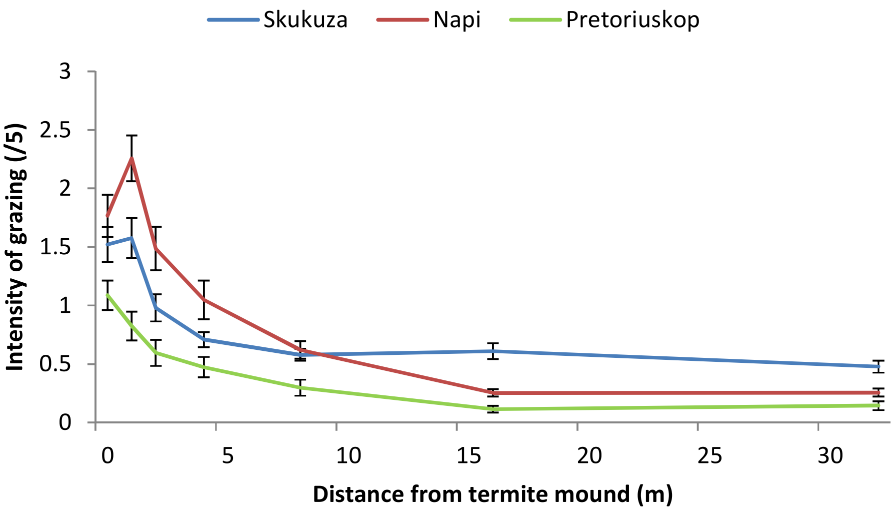
In order to determine the sphere of influence of mounds in each study site, the mean mound diameter was calculated and added to the extent of grazing determined from the distance transects to obtain a radius of influence from the centre of each termite mound. For each savanna site and in each season (April and September) separately, a generalised linear mixed-effects model with distance as a fixed factor was applied to each data set in order to determine thresholds in the intensity of tuft utilization. Transect identity nested within mound identity were random factors in each model. Following this, multiple comparisons of means *post-hoc* testing for mixed-effects models (using Tukey contrasts), was used to examine pairwise comparisons and detect thresholds. Once determined, this sphere of influence was assumed to be circular, and the area influenced by a termite mound calculated. Using LiDAR imagery from the CAO, mound densities on crests in each study area were estimated (see Chapter 2), and from this the area influenced by mounds in terms of grazing patterns was calculated for each study site. Due to the nature of remote sensing techniques, some small mounds (< 1m in height) will escape detection, thus these estimations can be considered minimum values.

Results

Tuft utilization

Grazing intensity decreased significantly with distance from mounds (X^2 = 1089.56, $p < 0.001$) at all three savanna sites and in both seasons, with significant interactions between distance and site (X^2 = 94.05, $p < 0.001$) as well as distance and season (X^2 = 17.16, $p < 0.01$); tuft utilization therefore decreases with distance from mounds, but the manner in which it does so differs with savanna site and season (Fig. 4.1).

a)



b)

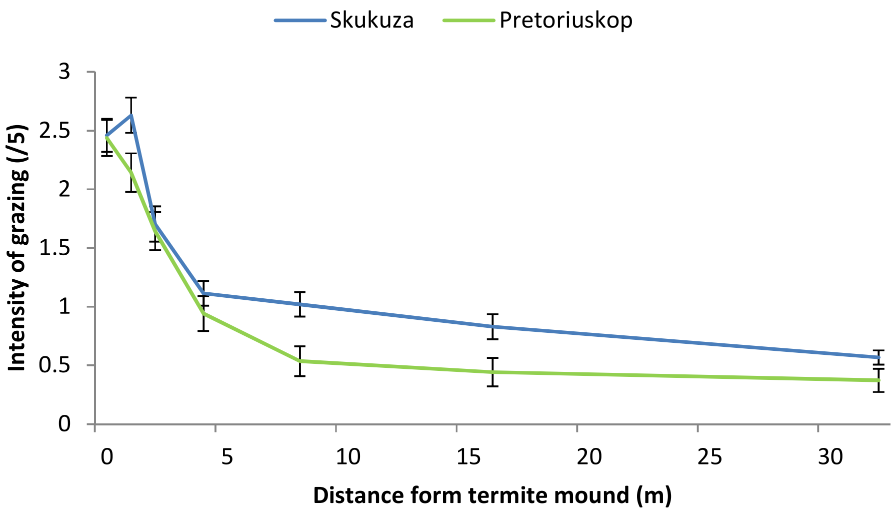


Figure 4.1: Intensity of grass tuft utilization along distance transects around termite mounds at three savanna sites during two seasons, a) the end of the growing season (April) and b) the end of the dry season (September). Grass tufts were ranked on a scale of 0 – 5 depending on the intensity of grazing.

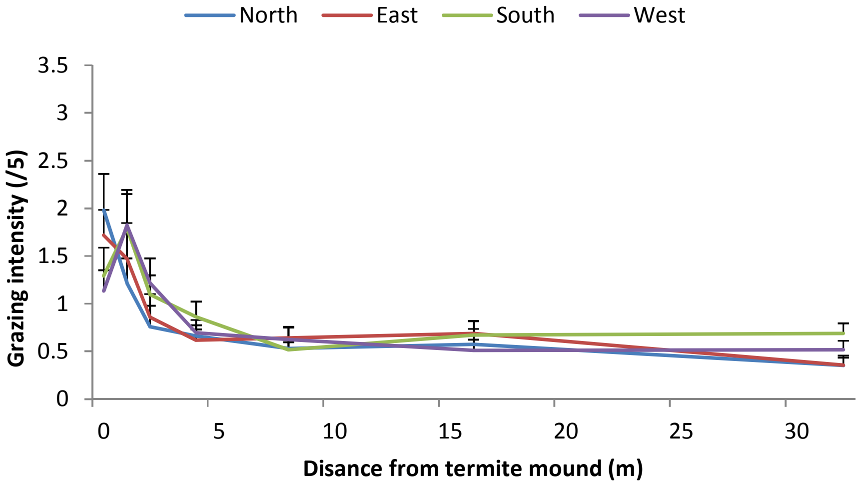
When considering the effect of the fixed factor distance, multiple comparisons testing revealed that tuft utilization was significantly higher on mounds than at distances of 2 m and greater ($p < 0.001$). Tuft utilization was highest 1 m from mounds compared to all distance categories apart from on termite mounds ($p < 0.001$). When comparing tuft utilization across distance categories with increasing distance from mounds, utilization was consistently lower between distance categories and significant up to 16 m from mounds (i.e. significantly lower tuft utilization at 4 m compared to 2 m ($p < 0.001$), lower at 8 m compared to 4 m ($p < 0.001$) and lower at 16 m compared to 8 m ($p < 0.001$)). Differences between 16 m and 32 m were not significant ($p = 0.866$); suggesting that a levelling off of tuft utilization occurs 16 m into the savanna matrix (Fig. 4.1).

Tuft utilization differed significantly with savanna site ($X^2 = 16.29$, $p < 0.001$), with the highest levels of grazing recorded on mounds at Napi, but the highest savanna matrix grazing was at Skukuza. Pretoriuskop had the lowest levels of grazing on mounds and in the savanna matrix (Fig. 4.1) and had significantly lower overall grazing than either Skukuza or Napi ($p < 0.001$ for both comparisons). The interaction between site and distance was significant ($X^2 = 94.05$, $p < 0.001$); tuft utilization levelled off closer to mounds at Skukuza (between 4 and 8 m during the wet season, Fig.4.1a), and Napi displayed the greatest differences between mound and savanna matrix (Fig. 4.1).

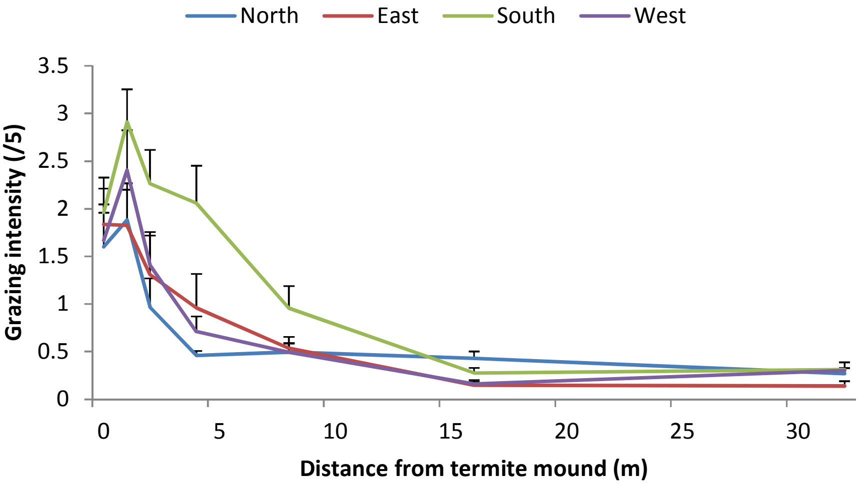
Recorded tuft utilization was significantly higher during the dry season (September) at both sites ($X^2 = 935.02$, $p < 0.001$) and a significant interaction existed between season and distance ($X^2 = 17.16$, $p < 0.01$); with the contrast between mound and savanna matrix greatest in September. Seasonal differences in tuft utilization were also more noticeable on mounds than in the savanna matrix (Fig. 4.1). Mound utilization did not differ between sites in September (Fig. 4.1b).

Tuft utilization around mounds differed significantly with cardinal direction ($X^2 = 35.57$, $p < 0.001$): higher utilization was recorded south of termite mounds compared to all other cardinal directions ($p < 0.001$). The other directions (north, east and west) did not differ from each other (Fig. 4.2). The interaction between cardinal direction and site was significant ($X^2 = 19.97$, $p < 0.01$), with direction being an important factor at Napi (Fig. 4.2b), but not at the other two sites (Fig. 4.2a and c). Similarly, direction was important during the wet (April) season, but not during the dry (September) season ($X^2 = 26.89$, $p < 0.001$) (Fig. 4.2d and e). No data were available for Napi during the dry season.

a)


North
East
South
West
Grazing intensity (/5)
3.5
3
2.5
2
1.5
1
0.5
0
0
5
10
15
20
25
30
Disance from termite mound (m)

b)


North
East
South
West
Grazing intensity (/5)
3.5
3
2.5
2
1.5
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0.5
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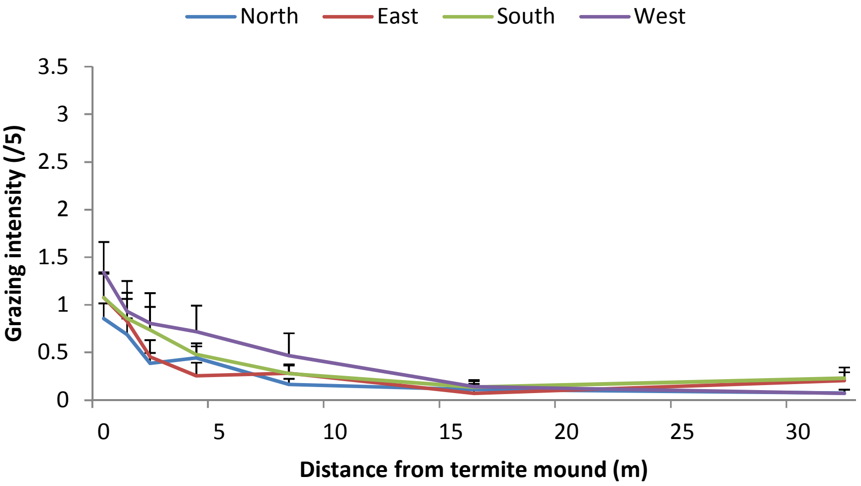
30
Distance from termite mound (m)

c)


North
East
South
West
Grazing intensity (/5)
3.5
3
2.5
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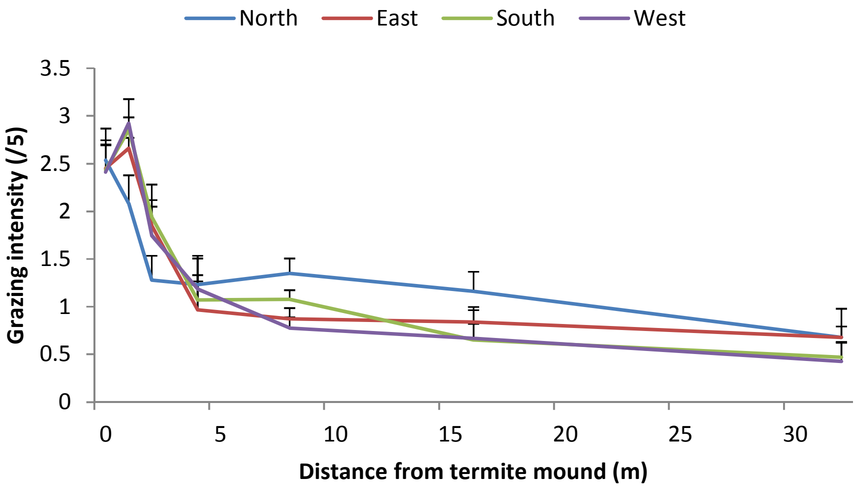
30
Distance from termite mound (m)

d)



e)

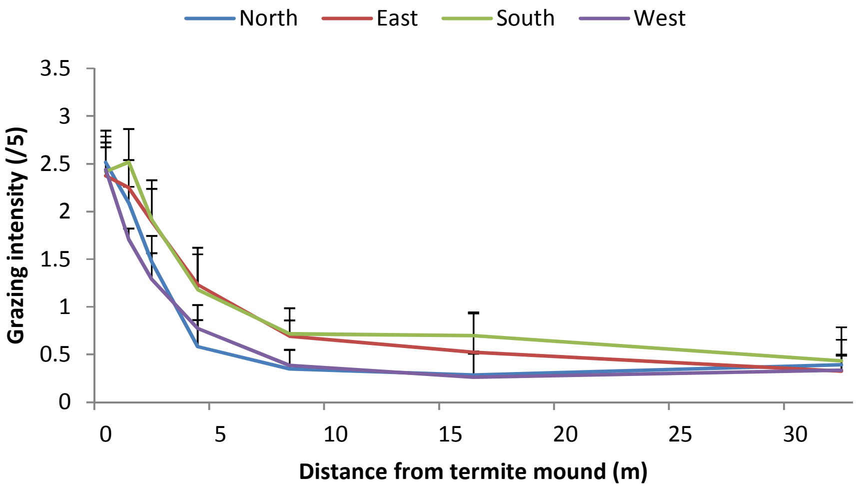


Figure 4.2: Intensity of grass tuft utilization along distance transects in the four cardinal directions around termite mounds during two seasons a) – c) the end of the growing season (April), and d) – e) the end of the dry season (September) and at three savanna sites, a) and d) Skukuza, b) Napi and c) and e) Pretoriuskop. Grass tufts were ranked on a scale of 0 – 5 depending on the intensity of grazing.

Grazing lawns

The extent of heavy grazing leading to grazing lawns around mounds varied significantly with savanna site, season (sampling date) and cardinal direction (site: $X^2 = 33.15$, $p < 0.001$; season: $X^2 = 9954.29$, $p < 0.001$; direction: $X^2 = 475.32$, $p < 0.001$). Grazing lawns were significantly and consistently larger at Napi than the other two sites ($p < 0.01$ for both comparisons). Differences between Skukuza and Pretoriuskop fluctuated with season, with more extensive lawns in the dry season (May – September) at Pretoriuskop and during the wet season (December – April) at Skukuza. Across seasons, however, Skukuza tended to have larger grazing lawns than Pretoriuskop ($p = 0.067$). Across sites, lawns displayed significant differences across all sampling dates ($p < 0.001$) and were larger during the drier months, with lawn extent peaking in September (Fig. 4.3).

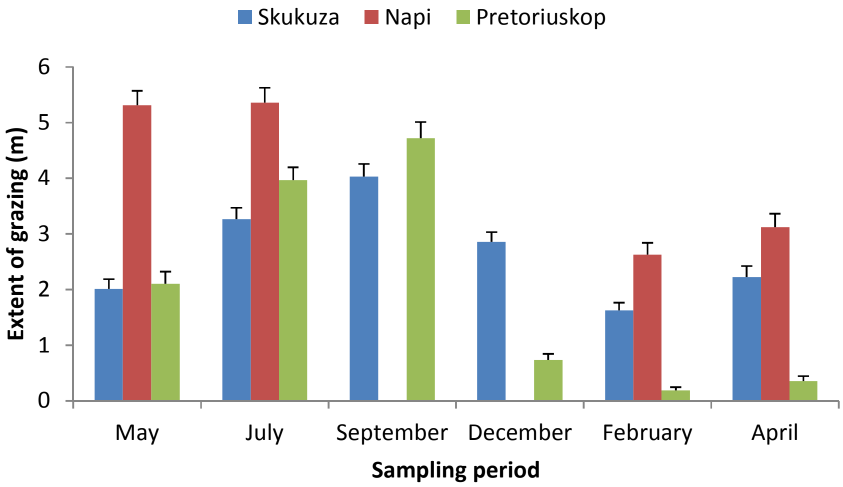


Figure 4.3: Extent of grazing lawns around termite mounds at three savanna sites across six sampling periods from May 2012 to April 2013. Sites are arranged (Skukuza to Pretoriuskop) in ascending order of mean annual precipitation received.

The size of grazing lawns varied significantly with cardinal direction ($X^2 = 475.32$ $p < 0.001$, Fig. 4.4). Overall, lawns were significantly larger on the southern sides of mounds (up to 1.5 m larger, Fig. 4.4) compared to all other sides ($p < 0.001$). Northern and eastern sides did not differ from each other ($p = 0.642$), but the western side was significantly larger than both northern ($p < 0.001$) and eastern ($p < 0.001$) sides. The interaction between direction and site was significant ($X^2 = 99.84$, $p < 0.001$); directional effects being less pronounced at Skukuza (Fig. 4.4). Similarly, the interaction between direction and season (sampling date) was significant ($X^2 = 48.30$, $p < 0.001$), differences being more pronounced during the drier months (May – September).

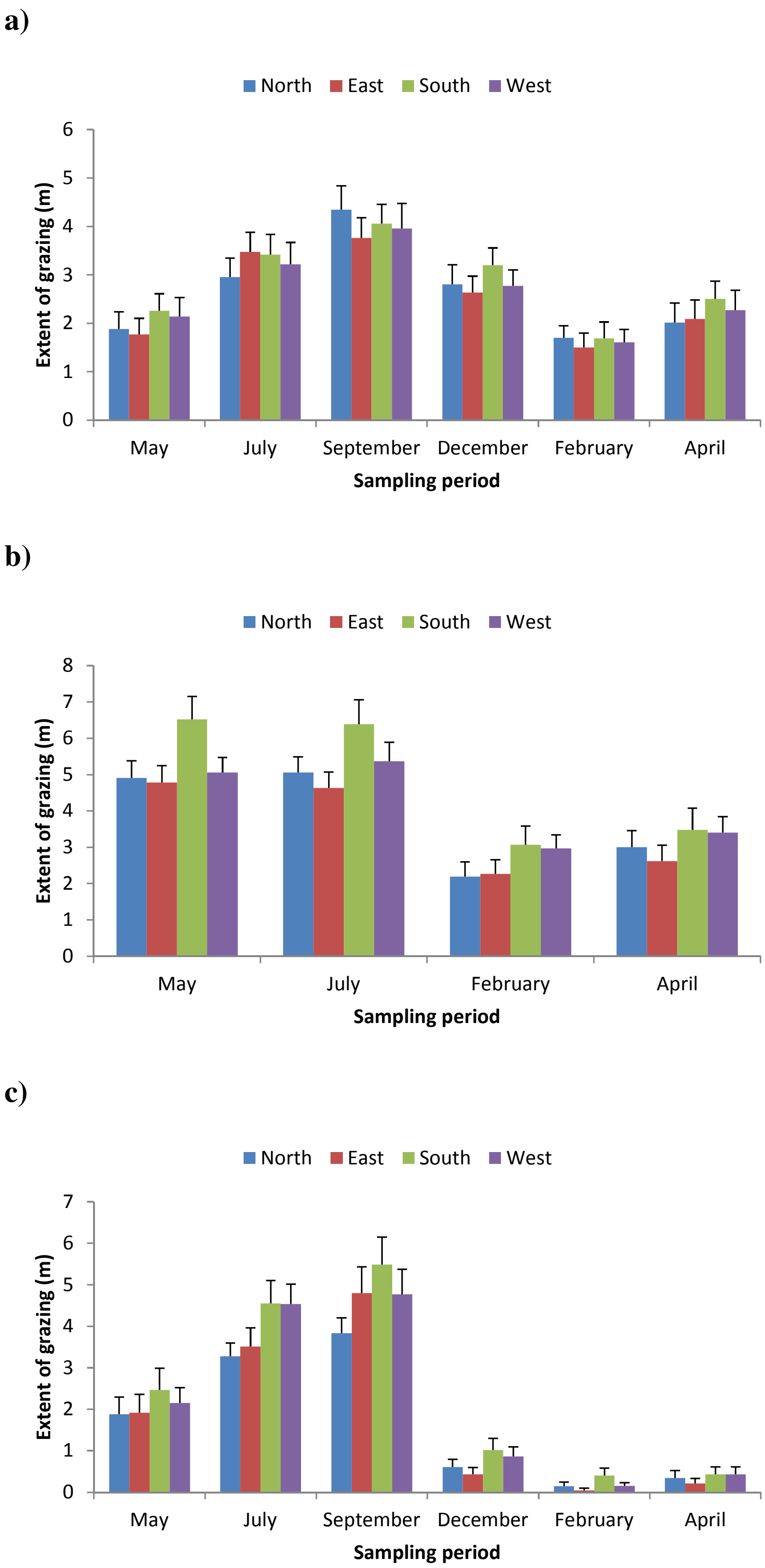


Figure 4.4: Extent of grazing lawns around termite mounds in the four cardinal directions at three savanna sites, a) Skukuza, b) Napi and c) Pretoriuskop at six surveying dates from May 2012 to April 2013.

Grazing exclosures

Neither temperature nor relative humidity differed between full and partial exclosures (temperature: Paired Wilcoxon Rank Sum Test, W = 1, $p = 0.25$, $n = 4$; humidity: W = 4, $p = 0.88$, $n = 4$), so microclimatic conditions were therefore considered similar between exclusion treatments. The only significant variable affecting standing grass biomass on termite mounds was exclusion treatment (i.e. full, partial or control) ($X^2 = 97.56$, $p < 0.001$). Biomass inside full (excluding mammalian and insect herbivores) and partial (excluding mammalian herbivores) exclosures was significantly greater than the control ($p < 0.001$ for both treatments), and was significantly higher ($p < 0.05$) in full than partial exclosure treatments (Fig. 4.5a). For the exclosures in the savanna matrix, exclusion treatment was again the only significant variable explaining variation in the data ($X^2 = 13.24$, $p < 0.01$) and was significantly higher inside full and partial exclosures compared to the control ($p < 0.01$ for full exclosures and $p < 0.05$ for partial exclosures). Biomass between exclosure treatments (full *vs.* partial) did not differ ($p = 0.581$) (Fig. 4.5b). When comparing control plots with exclosures on mounds and in the savanna matrix, the magnitude of difference between treatment and control was much lower in the savanna matrix (Fig. 4.5).

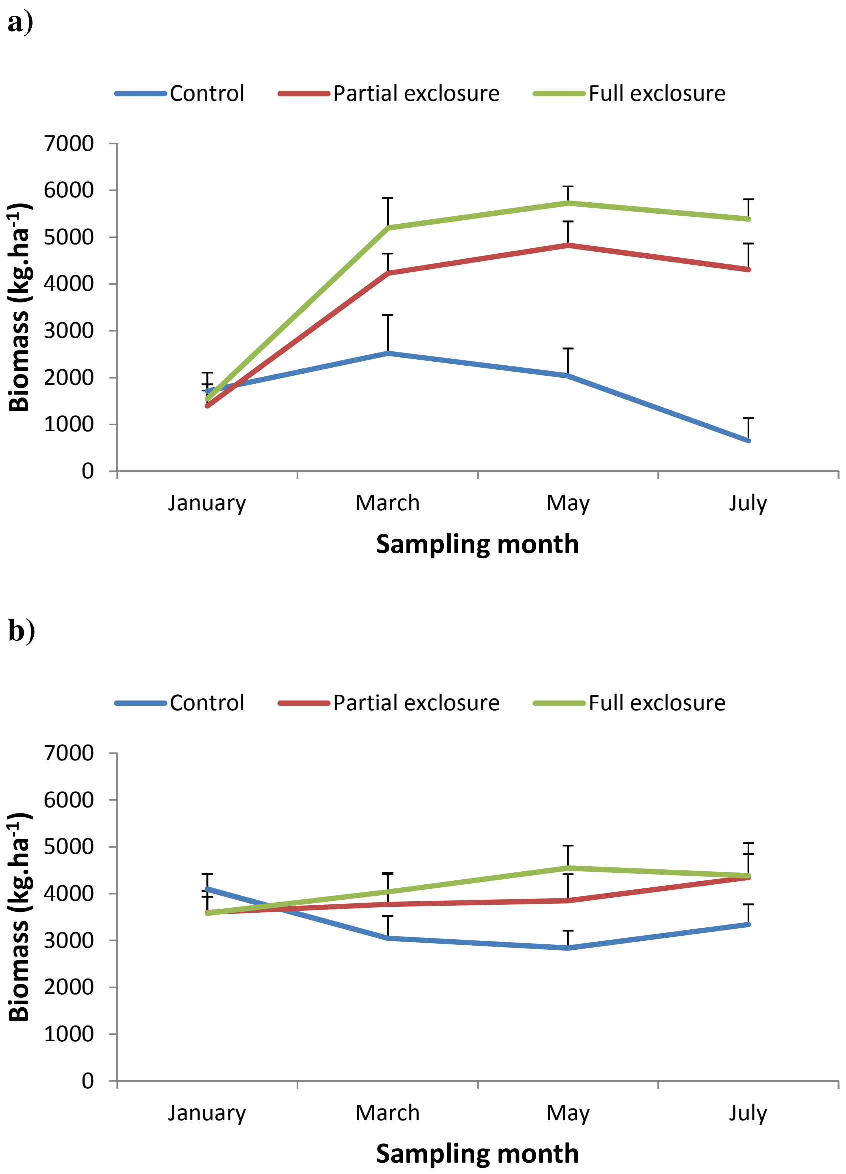


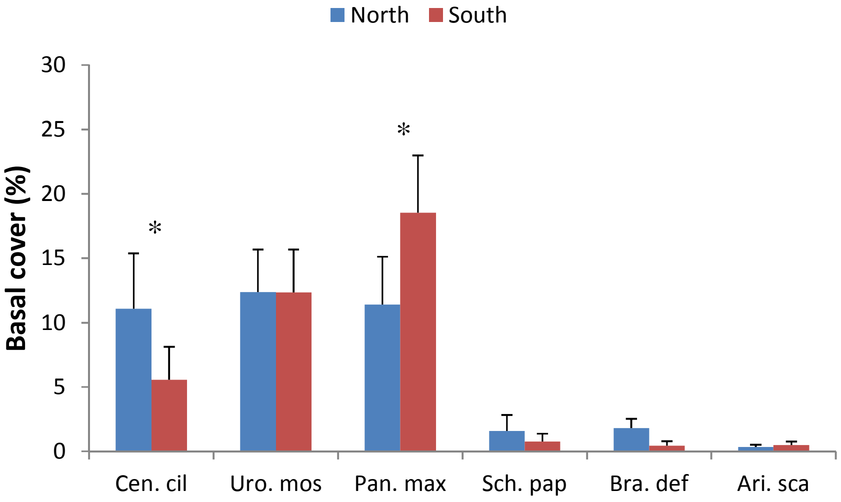
Figure 4.5: Standing biomass (kg.ha^{-1}) of grass in full herbivore exclosures (excluding both mammals and insects), partial exclosures (excluding mammals only) and control sites at a) termite mounds and b) savanna matrix plots.

Grass species on mounds

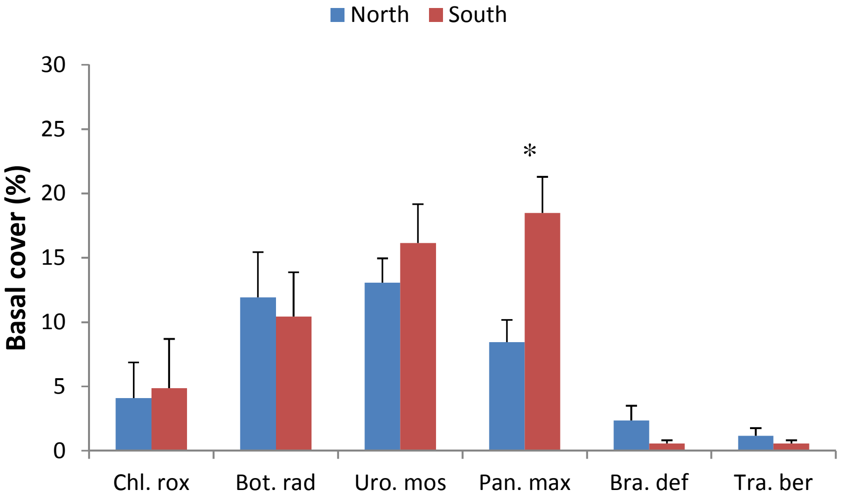
At Skukuza, *Cenchrus ciliaris* was significantly more abundant on the northern slope of termite mounds (Paired Wilcoxon Rank Sum Test, W = 21, $p < 0.05$, n = 10) while *Panicum maximum* was significantly more abundant on southern slopes (Paired Student's t-Test, t = -4.15, $p < 0.01$, n = 10) (Fig. 4.6a). At Napi, significantly more *P. maximum* was recorded on southern slopes (Paired Student's t-Test, t = -3.29, $p < 0.01$, n = 10) (Fig. 4.6b). At

Pretoriuskop, no grass species differed in abundance between northern and southern slopes (Fig. 4.6c).

a)



b)



c)

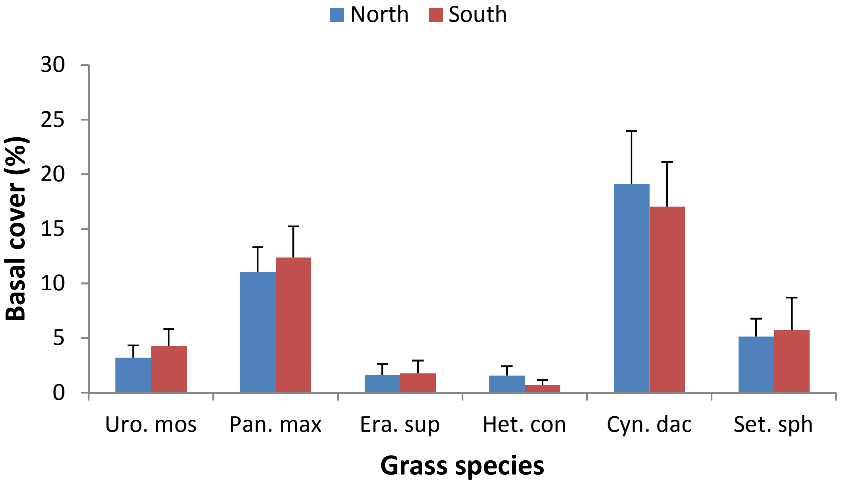


Figure 4.6: Mean (±SE) abundance (measured as percentage basal cover) of the dominant grass species occurring on northern and southern slopes of termite mounds in a) Skukuza, b) Napi and c) Pretoriuskop. Grass species abbreviations are as follows: Cen. cil = *Cenchrus ciliaris*; Uro. mos = *Urochloa mosambicensis*; Pan. max = *Panicum maximum*; Sch. pap = *Schmidtia pappophoroides*; Bra. def = *Brachiaria deflexa*; Ari. sca = *Aristida scabrivalvis*; Chl. rox = *Chloris roxburghiana*; Bot. rad = *Bothriochloa radicans*; Tra. ber = *Tragus berteronianus*; Era. sup = *Eragrostis superba*; Het. con = *Heteropogon contortus*; Cyn. dac = *Cynodon dactylon*; Set. sph = *Setaria sphacelata*.

Nutrient results

All nutrients measured (apart from Mg) varied with distance from termite mounds (Appendix 4.5, Fig 4.7). The C: N ratio increased significantly with distance from mounds up to 8 m (Appendix 4.5, Fig. 4.7) and also differed across sites, being highest at Pretoriuskop and lowest at Skukuza (Appendix 4.6, Fig. 4.7). All other nutrients, apart from Mg and Mn, decreased with distance from mounds, with most differences occurring between mounds and distances up to 2 m off mounds. P, Zn, Cu and S showed the strongest declines with distance. Mn was the only nutrient to significantly increase with distance from termite mounds, with significantly higher levels recorded at 8 m, 16 m and 32 m from mounds (Appendix 4.5, Fig. 4.7). All nutrients apart from Na, Ca and Fe differed significantly between sites (Appendix 4.6, Fig. 4.7). Of the nutrients to display site differences, Pretoriuskop had significantly lower levels compared to Skukuza for all nutrients, except for Mn. Napi had significantly less K, Mg, Al and Cu than Skukuza and significantly more P, Mg and Zn compared to Pretoriuskop. Pretoriuskop had significantly more Mn than Napi (Appendix 4.6, Fig. 4.7).

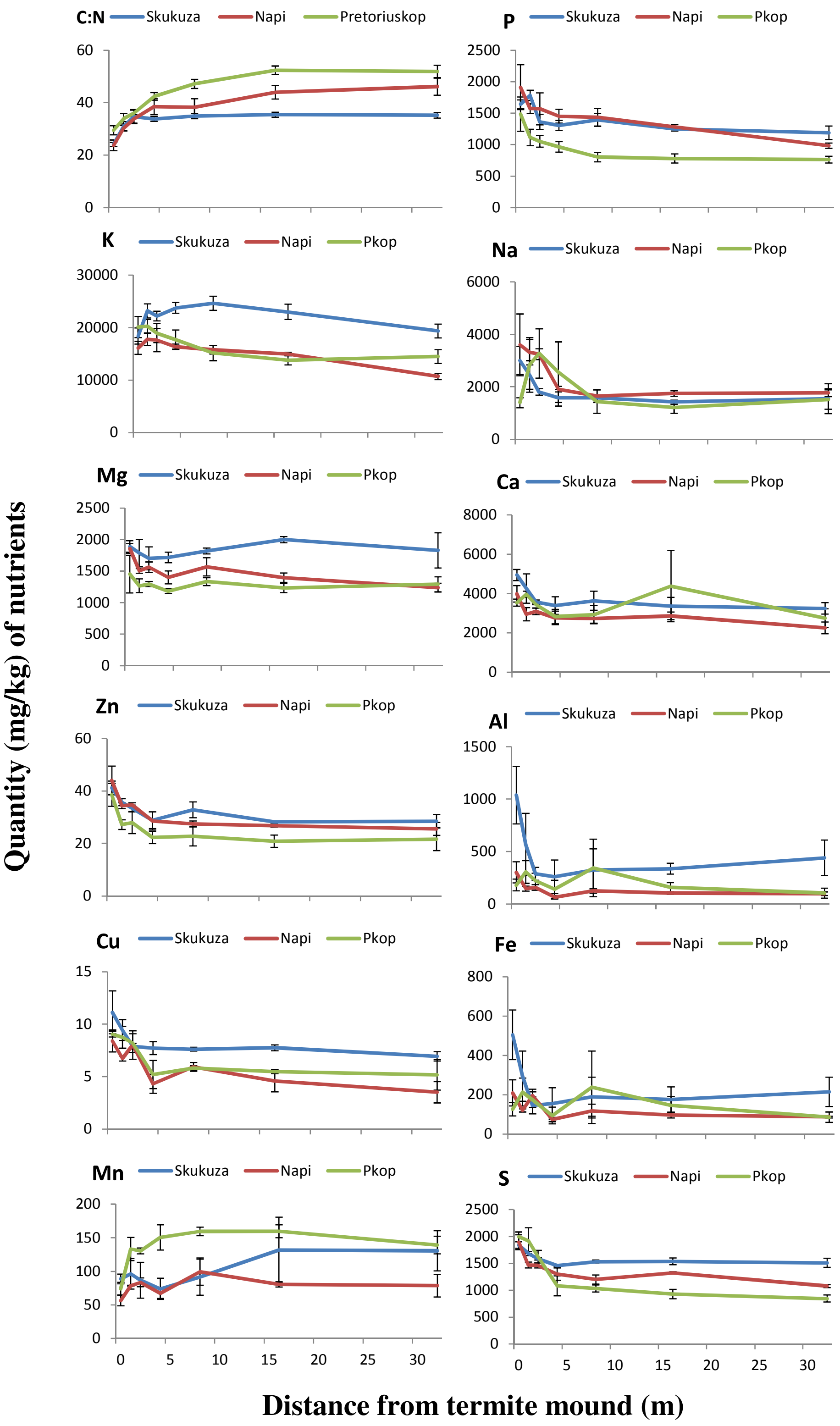


Figure 4.7: Carbon to nitrogen ratio (C: N) and nutrient quantities (mg/kg) from grass samples across distance transects away from termite mounds in three savanna sites. Data were pooled from homogenised samples taken from the four cardinal directions around mounds. For significant differences see Appendices 4.5 and 4.6.

Sphere of termite mound influence on grazing

Generalized linear mixed-effects models revealed that during the wet season tuft utilization around termite mounds is significantly greater up to 16 m into the savanna matrix at Napi and Pretoriuskop and 4 m at Skukuza (Fig. 4.1a). In the dry season, this increased at Skukuza, up to 16 m, while at Pretoriuskop it decreased to 8 m (Fig. 4.1b). For the sphere of influence calculations, mounds were assumed to be circular and the average mound diameter for each site calculated. The extent of grazing beyond the mound was then added to this diameter in order to calculate the total savanna area influenced by mounds during each season. These calculations revealed that during the wet season mounds have a more extensive landscape effect on grazing at the wettest site, Pretoriuskop, where more than 15 % of savanna landscapes on crests are affected. Although individual mounds had the largest sphere of influence at Napi, the overall landscape effect (7.78 % of the landscape) is smaller than Pretoriuskop due to lower mound densities. Skukuza had the smallest extent of landscape affected (7.08 %) because although mounds here are larger and occur at higher densities, the sphere of influence extends only to 4 m from mounds compared to 16 m at the wetter sites. However, during the dry season this pattern is reversed, with mounds at Skukuza influencing almost 20 % of the landscape, while at Pretoriuskop only 5.25 % is affected (Table 4.2).

Table 4.2: The mean area (sphere of influence [SoI]) around individual termite mounds (n = 10 for each savanna site) and the percentage of the landscape within which grazing is enhanced. The mound densities from which the percentage figures are calculated were attained from LiDAR terrain data and reflect densities on crests within the landscape, the landscape percentage influenced subsequently refers to percentages of crests influenced by mounds.

Savanna site (season)	**SoI around individual mound**	**Mound density**	**Percentage of landscape influenced by mounds**
Skukuza (wet)	204.03 m^2	1.55 ha^{-1}	3.16 %
Napi (wet)	1235.60 m^2	0.63 ha^{-1}	7.78 %
Pretoriuskop (wet)	1139.94 m^2	1.37 ha^{-1}	15.62 %
Skukuza (dry)	1264.04 m^2	1.55 ha^{-1}	19.59 %
Pretoriuskop (dry)	383.51 m^2	1.37 ha^{-1}	5.25 %

Discussion

My results clearly demonstrate that termite mounds are favoured foraging hotspots for grazing herbivores across markedly different savanna types, supporting previous studies and demonstrating the importance of these biotic drivers for savanna spatial heterogeneity. Furthermore, mounds are utilised more heavily than the savanna matrix across seasons when forage is both abundant (April) and restricted (September). Importantly, however, I show that the use of mounds varies substantially in time and space.

Termite mounds have been shown to harbour significantly different grass assemblages (Arshad 1982, Jouquet et al. 2004a, Moe et al. 2009, Chapter 3), which are also higher in nutritional content (Grant and Scholes 2006, Chapter 3) than the matrix. It is therefore not surprising that they are heavily utilized by grazers, as found in previous studies (Mobæk et al. 2005, Grant and Scholes 2006). Grass on termite mounds at all three savanna sites contained higher levels of all nutrients apart from Mg and Mn than the savanna matrix. In particular, nutrients known to be essential for wild mammalian herbivores (e.g., N, P and Na, see Owen-Smith and Novellie (1982) and Grant and Scholes (2006)) were found in significantly higher quantities on mounds and 1 m off mounds. The mechanism for increased grazing on and around termite mounds is therefore likely to be the increased nutrition available from mound grasses. Although mechanisms other than nutrition have been suggested for increased browsing, such as vegetation structure and shading (Loveridge and Moe 2004), these are not likely to play a role in grazing because the small sizes of the patches are unlikely to provide protection (visibility) against predators and although grass structure is modified, this is a result of the enhanced grazing and thus cannot be considered a driving mechanism itself. However, since browsers utilise mounds and reduce woody cover around them (Levick et al. 2010b), some degree of predator avoidance may also attract grazers to mounds.

Variation with landscape context and season

During the wet season, tuft utilization differed across the sites, with the heaviest utilization at the intermediate rainfall site (Napi) where mammalian herbivore biomass is also highest; differences between mound and matrix are also particularly pronounced here. The high herbivore biomass may lead to depletion of alternative high-quality forage patches in the savanna matrix, with termite mounds coming under greater pressure as animals are forced to utilise them. Mound utilization decreased with decreasing herbivore biomass across sites, with the lowest levels of mound utilization occurring at the wettest site (Pretoriuskop).

Differences between termite mound and savanna matrix utilization suggest that the relative importance of mounds for savanna herbivores varies across the rainfall gradient. Despite lower herbivore biomass at the driest, most nutrient-rich site (Skukuza), grazing in the savanna matrix is higher compared to Napi, with the lowest ratio of mound to matrix utilization here. In this nutrient-rich savanna, nutrient availability is higher in the savanna matrix and likely sufficient for herbivores during the wet season, with mounds being less important as foraging patches for maintaining populations. However, as nutritional content in the savanna matrix decreases (with increasing annual rainfall), nutritional differences between mound and matrix become more pronounced and the importance of mounds increases, with a higher ratio of mound to matrix utilization and a greater sphere of influence around mounds. Van der Plas et al., (2013) suggest that in high-nutrient savannas browsers are not reliant on mound vegetation and can source sufficient nutrition in the savanna matrix. My results provide some support for this notion in grazing herbivores, with less reliance on mounds in high-nutrient savanna; however, mounds were still always preferred as foraging sites. Further testing in even higher-nutrient areas (e.g., the basaltic plains of KNP or the nutrient-rich volcanic soils of east Africa) is necessary because although Skukuza represents a nutrient-rich savanna along the rainfall gradient in this study, it is still located on generally nutrient-poor granitic substrate.

During the dry season, however, herbivores are under increased pressure to find resources with sufficient nutrients, with tuft utilization and grazing lawn extent increasing on and around mounds across all sites. Differences in mound tuft utilization across sites are diminished, and termite mounds experience similar levels of utilization at both ends of the nutrient gradient. Grass nutritional value declines through the dry season (Treydte et al. 2008) and forage patches do not re-grow, placing pressure on grazers to locate resources (Owen-Smith and Novellie 1982). As a result, it is likely that during the dry season the matrix grasses at Skukuza no longer contain sufficient nutrients and many high-quality patches are exhausted, resulting in herbivores relying more heavily on mound vegetation. Consequently, the use of mounds increases dramatically and they become essential in maintaining herbivore populations (see also Grant and Scholes 2006).

Sphere of termite influence on grazing

The sphere of influence around mounds demonstrates that termites affect herbivore foraging at scales greater than the extent of their mounds. Levick et al., (2010b) measured termite influences on browsing herbivores up to 20 m into the savanna matrix at the end of the wet season (May) in nutrient-poor Pretoriuskop. My measurements for grazers in the same savanna site at a similar time of year are less, up to a maximum of 16 m. Woody plants have deeper, more extensive root systems than grasses with their roots extending well beyond their own canopy (Scholes and Archer 1997). It is likely that the larger rooting systems enable woody plants to access the nutrient and moisture enriched soil around termite mounds at greater distances than grasses, enlarging the sphere of influence that mounds have on browsing patterns. In Chapter 3, I showed that the direct sphere of mound influence on grass assemblages is much lower (between 2 and 4 m) than the grazing patterns from this study; as such, cascading effects of altered grass species composition and nutritional content are therefore larger than the direct effects of mounds on grass assemblages. The extent of grazing lawns around mounds, however, matched the extent of altered grass assemblages more closely, suggesting a two-layered effect. Intense grazing around mounds (lawns) is spatially restricted to the distinct grass assemblages around them, but enhanced, although less intense, grazing extends further into the savanna matrix.

Grazing lawns are recognised as important features in African savannas (Young et al. 1995, Archibald 2008, Stock et al. 2010), and are initiated by disturbance (including termite activity) rather than large migratory herds in southern Africa (Cromsigt and Olff 2008). Termite activity, rather than grazing, has been shown to alter grass species composition around mounds (Okullo and Moe 2012b), but once altered communities are established, grazing herbivores maintain and enhance such differences (Okullo and Moe 2012a), contributing to grazing lawn formation (Cromsigt and Olff 2008). Accordingly, the larger grazing lawns throughout the year at Napi are likely a result of increased herbivory here. Positive-feedback loops may then result, with termite activity leading to enhanced grazing which facilitates lawn establishment and causes herbivores to spend more time around mounds, adding nitrogen to the soil through increased levels of dung, further enhancing the nutritional value of the soil and vegetation, and attracting herbivores. Similar positive-feedback loops between mammals and termites have been previously suggested (Freymann et al. 2010, Levick et al. 2010b, Davies et al. 2012) and may be an important contributor to high herbivore densities. Indeed the highest herbivore biomass in my study was recorded at Napi, despite intermediate nutrient levels in the savanna matrix here.

As mounds become more important foraging patches for grazers during the dry season, the sphere of influence (measured with tuft utilization) around them increases at nutrient-rich Skukuza. In contrast, although mound utilization increases at the wet, nutrient-poor site, Pretoriuskop, the sphere of influence and extent into the savanna matrix of significantly enhanced grazing decreases and is in fact smaller during the dry season (8 m) compared to the wet season (16 m). Furthermore, grazing extent is less here than at Skukuza, in contrast to wet season patterns. Mounds at Pretoriuskop are smaller than Skukuza and occur at lower densities (Chapter 2). Such smaller mounds may result in lower rates of soil erosion into the matrix, leading to smaller spheres of influence. Moreover, the smaller mounds result in less nutrient-rich forage growing on them which is likely to be depleted faster than the more abundant forage on the larger Skukuza mounds. Fewer mounds (lower densities) also means less available termite-mound forage overall, forcing herbivores to seek forage in the matrix, resulting in increased matrix grazing and less clear thresholds in utilization between mounds and the matrix. At Skukuza, however, the larger mounds provide more forage, enough to be sustained throughout the dry season, and herbivores are thus able to use them throughout the season. Patch depletion at mounds in nutrient-poor landscapes implies that herbivores here will be more dependent on alternative nutrient-rich patches or must occur at lower densities. Indeed, such nutrient-rich patches have been described as “limited intake resources” that provide highly nutritious food but only in limited abundance (Owen-Smith 2002). Similarly, large savanna trees are important foraging patches for ungulates, but by themselves are not enough to sustain herbivore populations (Treydte et al. 2009). In such nutrient-poor landscapes, nutrient-rich patches are essential (and hence are depleted by the end of the dry season), but not enough to sustain large populations of herbivores, resulting in lower herbivore densities here.

Anisotropic effects

Anisotropy in grazing is most discernible at Napi, the intermediate rainfall site with the highest herbivore biomass. Due to termite mounds being so heavily utilised by herbivores, they are thought to be among the first sites to show signs of environmental degradation and have therefore been suggested as useful monitoring sites (Grant and Scholes 2006). The presence of anisotropy has implications for such monitoring; southern sides of mounds are more intensely grazed and thus would be more useful in monitoring exercises. Furthermore, anisotropy is mostly evident under high herbivore pressure (Napi), and when present may indicate increased herbivory (and potential over-grazing). This is substantiated by an increased trend for southern and eastern sides of mounds at Pretoriuskop (wet, nutrient-poor) been preferentially grazed during the dry season when mounds are under more pressure due to animals becoming nutritionally stressed. When anisotropy is present (at Napi), southern sides of mounds, with increased abundance of *Panicum maximum*, are preferred. *P. maximum* is a shade-loving grass species that is also high in nutrients and favoured by grazers (Treydte et al. 2007). When tall enough, termite mounds will provide shading on their southern slopes, and hence ideal conditions for *P. maximum*. At Pretoriuskop, mounds are shorter (Chapter 2) and likely not tall enough to create such shading effects, with less anisotropy evident in grazing. The tallest mounds are located at the driest site, Skukuza, (Chapter 2) and here *P. maximum* is more abundant on southern slopes and *Cenchrus ciliaris*, a nutritious, palatable grass species that prefers warm, dry areas (van Oudtshoorn 1999), on northern slopes, possibly occluding anisotropic effects. Indeed, there is a trend for increased grazing on northern slopes here during the dry season, likely a result of increased *C. ciliaris* cover.

Insect versus mammalian herbivory

My exclosure results demonstrate that herbivory on mounds (and biomass depletion) cannot be accredited to mammalian herbivores alone, but is rather a composite of insects and mammals. Insects generally receive less attention compared to vertebrates in savanna ecological research (Braack and Kryger 2003), but have been shown to contribute significantly to herbivory (Gandar 1982, Andersen and Lonsdale 1990). In my study, a significant difference between insect and mammalian herbivory was recorded on termite mound treatments only (not in the savanna matrix), demonstrating that insects are preferentially feeding on termite mounds in similar ways to mammals. Indeed, Leitner (2012) recorded higher grasshopper (a dominant insect herbivore) abundance on mounds than off them at the same study sites, likely driving patterns of increased use on mounds. Similarly, Pringle et al., (2010) recorded higher abundance of herbivorous insects on termite mounds in east Africa. Mobæk, et al., (2005) found a wide range of ungulate species and both sexes to preferentially graze on termite mounds despite large differences in body size. My results indicate that such general preferences apply to insects as well as mammals. The lower herbivore pressure in the savanna matrix (by both mammals and insects) results in no differences in herbivory between these groups; differences are only evident under heavy grazing pressure at productive sites.

Conclusion

My findings demonstrate that termite mounds are preferred foraging sites across nutritionally different savanna types and thus enhance the value of savanna landscapes for grazing herbivores. Increased utilisation of mounds also makes them useful for conservation monitoring programmes. The presence of anisotropy should also be considered in such programmes. I further demonstrate that, similar to browsing patterns (Levick et al. 2010b), the influence of *Macrotermes* mounds on savanna grazing patterns extends beyond the mound itself, influencing up to 19% of the landscape. Mounds thus act as keystone structures and contribute significantly to savanna heterogeneity. Cromsigt et al., (2009) suggest that habitat heterogeneity facilitates herbivore diversity and that high levels of heterogeneity may counterbalance effects of landscape fragmentation and declining reserve size. Areas with increased mound densities or larger termite mounds are thus likely to support larger and more diverse populations of both mammalian and insect herbivores and should be incorporated into habitat quality measurements and management objectives.

However, the importance of termite mounds as keystone structures will vary with landscape context (nutritional availability), mound structure (size) and herbivore biomass. In nutrient-rich landscapes mounds are less important, and in even more nutritious landscapes than the ones investigated here they are likely to play an even smaller role. Mound size also affects the relative importance of mounds for herbivore foraging. When mounds are small they are likely to be depleted faster and therefore their importance for sustaining herbivore populations will not persist throughout the year. Joseph et al., (2013a) showed that larger termite mounds support more distinct woody plant assemblages compared to the savanna matrix than smaller mounds. Whether such patterns extend to grasses and thus further influence grazing warrants investigation. Relative herbivore biomass is also of relevance. In areas of very high herbivore biomass (e.g., the Serengeti plains), mounds and other similar sized nutrient-hotspots will be depleted early in the dry season and thus possibly play less of a role in heterogeneity. When conceptualising the role of termite mounds in different savanna ecosystems such factors require consideration. Mounds are likely to be most important in landscapes that are relatively nutrient-poor, and expressly where mounds are large enough to sustain high levels of herbivory throughout the year, as is the case at my intermediate-nutrient site, Napi.

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Appendix 4.1: The top three regression models for grazing intensity that received considerable empirical support ($\Delta_i < 8$) according to the second order Akaike Information Criterion (AIC*c*). The top selected model I used in the final analysis is in bold. Δ_i is the difference between a model's AIC*c* value and that of the model with the lowest AIC*c*; the Akaike weight w_i is the likelihood of a given model's being the best model in the set. For all models, line transect was a random effect nested within termite mound identity.

Rank	Form of regression model	AIC_c	No. parameters	Δ_i	w_i
1	**Site + Distance + Season + Direction + Site*Distance + Season*Distance + Site*Direction + Season*Direction**	**11222.8**	**9**	**0.00**	**0.904**
2	Site + Distance + Season + Direction + Site*Distance + Site*Direction + Season*Direction	11227.8	8	5.07	0.072
3	Site + Distance + Season + Direction + Site*Distance + Season*Distance + Season*Direction	11230.3	8	7.56	0.021

Appendix 4.2: The top three regression models for grazing lawn extent. Only the top performing model received considerable empirical support according to the second order Akaike Information Criterion (AIC*c*). The top selected model I used in the final analysis is in bold. Δ_i is the difference between a model's AIC*c* value and that of the model with the lowest AIC*c*; the Akaike weight w_i is the likelihood of a given model's being the best model in the set. For all models, termite mound identity was a random effect.

Rank	Form of regression model	AIC$_c$	No. parameters	Δ_i	w_i
1	**Site + Time + Direction + Site*Direction + Time*Direction**	**24357.0**	**6**	**0.00**	**1.000**
2	Site + Time + Direction + Site*Direction	24374.5	5	17.54	0.000
3	Site + Time + Direction + Time*Direction	24445.5	5	88.45	0.000

Appendix 4.3: The set of regression models applied for standing biomass on termite mounds in full and partial herbivore exclosures and control sites. Models are ranked according to the second order Akaike Information Criterion (AIC*c*). The top selected model I used in the final analysis is in bold. Δ_i is the difference between a model's AIC*c* value and that of the model with the lowest AIC*c*; the Akaike weight w_i is the likelihood of a given model's being the best model in the set. For all models, termite mound identity was a random effect.

Rank	**Form of regression model**	**AIC$_c$**	**No. parameters**	**Δ_i**	**w_i**
1	**Exclosure treatment + Sampling month + Exclosure treatment * Sampling month**	**1438.1**	**4**	**0.00**	**1.000**
2	Exclosure treatment + Sampling month	1495.4	3	57.27	0.000
3	Exclosure treatment	1521.5	2	83.41	0.000
4	Sampling month	1580.5	2	142.39	0.000
5	Intercept	1606.9	1	168.75	0.000

Appendix 4.4: The set of regression models applied for standing biomass in the savanna matrix in full and partial herbivore exclosures and control sites. Models are ranked according to the second order Akaike Information Criterion (AIC*c*). The top selected model I used in the final analysis is in bold. Δ_i is the difference between a model's AIC*c* value and that of the model with the lowest AIC*c*; the Akaike weight w_i is the likelihood of a given model's being the best model in the set. For all models, termite mound identity was a random effect.

Rank	**Form of regression model**	**AIC_c**	**No. parameters**	**Δ_i**	**w_i**
1	**Exclosure treatment + Sampling month + Exclosure treatment * Sampling month**	**1423.6**	**4**	**0.00**	**1.000**
2	Exclosure treatment + Sampling month	1474.9	3	51.28	0.000
3	Exclosure treatment	1498.3	2	74.75	0.000
4	Sampling month	1510.0	2	86.40	0.000
5	Intercept	1533.8	1	110.19	0.000

Appendix 4.5: Pairwise comparisons of C: N ratio and quantities (mg/kg) of other nutrients across distance transects from termite mounds; data are from all savanna sites pooled. Linear mixed-effects models were applied to the data and following model selection, multiple comparisons of means *post hoc* testing was conducted on the top performing model using Tukey contrasts averaged across interaction terms when present. Bold p values represent significant differences between the distance categories compared (top distance *vs.* bottom distance in the table), italics refer to variable increase with distance (positive z value) and non-italics variable decrease with distance (negative z value).

Nutrient		0 m						1 m				
		1 m	2 m	4 m	8 m	16 m	32 m	2 m	4 m	8 m	16 m	32 m
C: N ratio	z statistic	4.045	6.464	9.111	10.964	12.727	13.611	2.442	5.115	6.985	8.734	9.627
	p value	***< 0.001***	***< 0.001***	***< 0.001***	***< 0.001***	***< 0.001***	***< 0.001***	0.181	***< 0.001***	***< 0.001***	***< 0.001***	***< 0.001***
P (mg/kg)	z statistic	-2.016	-3.745	-4.680	-5.000	-6.143	-7.468	-1.729	-2.663	-2.984	-4.127	-5.452
	p value	0.404	**0.003**	**< 0.001**	**0.001**	**< 0.001**	**< 0.001**	0.596	0.108	**0.045**	**< 0.001**	**< 0.001**
K (mg/kg)	z statistic	2.493	1.574	1.204	0.355	-1.084	-3.800	-0.919	-1.289	-2.138	-3.577	-6.293
	p value	0.162	0.699	0.893	1.000	0.933	**0.003**	0.970	0.857	0.330	**0.006**	**< 0.001**
Na (mg/kg)	z statistic	0.503	0.266	-1.638	-2.803	-3.034	-2.653	-0.236	-2.141	-3.306	-3.537	-3.155
	p value	0.999	1.000	0.657	0.075	**0.039**	0.110	1.000	0.328	**0.017**	**0.008**	**0.027**
Mg (mg/kg)	z statistic	-2.008	-1.997	-2.813	-1.488	-1.789	-2.622	0.010	-0.805	0.520	0.219	-0.614
	p value	0.410	0.416	0.073	0.752	0.555	0.119	1.000	0.985	0.999	1.000	0.996
Ca (mg/kg)	z statistic	-1.104	-2.016	-2.991	-2.719	-1.597	-3.605	-0.912	-1.887	-1.615	-0.492	-2.501
	p value	0.927	0.404	**0.044**	0.093	0.685	**0.006**	0.971	0.489	0.673	0.999	0.159
Zn (mg/kg)	z statistic	-3.778	-3.958	-6.294	-5.819	-6.841	-6.870	-0.181	-2.517	-2.041	-3.064	-3.092
	p value	**0.003**	**0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	1.000	0.153	0.389	**0.036**	**0.033**

Al (mg/kg)	z statistic	-1.583	-2.702	-3.339	-2.298	-2.906	-2.770	-1.119	-1.757	-0.716	-1.324	-1.188
	p value	0.694	0.098	**0.015**	0.245	0.057	0.082	0.923	0.578	0.992	0.841	0.899
Cu (mg/kg)	z statistic	-1.790	-2.186	-5.545	-4.506	-5.260	-6.331	-0.396	-3.755	-2.716	-3.470	-4.540
	p value	0.554	0.303	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	1.000	**0.003**	0.094	**0.009**	**< 0.001**
Fe (mg/kg)	z statistic	-1.237	-1.886	-3.012	-1.717	-2.459	-2.631	-0.649	-1.776	-0.481	-1.222	-1.395
	p value	0.880	0.490	**0.042**	0.604	0.175	0.117	0.995	0.565	0.999	0.886	0.805
Mn (mg/kg)	z statistic	2.466	2.261	2.006	3.630	4.239	3.586	-0.205	-0.461	1.164	1.773	1.119
	p value	0.171	0.263	0.411	***0.005***	***< 0.001***	***0.006***	1.000	0.999	0.908	0.567	0.922
S (mg/kg)	z statistic	-3.742	-6.066	-10.813	-11.240	-11.110	-13.156	-2.324	-7.071	-7.501	-7.373	-9.414
	p value	**0.003**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.233	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**

Nutrient		2 m				4 m			8 m		16 m
		4 m	8 m	16 m	32 m	8 m	16 m	32 m	16 m	32 m	32 m
C: N ratio	z statistic	2.673	4.543	6.273	7.165	1.870	3.579	4.471	1.693	2.586	0.905
	p value	0.105	***< 0.001***	***< 0.001***	***< 0.001***	0.500	***0.006***	***< 0.001***	0.621	0.130	0.972
P (mg/kg)	z statistic	-0.934	-1.254	-2.398	-3.723	-0.320	-1.463	-2.789	-1.143	-2.469	-1.325
	p value	0.967	0.873	0.200	**0.004**	1.000	0.767	0.078	0.915	0.170	0.840
K (mg/kg)	z statistic	-0.370	-1.220	-2.658	-5.375	-0.849	-2.288	-5.004	-1.438	-4.155	-2.717
	p value	1.000	0.887	0.110	**< 0.001**	0.980	0.250	**< 0.001**	0.781	**< 0.001**	0.094
Na (mg/kg)	z statistic	-1.905	-3.070	-3.301	-2.919	-1.165	-1.396	-1.014	-0.231	0.151	0.382
	p value	0.477	**0.035**	**0.017**	0.055	0.907	0.804	0.951	1.000	1.000	1.000

Mg (mg/kg)	z statistic	-0.815	0.510	0.208	-0.625	1.325	1.024	0.191	-0.301	-1.134	-0.833
	p value	0.983	0.999	1.000	0.996	0.840	0.949	1.000	1.000	0.918	0.982
Ca (mg/kg)	z statistic	-0.975	-0.703	0.419	-1.589	0.272	1.394	-0.614	1.123	-0.886	-2.009
	p value	0.959	0.992	1.000	0.689	1.000	0.805	0.996	0.921	0.975	0.409
Zn (mg/kg)	z statistic	-2.336	-1.860	-2.883	-2.912	0.476	-0.547	-0.576	-1.023	-1.051	-0.029
	p value	0.226	0.507	0.060	0.056	0.999	0.998	0.997	0.949	0.942	1.000
Al (mg/kg)	z statistic	-0.638	0.403	-0.205	-0.069	1.041	0.433	0.569	-0.608	-0.472	0.136
	p value	0.996	1.000	1.000	1.000	0.945	1.000	0.998	0.997	0.999	1.000
Cu (mg/kg)	z statistic	-3.359	-2.320	-3.074	-4.144	1.039	0.285	-0.785	-0.754	-1.825	-1.070
	p value	**0.014**	0.235	**0.035**	**< 0.001**	0.945	1.000	0.986	0.989	0.531	0.937
Fe (mg/kg)	z statistic	-1.127	0.168	-0.573	-0.746	1.295	0.554	0.381	-0.741	-0.914	-0.173
	p value	0.920	1.000	0.998	0.990	0.855	0.998	1.000	0.990	0.971	1.000
Mn (mg/kg)	z statistic	-0.255	1.369	1.978	1.325	1.625	2.233	1.580	0.609	-0.044	-0.653
	p value	1.000	0.818	0.429	0.840	0.666	0.277	0.695	0.997	1.000	0.995
S (mg/kg)	z statistic	-4.747	-5.177	-5.049	-7.090	-0.429	-0.301	-2.343	0.128	-1.914	-2.042
	p value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	1.000	1.000	0.223	1.000	0.471	0.388

Appendix 4.6: Pairwise comparisons of C: N ratio and quantities (mg/kg) of other nutrients across savanna sites; data are from all distance categories pooled. Linear mixed-effects models were applied to the data and following model selection, multiple comparisons of means *post hoc* testing was conducted on the top performing model using Tukey contrasts averaged across interaction terms when present. Bold p values represent significant differences between the sites compared (base level *vs.* site compared). Na, Ca and Fe are not included because site was not an important variable in the top performing model for these nutrients.

Nutrient	Site (base level)	Skukuza		Pretoriuskop
	Site compared	Napi	Pretoriuskop	Napi
C: N ratio	z statistic	-3.545	-4.287	0.875
	p value	**0.001**	**<0.001**	0.656
P (mg/kg)	z statistic	-0.328	3.356	-3.684
	p value	0.943	**0.002**	**<0.001**
K (mg/kg)	z statistic	5.016	3.780	1.235
	p value	**<0.001**	**<0.001**	0.432
Mg (mg/kg)	z statistic	4.530	7.534	-3.004
	p value	**<0.001**	**<0.001**	**0.007**
Zn (mg/kg)	z statistic	0.663	4.438	-3.775
	p value	0.785	**<0.001**	**<0.001**
Al (mg/kg)	z statistic	3.579	2.861	0.719
	p value	**<0.001**	**0.012**	0.752
Cu (mg/kg)	z statistic	3.736	2.383	1.354
	p value	**<0.001**	**0.045**	0.366
Mn (mg/kg)	z statistic	1.201	-1.918	3.122
	p value	0.451	0.133	**0.005**
S (mg/kg)	z statistic	2.068	2.495	-0.427
	p value	0.097	**0.034**	0.905

Appendix 4.7: Heavily grazed *Macrotermes* mound, depicting a) an example of the grazing lawns measured during the study, and b) the definite boundaries between grazing lawn and savanna matrix.

a)

b)

Chapter 5

Interactive effects of fire, rainfall and litter quality on decomposition in savannas: frequent fire leads to contrasting effects

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Abstract

One of the many ecological processes expected to undergo alteration due to global change is the decomposition of organic matter, with little known concerning the effects that changing disturbance regimes may have. Fire, a critical process in many habitats, is expected to become more common. I measured the decomposition rates of four grass species that differed in litter quality, investigating them under different fire regimes across a savanna rainfall gradient in South Africa. I also collected data on the abundance and activity of fungus-growing termites and recorded measurements of temperature and canopy cover. Overall, decomposition rate followed global models, increasing under warmer and wetter conditions. Litter quality was also significant with higher quality grasses decomposing faster; however, this effect was less pronounced than expected. Fire regimes did not have a consistent effect on decomposition rate along the rainfall gradient. In the most arid savanna type examined, fire had no effect, whereas in the intermediate-rainfall savanna burning increased decomposition rate under higher levels of fungus-growing termite activity. In the wetter savannas, fire slowed decomposition, possibly through modification of vegetation structure and potential effects on other invertebrates. Our results demonstrate that grass decomposition in African savannas varies significantly along precipitation gradients, with different factors becoming influential in different habitats. Importantly, I demonstrate that fire does not always act to slow decomposition and that it interacts with other factors to influence the process. These findings have important implications for decomposition in the light of global change models that predict wetter climates and a higher frequency of fires for southern African savannas.

Keywords: burning; crude protein content; disturbance; global change; grass decomposition; mean annual precipitation; termites

Introduction

Understanding how ecosystem functioning will be affected by global change has attracted much interest and concern. One function likely to change considerably is the decomposition of organic matter, a critical ecological process essential for nutrient cycling (Swift and others 1979; Sayer 2006), in particular for returning carbon fixed by plants during photosynthesis to the atmosphere (Schimel and others 1996; Hättenschwiler and others 2005). Much literature exists examining how litter decomposition varies with, and is driven by, climate (Couteaûx and others 1995; Taylor and others 2004), however far less well understood is how changes in the frequency of disturbance phenomena, such as fire, will affect the process (Brennan and others 2009).

Fire is a widespread disturbance in many ecosystems across the globe (Chapin and others 2002), where it acts to alter vegetation structure and composition (Bond and Keeley 2005), nutrient cycling (Van de Vijver and others 1999) and aboveground net primary productivity (Buis and others 2009). Effects of fire on ecosystem functioning therefore cannot be ignored and changing fire regimes may be even more influential than the direct effects of a changing climate (Flannigan and others 2000; Brennan and others 2009). However, the influence of fire on many ecological dynamics and processes, ranging from biodiversity (Parr and Chown 2003; Davies and others 2010) to ecosystem functioning (Bond and others 2005) is thus far poorly understood.

It is generally accepted that in many fire-prone biomes across the globe the frequency of fires will increase under global climate change. This due to, among other things, an increase in fuel load and aridity caused by increasing CO_2 and temperature levels, decreasing rainfall and relative humidity (Hughes 2003), and an increase in lighting strikes in some areas (Goldammer and Price 1998; Cary 2002). Furthermore, more frequent fires are expected as a result of increasing human populations in many parts of the world (Williams and others 2009). This suggests that a clearer understanding of how fire affects important ecosystem functions, such as decomposition, is necessary if we are successfully to anticipate and mitigate effects of future global change (Krawchuk and others 2009).

The main direct agents of decomposition are decomposer organisms: predominantly fungi, bacteria, and soil/litter invertebrates, although some breakdown of dead plant material is caused by photodegradation. At global scales, the rate of decomposition by these decomposer agents is principally mediated by climate (rainfall and temperature), and secondarily litter quality (chemical composition) (Lavelle and others 1993; Couteaûx and others 1995; Aerts 1997). Decomposition is thought to be predominantly a microbial process, with important contributions made by invertebrates when conditions are suitable, with climate creating the conditions (temperature and moisture levels) under which decomposition occurs. Under extremes of temperature and moisture, decomposition takes place slowly because microbial communities are sensitive to such extremes (becoming inactive under unfavourable conditions) (Couteaûx and others 1995). Litter quality defines how important the substrate material is to the microbial community (Murphy and others 1998) and hence influences the rate of decomposition. Soil/litter animals, when they are relatively abundant, in turn enhance decomposition through direct consumption of dead plant material, litter comminution and soil mixing, increasing surface area for microbes and bringing them into contact with litter (Couteaûx and others 1995). However, faunal communities are even more constrained than microbial communities by climatic factors and litter quality, and are therefore often only considered important in ecosystems that are unconstrained by temperature and moisture availability (Lavelle and others 1993; Wall and others 2008). Furthermore, because most decomposition models assume that all decomposition is microbial, they focus solely on climate and litter quality (Meentemeyer 1978; Rastetter and others 1991; Gholz and others 2000), with little regard to other factors such as soil animals and disturbance phenomena.

At local and regional scales other factors have been shown to have a significant influence on decomposition (Wall and others 2008; Powers and others 2009). These factors include soil animals (Whitford and others 1982; Schuurman 2005), photodegradation in arid regions (Austin and Vivanco 2006; Brandt and others 2010; Austin 2011), litter type interactions (Hättenschwiler and Gasser 2005), and the “home-field advantage” hypothesis, whereby litter decomposes faster under cover of the same species it is derived from (e.g. Ayres and others 2009). At such regional scales, disturbances such as fire may also play an important role through interactions with other mediating factors. Several studies have shown that frequent burning slows decomposition rates through a variety of mechanisms. In *Eucalyptus* forest, Brennan and others (2009) attributed slower rates of decomposition to negative effects of frequent fire on invertebrate decomposer abundance, while in seasonal Amazonian forest repeated burning was thought to have slowed decomposition rates through altered micro-climatic conditions (particularly by increasing temperature and decreasing relative humidity, resulting in a drier environment) (Silveira and others 2009). Other potential mechanisms include interactions with herbivory (Kay and others 2008), and long-term alterations of litter quality by fire (Hernández and Hobbie 2008).

The majority of decomposition studies (both global and regional) have taken place in forested areas, with fewer in grassy biomes, despite these biomes being globally dominant habitats (Bond and Parr 2010). The few decomposition studies from grassy systems have shown that drivers vary regionally, with, for example, photodegradation playing larger roles in arid than mesic regions (Brandt and others 2010). Tian and others (2007) measured decomposition as a function of climate and litter quality along a rainfall gradient from rainforest to the Sahel in west Africa (including grassy systems) and found the two factors to interact in their influence: high quality grasses decomposed more rapidly in wetter environments while low quality grasses decomposed faster in dry areas. They attributed this effect to higher termite abundance and increased photodegradation in arid regions.

Decomposition work in savannas (which extend over more than half the African continent and range from mesic, humid habitats to semi-arid ones (Scholes and Archer 1997)) has also demonstrated the important role played by soil fauna, in particular termites (Ohiagu and Wood 1979; Collins 1981; Schuurman 2005; Freymann and others 2010; Buitenwerf and others 2011). However the lack of published studies across environmental gradients, particularly in relation to potential effects of disturbance phenomena such as fire on decomposition, means decomposition processes in African savannas remain poorly understood. In the current study, grass decomposition rates were investigated along environmental gradients in southern African savannas. I examined differences in decomposition rates at four sites along an extended rainfall gradient during two seasons to (1) investigate the influence of climate; (2) litter quality and (3) long-term fire regimes, on decomposition, including how fire interacts with climate and litter quality. To explore potential mechanisms underlying the effects of fire, I collected data on the abundance and activity of a major decomposer animal group (fungus-growing termites) as well as other explanatory variables that have previously been shown to be important (temperature and canopy cover). While I was unable to tease apart the direct mechanisms of the patterns observed based on my data, I do suggest testable hypotheses for the main factors influencing decomposition across the rainfall gradient.

In line with global models, I expected to find faster rates of decomposition in wetter savannas and during the wet season due to increased temperatures and moisture availability favouring microbial communities and soil animals. I also expected high quality grasses to decompose faster, irrespective of climate, as soil animals and microbes would be better able to break them down. The effect of frequent burning was expected to decrease decomposition rates through interactions with other mediating factors such as decomposer organisms and microclimatic conditions, as found in previous studies (see for e.g. Brennan and others 2009; Silveira and others 2009); but this effect was expected to interact with mean annual precipitation, being more influential in wetter areas where fire effects are more noticeable (see for e.g. Parr and others 2004; Davies and others 2012).

Methods

Study site

The experiment was undertaken in four distinct savanna types across two of South Africa's major reserves: Kruger National Park (KNP, 22° 25' - 25° 32' S; 30° 50' - 32° 02' E) and Hluhluwe-iMfolozi Park (HiP, 28° 01' - 28° 25' S; 32° 15' - 32° 26' E). These sites are spread over a distance of *ca.* 700 kilometres and are situated along a rainfall gradient from 450 $mm.yr^{-1}$ in the north to 900 $mm.yr^{-1}$ in the south. The two parks are located in the eastern part of South Africa and have a sub-tropical climate with a distinct summer rainfall pattern.

The four savanna types, in ascending order of mean annual rainfall, were: *Colophospermum mopane* savanna (Mopani, northern KNP, 450 mm mean annual precipitation (MAP)), *Acacia* savanna (Satara, central KNP, 550 mm MAP), *Terminalia* savanna (Pretoriuskop, southern KNP, 750 mm MAP) and mesic *Acacia* savanna (Hluhluwe, northern HiP, 900 mm MAP). Sampling in KNP was carried out on a series of long-term experimental burning plots; enabling me to test for effects of long-term burning regimes on decomposition rates. Because no such formal burning experiment exists in HiP, fire map records were used to identify sites in the landscape with fire histories that, as best as possible, match those of the burn plots utilised in KNP (i.e., areas burnt with low and high fire frequency). Six replicated sampling plots (except for Hluhluwe where four plots were used) were selected from within each of the four savanna habitats. Of these six plots, three in each savanna type have been burnt on a triennial basis during the late dry season (August) since 1954 and the other three have remained essentially unburnt for the same time period. Each plot is approximately 7 ha in size and protected from outside fires by a double fire break. The plots are located within a string of other plots subjected to different fire regimes, thus in my study, each burnt plot is paired to an unburnt one, with such pairs spaced 10 – 20 km apart (for more information on this fire experiment see Biggs and others 2003). The plots at Satara and Pretoriuskop are on the same burning cycle, while Mopani is a year ahead, meaning that plots at Mopani were burnt a year earlier. At Hluhluwe, reliable estimates of time-since-fire are difficult to obtain. However, previous work (Parr and others 2004; Radford and Andersen 2012) has shown that time-since-fire is only relevant for the first few months, after this vegetation regrows and differences disappear. Thus time-since-fire was not considered as important for this study as the burning regime.

Grass species, litter collection and treatment

Four grass species of differing quality were used in the study (Table 5.1). Grass quality was measured according to crude protein content and general palatability. Crude protein is known to be necessary for many ungulates to maintain normal physiological functions (Bowers 2006), and although its importance for invertebrates and microbes involved in decomposition is less clear, it does provide a general estimate of litter quality (Radford and Andersen 2012). The four selected grass species can be ranked on a gradient of litter quality by their crude protein content and palatability: (1) *Urochloa mosambicensis* (highest quality), (2) *Cenchrus ciliaris*, (3) *Themeda triandra* and (4) *Cymbopogon excavatus* (lowest quality) (Table 5.1).

Table 5.1: Estimates of percentage crude protein content and palatability of the four grass species used in this study. The species represent a gradient of litter quality from low (*C. excavatus*) to very high (*U. mosambicensis*).

Grass species	**Crude protein content (%)**	**Palatability**
Cymbopogon excavatus	6.19[a]	Poor[b,c,d,e]
Themeda triandra	6.90[a], 5.3 – 10.4[b]	Moderate[c,d,e] - High[b]
Cenchrus ciliaris	12.00[a], 7.4 – 12.27[b]	High[b,c,e]
Urochloa mosambicensis	13.83[a], 10 – 20[b]	Very high[b,e]

References: a – Bowers 2006; b - Survey of economic plants for arid and semi-arid lands (SEPASAL) database (1999); c – Macandza and others 2004; d – Fourie and others 1985; e – van Oudtshoorn 1999

Plant material was harvested from KNP during May 2008 for the dry season experiment and January 2010 for the wet season experiment. As far as possible each species was harvested from the same location to minimise variation in chemical composition between samples. After harvesting, grass material was cut into segments of approximately 5 cm, mixing stems, inflorescences, green and dried leaves, and placed in brown paper bags. The material was then taken to the laboratory and dried at 60° C for 48 hours. After drying, 8 – 10 grams of grass material was placed in individually numbered litter bags, measuring 200 mm x 200 mm, constructed from aluminium mesh with a mesh size of approximately 2 mm x 2 mm. This material allowed enlargement of the holes relatively easily to aid access by soil animals such as the larger termite genera. Each bag was then placed in the field, using a nail at opposite corners to secure it to the ground. During each placement the ground surface was cleared of grass or leaf litter to ensure the bag was in direct contact with the soil. For the dry season experiment, bags were placed during the austral winter in June 2008 and for the wet season experiment, placement was during the austral summer in January 2010.

Experimental design

Litter bags were placed in sets of four during the dry season when decomposition was expected to be slower, and three during the wet season. At monthly intervals, one bag from each set was removed with minimal disturbance to the surrounding bags, hence the experiment lasted four months during the dry season and three months during the wet season when decomposition was expected to be faster. Each set consisted of bags containing the same species placed adjacent to each other. These sets (of either four or three bags depending on the season) were placed on the experimental burning plots in a grid formation of six by four sets (24 sets per plot). Each set was spaced 10 metres apart. Species sets of bags were alternated so that at no point were two sets of the same species adjacent to each other in the grid. There were therefore 96 bags on each plot during the dry season (n = 2112) and 72 bags per plot in the wet season (n = 1584), with six bags from each grass species collected each month (24 bags collected per month).

After collection, the litter bags were placed in paper bags and taken to the laboratory where they were oven dried for 48 hours at 60° C. Many bags were sufficiently dry during the dry season and hence drying in an oven was not necessary, however, all wet season samples and dry season samples where moisture was present, were dried. After drying, all material was removed from the bags and the grass was manually separated from any foreign plant material, soil or gallery material taken into the bags by termites. Following this, the grass was weighed and the amount remaining measured.

Additional biotic and environmental measurements

In addition to measuring decomposition rate with litter bags, I collected data on fungus-growing termite (a major invertebrate decomposer in African savannas) abundance and activity using cellulose baits. During the wet season, when termites are more active (Dawes-Gromadzki and Spain 2003; Davies 2010), 40 toilet rolls (baits) were placed on each experimental plot in an eight by five grid formation. Half (20) of these baits were buried 2 cm below the ground and the other half placed on the surface, secured with an aluminium tent peg and wrapped with tape to prevent unravelling (La Fage 1973). At pre-determined time intervals of 5, 14, 28 and 56 days after placement, baits (five buried and five surface at each sampling interval) were removed and inspected for termites. Abundance of termites per plot was defined as the number of termite encounters, with a single encounter defined as one attacked bait (due to difficulties in counting all the termites at a particular bait). The intensity of termite foraging activity was assessed by assigning each bait a score based on the intensity of termite attack, following Dawes-Gromadzki (2003): 0 = no evidence of attack, 1 = 1 – 24% of bait consumed, 2 = 25 – 49% consumed, 3 = 50 – 74% consumed, 4 = 75 – 99% consumed and 5 = bait completely consumed. Hourly temperature readings were also recorded in each savanna site for burnt and unburnt sites using Thermochron iButtons® (Maxim/Dallas Semiconductor Corp., USA) placed approximately 2 cm below the soil surface. Finally, canopy cover on each experimental burn plot was estimated during the wet season by placing twenty 1x1 metre quadrats in a grid of five by four quadrats in the centre of each plot and visually estimating canopy cover above each quadrat.

Data analysis

The amount of grass remaining in each bag after collection was used to calculate the decomposition constant *k* assuming the exponential decomposition model (Olson 1963), i.e.

$$W_t = W_0 e^{-kt}$$

where W_0 is the amount of grass at the start of the experiment and W_t the amount of grass at time *t*. In this case I calculated the constant *k* with the unit month^{-1} and it was calculated for each litter bag for each month. This variable was then used for the statistical analysis.

In order to avoid spatial autocorrelation, litter bags from each species from each plot were pooled to produce a mean organic mass remaining at collection for each experimental plot per grass species. The decomposition rates in relation to potential explanatory variables (mean annual precipitation (hereafter referred to as precipitation), season, litter quality and fire regime) and the interactions between them were then analysed using a generalised linear model (GLM), corrected for overdispersion, with a Poisson error distribution and log-link function. Model fit was assessed for goodness of fit, homogeneity of variance and normality of residuals using model-checking plots (observed *vs.* fitted values, residuals *vs.* fitted values, QQ plots, scale-location plots and residual-leverage plots).

Differences in termite abundance and intensity of termite attack across the two fire regimes in each savanna site were assessed with Wilcoxon signed-rank tests. In order to compare differences in recorded hourly temperature, Student's t tests were applied. Differences in canopy cover across fire regimes were compared with Wilcoxon signed-rank tests. All statistical analyses were performed in the software package R, version 2.11.1 (R development core team 2010).

Results

Variation along climatic and litter quality gradients

The GLM revealed that precipitation, season and litter quality had a significant effect on the decomposition constant (*k*) recorded, and hence on the rate of grass decomposition (Table 5.2). Overall, my recorded rates were very slow, with decomposition being the slowest at the driest site (Mopani) and the most rapid at the wettest site (Hluhluwe); this was the case for all grass species (Figs. 5.1, 5.2). Decomposition rates were intermediate at Satara (semi-arid to intermediate precipitation) and Pretoriuskop (intermediate to higher precipitation), although the decomposition rate of the highest quality grass (*U. mosambicensis*) was similar at Satara and Hluhluwe (Figs. 5.1, 5.2). Compared with the dry season, decomposition proceeded significantly more rapidly during the wet season, and differences between savanna site and grass species were easier to detect during this season (Table 5.2, Figs. 5.1, 5.2). In all savanna types and both seasons, *U. mosambicensis* decomposed the fastest and there was a trend of increased decomposition with increasing precipitation (Figs. 5.1, 5.2). *C. excavatus* was the second most removed species, although removal was markedly less than *U. mosambicensis*.

The interaction between precipitation and season was close to significant ($p = 0.08$), indicating that season had a stronger effect on decomposition under some precipitation regimes (i.e. savanna types) than others (Table 5.2). This stronger effect was evident at the intermediate to high rainfall savannas while at the driest savanna (Mopani) seasonal effects were not present (Figs. 5.1, 5.2). Similarly, the interaction between precipitation and litter quality was significant (Table 5.2), meaning that the rate at which certain grass species decomposed relative to the others depended on the precipitation regime. This is clear when *U. mosambicensis* is considered: it decomposed at a similar rate to the other grass species at

Mopani (the driest site) but at much faster rates at all other savanna sites (Figs. 5.1, 5.2). The interaction between litter quality and season was also significant (Table 5.2), which is most likely because the litter that does not decay rapidly in the wet season (*T. triandra* and *C. ciliaris*) does not decompose any slower in the dry season. However, the litter that decomposed faster in the wet season (especially *U. mosambicensis*) decomposed much more slowly in the dry season, hence the significant interaction term (Figs. 5.1, 5.2). Therefore, different seasonal effects for different grass litter types are present, but are driven by the low quality grasses displaying no clear seasonal patterns, rather than high quality litter which do.

Table 5.2: Statistical (GLM) analysis of decomposition rate (*k* values) in relation to the fixed factors precipitation, season, litter quality and fire regime. Asterisks (*) signify statistical significance, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Factor	*df*	*F*	*P*
Precipitation	3	42.92	<0.0001***
Season	1	42.23	<0.0001***
Litter quality	3	52.99	<0.0001***
Fire regime	1	0.87	0.3523
Precipitation x Season	3	2.23	0.0840
Precipitation x Litter quality	9	1.94	0.0449 *
Precipitation x Fire regime	3	10.10	<0.0001***
Season x Litter quality	3	24.09	<0.0001***
Season x Fire regime	1	1.30	0.2552
Litter quality x Fire regime	3	4.83	0.0025 **
Precipitation x Season x Litter quality	9	1.41	0.1819
Precipitation x Season x Fire regime	3	0.92	0.4288
Precipitation x Litter quality x Fire regime	9	0.86	0.5617
Season x Litter quality x Fire regime	3	1.37	0.2499
Precipitation x Litter quality x Season x Fire regime	9	0.81	0.6092

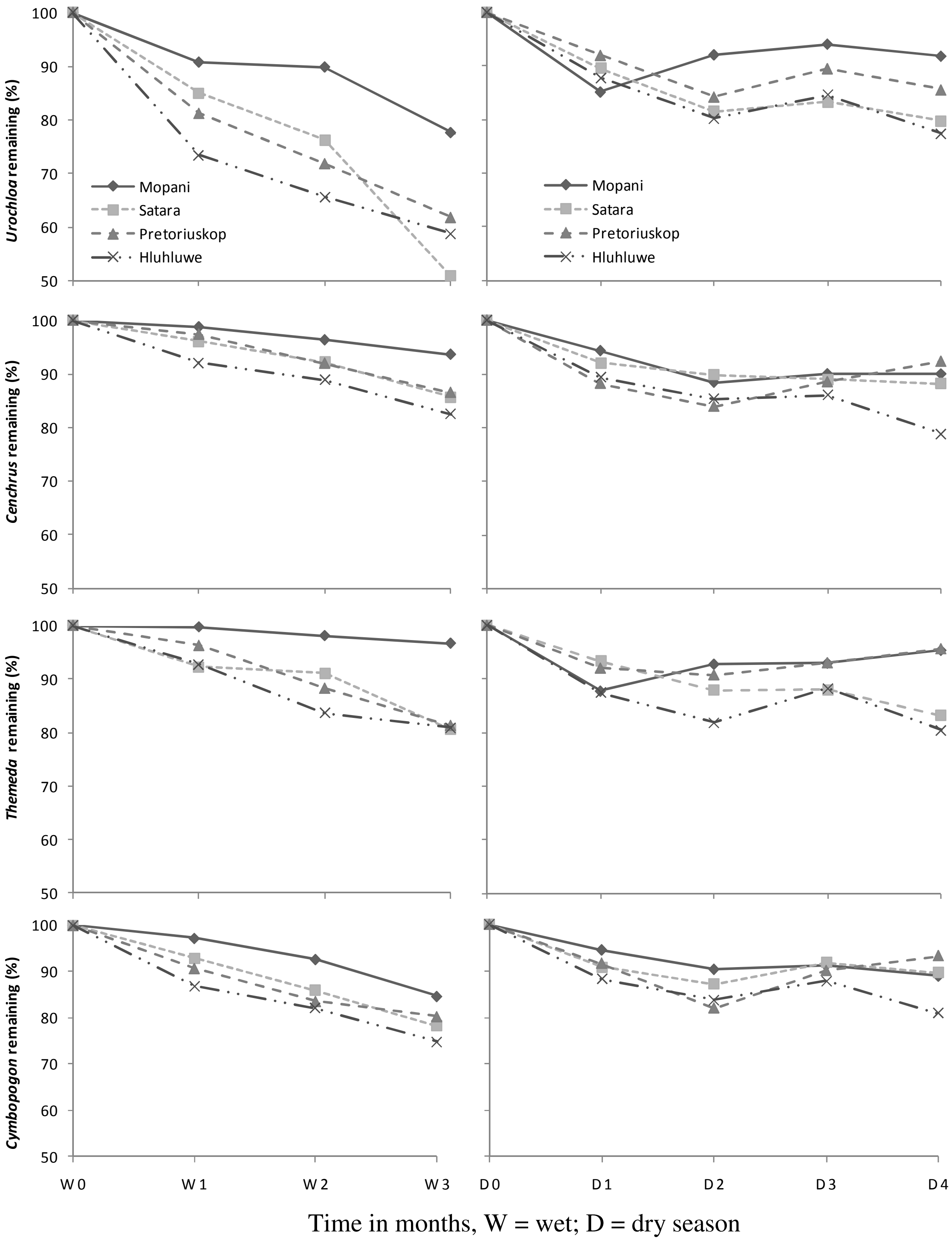


Figure 5.1: Mass loss of four grass species measured as a percentage of litter remaining across four savanna types and two seasons (left: wet, right: dry season). Savanna types are arranged along a gradient of increasing mean annual precipitation. Standard error bars are smaller than data points. Data points are joined by lines for reader convenience only and do not reflect a time sequence, each point rather indicating an independent sampling event.

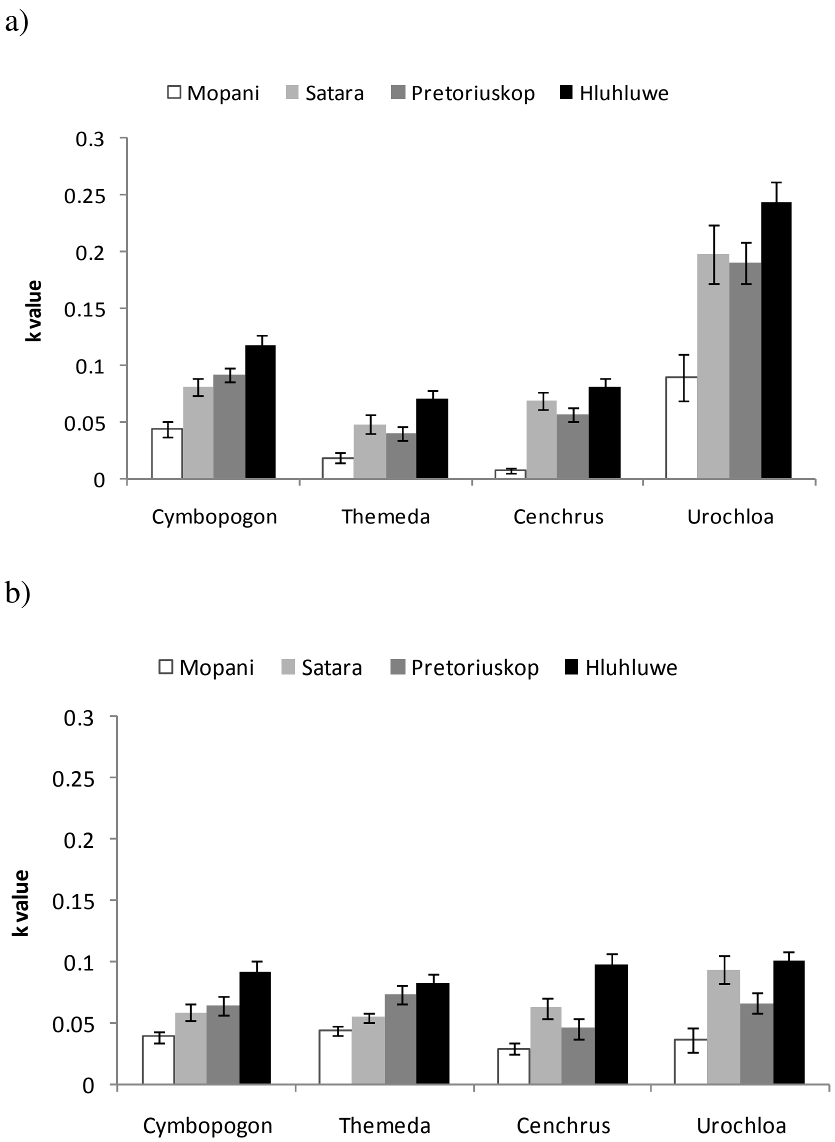


Figure 5.2: Mean (± SE) decomposition constants (*k*) for four grass species (x-axis) across four savanna types in South Africa during a) the wet and b) the dry season. Savanna types are arranged along a gradient of increasing mean annual precipitation.

Effects of fire regime on decomposition

Although the GLM showed that overall fire regime did not have a significant effect on decomposition rates (all grass species and precipitation regimes combined), there were significant interactions between fire and precipitation, i.e. savanna site, and fire and litter quality (Table 5.2). Thus, fire regime (triennially burnt *vs.* long unburnt) affects decomposition rates at some savanna sites, but not others, and also affects decomposition rates of some grass species but not others. Decomposition rates were higher on unburnt plots in the wet savannas for some grass species at Pretoriuskop and all species at Hluhluwe, while the opposite was recorded in the intermediate-arid savanna, Satara: here there were significantly faster rates of decomposition on burnt sites (Fig. 5.3) for *U. mosambicensis* (and to a lesser extent *C. excavatus*). At the most arid site (Mopani), no differences were recorded.

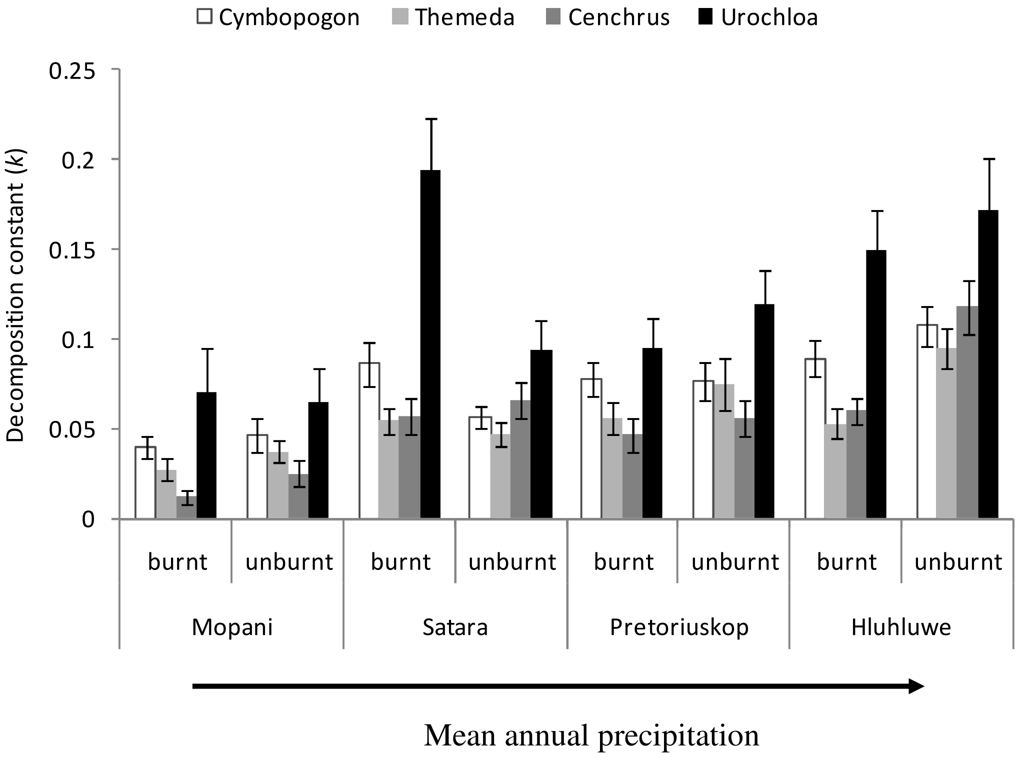
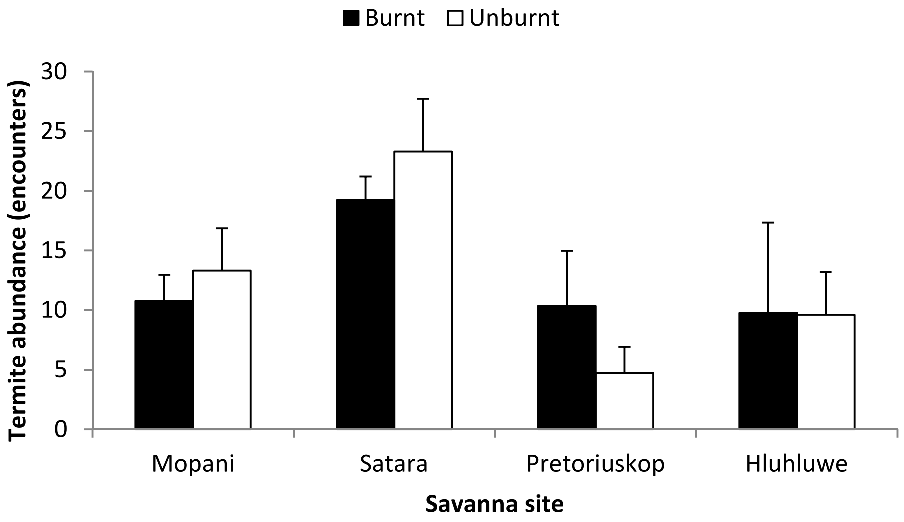


Figure 5.3: Mean (± SE) decomposition constants (*k*) of four grass species across four savanna types in South Africa on sites which were either burnt triennially (burnt) or remained unburnt (unburnt) for *ca.* 57 years. Data are for both the wet and dry seasons combined. Savanna types are arranged along a gradient of increasing mean annual precipitation.

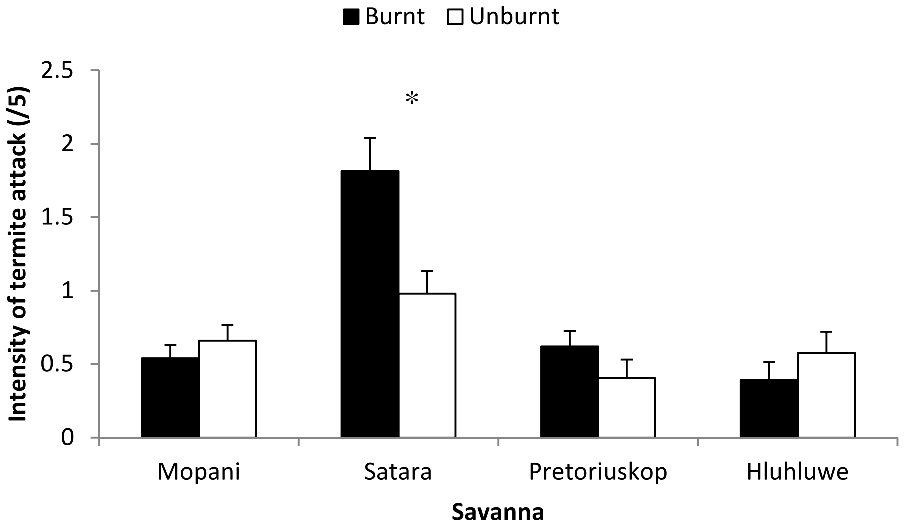
Additional biotic and environmental measurements

Termite abundance did not differ significantly across burning regimes in any of the savanna types (Fig. 5.4a). However, intensity of termite attack was significantly higher ($W = 9.75$, $p < 0.05$) on burnt sites at Satara (intermediate-arid savanna), but did not differ significantly in any other savanna type (Fig. 5.4b). Hourly temperature differed significantly between fire regimes at all sites except Pretoriuskop (Mopani: $t = -5.63$, $p < 0.001$; Satara: $t = -8.12$, $p < 0.001$; Pretoriuskop: $t = -0.39$, $p = 0.70$; Hluhluwe: $t = 6.15$, $p < 0.001$). At the dry sites (Mopani and Satara) temperatures were higher on burnt sites while at the wettest site (Hluhluwe), higher temperatures were recorded on unburnt sites (Fig. 5.4c). Canopy cover differed significantly only at Pretoriuskop (a wet savanna) with greater cover on unburnt sites (W = 1318, $p < 0.001$, Fig. 5.4d).

a)



b)



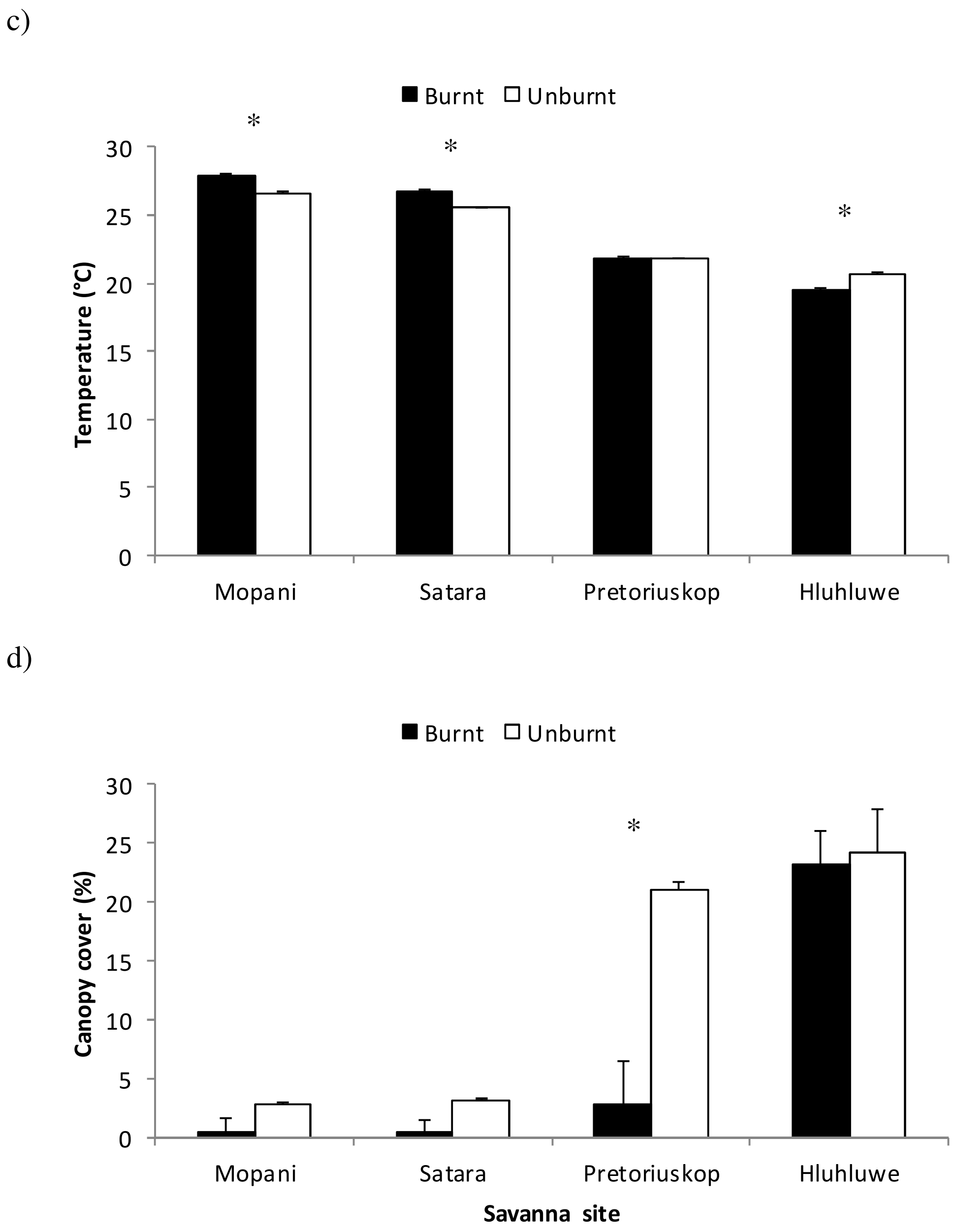


Figure 5.4: Mean (± SE) a) termite abundance recorded with cellulose baits, b) intensity of termite attack at cellulose baits, c) temperature recorded hourly and d) canopy cover at burnt and unburnt sites in four savanna types. Sites are arranged along a gradient of increasing mean annual precipitation. An asterisk denotes a significant difference between fire regimes at each site.

Discussion

A striking finding from my study is the mostly very slow rates of absolute decomposition recorded for grass litter. Although such slow rates could be attributable to the relatively short temporal scale of my study (following the exponential decay model (Olson 1963)), they do reflect patterns for low quality (i.e. highly refractory) grass decomposition. Such slow turnover rates will result in organic matter persisting in the system for a long time: this underscores the importance of single fire events for removal of dead grass and litter in savannas, particularly in the dry season when decomposition is particularly slow.

Decomposition along the rainfall and litter quality gradients

My results generally support global decomposition models that suggest climate and litter quality have a dominant effect on the agents of decomposition and therefore decomposition rates (Meentemeyer 1978; Lavelle and others 1993; Couteaûx and others 1995; Gholz and others 2000). Faster rates of decomposition were recorded at the wet sites (Pretoriuskop and Hluhluwe), which is in line with predictions. Similarly, decomposition during the wet season was generally faster at all savanna sites and for all grass species. These results point to an overarching influence of climate over the agents of savanna decomposition, with higher levels of mean annual precipitation, and hence moisture, as well as higher temperatures during the summer wet season, leading to increased decomposition rates. In addition, faunal decomposers, such as earthworms and termites, are sensitive to moisture and temperature levels (Smith and Rust 1994; Curry 1998), becoming less active in cold and dry environments. They are consequently more active during the wet season (Garnsey 1994; Dawes-Gromadzki and Spain 2003; Davies 2010). Warmer and wetter areas (as well as the wet season) are therefore more conducive to high decomposer diversity and activity, potentially contributing to faster rates of decomposition in such areas and seasons.

An exception, however, to this climate driven model of decomposition is my recorded rates at Satara, a semi-arid savanna receiving intermediate rainfall. Here decomposition proceeded at similar rates comparable, or even faster in some cases, to Pretoriuskop, a savanna receiving markedly more rainfall. Although not explicitly tested for, a plausible explanation is that this unexpectedly higher rate of decomposition may be due to higher abundance of fungus-growing termites at Satara (Fig. 5.4a, Davies and others 2012). Fungus-growing termites have been shown to be important decomposers in savannas (Collins 1981; Holt and Coventry 1990), contributing up to 60% of wood litter removal (Collins 1981). Indeed Schuurman (2005) found that in a semi-arid Botswana savanna with similar annual rainfall to Satara, variation in fungus-growing termite abundance was the only factor affecting decomposition rates, and hence the potentially important role they play as decomposers in these savannas cannot be ignored. Although no direct data on termite decomposition are available for this study, given that other studies have highlighted the importance of termites in African savannas, I hypothesise that the higher than expected decomposition rates at Satara are suggestive of a termite mediated role. Future research testing more explicitly the role of termites in savanna decomposition is, however, necessary.

Overall differences in decomposition rates between grass species (litter quality) partially followed my predictions. The highest quality grass, *U. mosambicensis*, (i.e., with the highest crude protein content) decomposed fastest in all savanna types. However, the decomposition rate of *C. excavatus*, the species considered to have the lowest litter quality for my study, was the second fastest and hence went against my predictions. *C. excavatus* contains high levels of terpenes and is subsequently usually considered unpalatable (Ellis 1990). The faster than expected decomposition of this species indicates that secondary metabolites (terpenes in this case) may be of less importance in savanna decomposition than anticipated. Bengtsson and others (2011) also found secondary metabolites to have minimal effect on decomposition in the fynbos biome of South Africa, attributing this to rapid leaching of such substances out of the litter (Schönholzer and others 1998). Furthermore, some groups of soil animals (e.g. termites and earthworms) can partly digest secondary metabolites (Hättenschwiler and Vitousek 2000), and thus their activity may not be inhibited by such compounds, precluding effects of polyphenols on the rate of decomposition. Crude protein content is also perhaps less important for invertebrate herbivores than vertebrate ones, and thus not a critical determinant for decomposition rates. Indeed, Radford and Andersen (2012) found that invertebrate population trends following fire events in Australian savanna did not correspond to changes in grass quality (including protein content), recovering much faster than grass nutrition levels. Thus, although litter quality does influence decomposition rates (*U. mosambicensis* decomposed the fastest) this is only discernible when litter quality is exceptionally high; at lower quality levels the effects are negligible.

The significant interaction terms in my model indicate that different factors are important in different areas and seasons. At the driest site (Mopani), neither seasonality nor litter quality affected decomposition, however, with increasing mean annual precipitation; season becomes an increasingly important factor for high quality litter. In arid regions such as Mopani, rainfall is sporadic and insufficient to sustain large populations of decomposer invertebrates or fungi, resulting in neither seasonality nor quality being important here. Tian and others (2007) recorded a similar pattern in west Africa, where high quality litter decomposed faster in wetter regions only and similar results (no effect of season or litter quality) were also recorded in arid New Mexico during a long-term decomposition study (Vanderbilt and others 2008). In such areas, factors other than water availability and litter quality need to be considered in relation to litter decomposition (Austin 2011). Photodegradation is likely to be relatively more important here; indeed Mlambo and Mwenje (2010) found that photodegradation was an important agent of tree litter decay in mopane woodland, and other studies have demonstrated that it is the most important mechanism in arid regions (Austin and Vivanco 2006; Henry and others 2008; Gallo and others 2008; Brandt 2010 and others 2010).

Seasonality is important for high quality litter, but not for low quality litter, this being particularly evident with *U. mosambicensis*. I suggest that this may be due to decomposer invertebrates favouring high quality litter (*U. mosambicensis*); since they would be more active during the wet season, rapid mass loss of high quality grass would occur then. However, when such organisms become inactive during the dry season, high quality litter is not removed by them and thus does not decompose any faster than low quality litter.

The effect of fire regime

Overall, fire regime had no significant effect on decomposition rate, which is partly expected given the high levels of resistance to burning shown by other savanna attributes (see Parr and Andersen 2006). However, my results indicate that the effect of fire regimes on the decomposition process is much more complex than shown in previous studies; and this is because the magnitude and direction of the effects varied with mean annual precipitation and litter quality. In the most arid region, Mopani, burning had no effect, demonstrating the exceptionally high resistance to disturbance of both biodiversity and ecosystem processes in these arid regions. Indeed, apart from temperature, none of the other recorded variables showed differences between fire regimes. At these same sites, Davies and others (2012) and Parr and others (2004) found similarly high resistance to fire for termites and ants respectively, with little difference in diversity and composition across fire regimes. My results suggest, therefore, that in such systems, ecosystem function responses to fire closely match faunal responses.

In the less arid savanna habitats, fire regime had significant effects on decomposition rates. At Satara (semi-arid to intermediate rainfall), faster levels of decomposition were recorded on burnt than unburnt sites. Although no direct data related to termite decomposition are available, termite activity was higher on burnt sites (Fig. 5.4b), and given the important role they play as decomposers, I hypothesise that higher rates of decomposition on frequently burnt plots may be a result of increased termite activity. Frequent fire in these savannas leads to an increase in fungus-growing termite activity with a concomitant increase in decomposition rate (the combined effect of fungus-growing termites outcompeting fungi, and greater nutrient cycling due to increased grazing activity, enhances termite activity, see Davies and others 2012). The highest quality grass litter (*U. mosambicensis*) showed the greatest differences in decomposition rate across the burning regimes, hence driving the pattern and the interaction between litter quality and fire regime. Thus, some litter types are affected by fire, but not others; possibly due to termites favouring high quality litter and being more abundant on frequently burnt plots.

In contrast, at the wetter savanna sites (Pretoriuskop and Hluhluwe), decomposition generally took place more rapidly on unburnt sites with frequent fire slowing decomposition; there was also no noticeable interaction between fire regime and litter quality. The higher decomposition rate on unburnt sites is likely to be because in systems with no, or low fungus-grower termite abundance, other factors are more important for determining decomposition rates. Silveira and others (2009) found that fire slowed decomposition in seasonal Amazonian forest, a system with no fungus-growing termites present, and attributed this to an altered, drier microclimate: temperature increased and humidity decreased as a result of an opening up of the canopy by frequent fire, producing an unfavourable environment for soil animals and microbial communities, particularly as they may normally be adapted to a more buffered microclimate. The joint effect of fewer fungus-growing termites and the lower canopy cover (which alters microclimate) on burnt plots at Pretoriuskop are thus likely to contribute to slower decomposition. Other studies (e.g., Brennan and others 2009) found that slowed decomposition under high frequency fire regimes was a result of the detrimental effects of fire on decomposer organisms. Although fire had little effect on fungus-growing termites (major savanna decomposers) at these wetter sites (Figure 5.4a,b and Davies and others 2012), burning may have reduced the diversity of other non-termite litter-consumers, including fungi, that are more abundant in wetter, more humid environments (Aanen and Eggleton 2005). Indeed, Brennan and others (2009) attribute changes to decomposition rate by fire to such non-termite invertebrate groups. At my wetter sites, fungus-growing termite diversity was lower than at the intermediate rainfall sites (Fig. 5.4a and Davies and others 2012). Consequently, I suggest that when mesic savanna sites are frequently burnt, decomposition rates decrease because other invertebrate groups (including non-fungus-growing termites) and fungi are negatively affected, and fungus-growing termites are not sufficiently abundant to come into prominence and increase decomposition rates (see Fig. 5.5 for a conceptual model hypothesising how burning interacts with mean annual precipitation to affect decomposition).

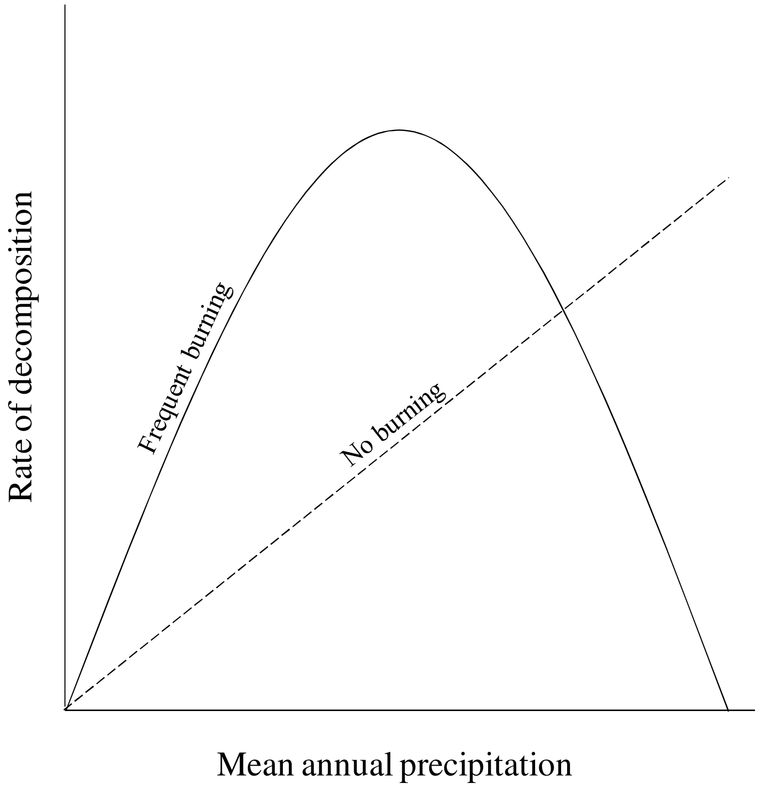


Figure 5.5: Conceptual diagram presenting a testable hypothesis I put forward for how burning influences grass decomposition rates in southern African savannas across a gradient of mean annual precipitation (frequent burning increasing decomposition in semi-arid savannas and decreasing it in wet savanna habitats, with no effect in arid savannas).

Conclusions and future directions

I conclude that, in line with global models, the rate of grass decomposition in African savannas is primarily governed by the effects of climate and litter quality on decomposer activity. Although much of this decomposition is likely to be microbial, I hypothesise that the role of larger decomposer organisms (particularly fungus-growing termites) may become important at local scales in areas of intermediate rainfall (e.g. Satara) where moisture levels are low enough to limit external microbial decomposition, but not too low to constrain termite activity. This then facilitates the dominance of fungus-growing termites where they can out-compete free-living fungi (Aanen and Eggleton 2005). Disturbance regimes (fire) also play an important role locally in mediating decomposition under certain climatic and litter quality conditions; this is likely to be through effects on termite activity, vegetation structural, and hence microclimatic, alterations, and possible effects on the diversity of other invertebrates, with the direction of these effects dependent on the amount of mean annual precipitation received (see Fig. 5.5).

Southern African savannas are predicted to become wetter with future climate change (Senior and others 2002). Consequently, following my results, overall faster rates of decomposition can be expected, potentially resulting in a reduced ability to store carbon and consequently an increased rate of carbon return to the atmosphere. Furthermore, under global change models and increased human population pressure, fires are likely to become more frequent (Williams and others 2009). Since fire regime has an effect on decomposition in all but the most arid savanna habitats, shifts in decomposition rates can be expected. Frequent fire was found to slow decomposition in wetter savannas, meaning that across many savanna areas increased fire occurrence could result in slower decomposition. Conversely, in arid or semi-arid savannas where fire increases decomposition rates the opposite could occur, leading to increased carbon turnover rates. Changing climate and fire regimes may thus act in opposite directions to affect decomposition, but currently I do not have enough data to predict accurately which, if either, will be most influential. Further studies are required to test more explicitly the ideas presented here, particularly to unravel the roles of termites and other factors in savanna decomposition using appropriate multiple mesh size litter bag exclusion experiments. Shading experiments will also be useful to elucidate the relative importance of photodegradation in these systems and interactions between processes (e.g. infrequent fire in mesic savannas increases woody cover which reduces light penetration to ground layer). Such research will improve our understanding of the mechanistic processes influencing decomposition under different fire-regimes, and enable more accurate predictions for future ecosystem changes.

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Chapter 6

General Discussion

This thesis has demonstrated the important functional roles *Macrotermes* mounds play as contributors to savanna spatial heterogeneity across a range of savanna types differing markedly in annual rainfall and nutrient status. In doing so, the importance not only of termites, but biotic agents more generally in creating heterogeneity, with cascading ecosystem effects, has been demonstrated. My work thus supports the idea that *Macrotermes* mounds can be thought of as keystone structures that have a profound influence on various dynamics of savanna ecosystems. However, I have also shown that the influence these mounds exert varies with savanna context, with their relative importance decreasing as the nutrient concentration of the savanna matrix increases. This is further reflected in the size of the sphere of influence mounds have, with less of the overall landscape affected by mounds in nutrient-rich savanna areas and during the wet season when nutritious grasses are more readily available in the savanna matrix.

My work conducted on termite mound distributions and their contribution to grass diversity and subsequent grazing patterns is the most comprehensive of its kind for savanna ecosystems, and indeed throughout the world. Likewise, the decomposition study stands out as the most complete on savanna grass decomposition to-date. A major contributing factor to this novelty is that each study was undertaken across a rainfall and nutrient gradient, enabling our understanding of termite-driven heterogeneity to advance beyond a collection of useful single-site studies to one that incorporates landscape context and thus enables a deeper, more process-based appreciation. Moreover, the investigation of the spatial dynamics of termite mounds and their influence on ecosystems has deepened our knowledge of the extent of their importance, both locally around mounds and up to a landscape scale.

Notwithstanding the contribution *Macrotermes* mounds make to fine-scale savanna heterogeneity, their influence is spatially restricted across landscapes. In Chapter 2, it was revealed that termite mound distributions are not uniform across savannas, but respond to abiotic factors at both regional and local scales. Not only did different areas of the catchment support higher or lower densities, with an apparent complete absence of mounds from the gabbro intrusion, but within these areas mounds were largely located on crests above seeplines. The implication of this is that the positive effect of enhancing spatial heterogeneity that mounds have is largely restricted to crests. However, these areas are generally nutrient-poor and not conducive to sustaining sizeable herbivore populations (Grant and Scholes 2006). The creation of nutrient-hotspots by termite mounds therefore makes a substantive contribution by enhancing the suitability of crests (dominant features in these landscapes) for utilisation by plant and animal species.

Termite mound distributions mapped with LiDAR terrain data are restricted, however, to larger mounds (>0.5 m). Although suitable for *Macrotermes*, mounds built by other termite genera, such as *Odontotermes*, that have been shown to influence savanna dynamics (Palmer 2003, Jouquet et al. 2004a, Brody et al. 2010, Fox-Dobbs et al. 2010, Pringle et al. 2010), will escape detection due to their smaller sizes and shorter heights. Distribution patterns of these mounds, as well as subterranean, non-mound building termite colonies, remain to be investigated across large spatial scales comparable to those of Chapter 2. Meyer et al. (2000a) found *Cubitermes* to prefer sandy soils (similar to the crests of the N'waswitshaka catchment), indicating that topographical preference may be similar at least for this genus. However, such field-based studies are unable to match the extensive coverage provided by remote sensing techniques, and are thus unable to map mound distributions across large spatial scales. Preliminary data from the Kruger National Park (KNP) suggest that *Odontotermes* may extend lower down hillslopes than our documented patterns for *Macrotermes* (B. Lind, *unpublished data*), warranting further investigation. If other termite genera do indeed occupy different topographical areas, the creation of nutrient-hotspots will be facilitated more broadly in landscapes, augmenting the contribution made by *Macrotermes*.

Not only do distribution patterns of mounds vary across savanna landscapes, but so does the relative contribution they make to spatial heterogeneity. In Chapter 3, I documented how grass diversity is significantly different on termite mounds compared to the savanna matrix at all three sites across the rainfall gradient. However, the distance into the savanna matrix that these different grass communities extend differs with landscape context. In relatively nutrient-rich savannas this spatial extent is less, up to two metres for the Skukuza site in this study. As annual rainfall increases and landscapes concomitantly become dystrophic this distance increases, being up to four metres in this study. I largely attribute this variation to differences in the nutrient content of the savanna matrix. Where savannas are nutrient-rich the difference between mound and matrix soil nutrients will be less, resulting in a smaller sphere of influence around mounds here because soil nutrients will level off closer to mounds. Although I present nutrient data in support of this hypothesis, and Treydte et al.

(2007) found similar patterns, and followed similar reasoning, for grass nutrients below large savanna trees, other plausible explanations need to be considered and tested.

These include factors such as termite mound size, which has been shown to affect the woody plant assemblages growing on them, with more distinct communities compared to the savanna matrix present on larger mounds (Joseph et al. 2013a); whether this also applies to savanna grasses remains to be investigated. Larger mounds may also be conducive to higher rates of erosion of nutrient-enriched soil into the savanna matrix around the mounds due to more soil being available, leading to a larger sphere of influence around larger mounds. However, the largest mounds in my study area were located in the nutrient-rich site Skukuza (Chapter 2) and yet had the smallest spheres of influence around them, indicating that mound size is possibly not an important factor, at least not at a landscape scale. Tests of mound size within single, homogeneous areas are necessary to test this hypothesis appropriately. Another factor which could affect the sphere of influence around mounds is whether the mounds are active (inhabited by *Macrotermes*) or not. Active mounds could be expected to have larger spheres of influence because the constant conveying of organic material to the nest will mean that nutrient cycling is on-going, enriching the soil around mounds. However, it is difficult, if not impossible, to ascertain when last an abandoned mound was active, which would confound these types of measurements. Nevertheless, activity status could be an important factor worth testing.

Grazing patterns around termite mounds followed similar patterns. Although mounds were always preferred by grazing herbivores (both mammalian and insect, see also Leitner (2012)), the extent of increased grazing differed both spatially and temporally across the savanna sites tested. At the end of the wet season, when forage is abundant, mounds in the nutrient-poor savanna sites had larger spheres of influence around them, with this pattern reversed in the dry season, possibly because of food patch depletion on and around the smaller mounds in the nutrient-poor site. Mounds are most likely preferred by grazers because they are responding to the increased nutrition of mound grasses, which were more nutritious than grasses of the savanna matrix at all sites. Van der Plas et al. (2013) recorded preferential browsing in Hluhluwe-Mfolozi Game Reserve of off-mound vegetation, ascribing this to increased nutrition in savanna matrix woody plants compared to mound vegetation. This thesis supports the findings of Van der Plas et al. (2013) because mounds in the wetter, nutrient-poor savanna site were more preferred until the resource was depleted, and grazing on mounds across sites was higher during the dry season when savanna nutrients are likely to be lower. However, I consistently recorded higher grazing on mounds than off them at all sites and in both seasons, in contrast to the findings of Van der Plas et al. (2013) for browsing. Although this study was conducted across a nutritional gradient, all sites were located on generally nutrient-poor granitic substrate. Further testing of grazing patterns around mounds in areas of higher savanna matrix nutrition, such as the basaltic plains of the Kruger National Park, parts of Hluhluwe-iMfolozi, or the volcanic plains of east Africa, will elucidate more clearly the relevance of landscape context and compare more directly to the results of Van der Plas et al. (2013).

Interactions between grazers and termites in the establishment of distinct and nutritionally enhanced grass assemblages around mounds are also worth considering. Okullo & Moe (2012b) showed that it is the termites themselves, not the mammalian herbivores, that facilitate and create the conditions for different grass communities, but these authors also documented that, once established, these distinct communities are maintained by mammalian herbivores (Okullo and Moe 2012a). Furthermore, Cromsigt & Olff (2008) showed that biotic disturbance, including termite activity, initiates the establishment of grazing lawns in African savannas, but once established they are maintained and enhanced by mammalian grazing. The use of herbivore exclosure plots (such as the long-term ones already established in KNP) will enable further testing of these processes, and the KNP exclosures afford an excellent opportunity to test them across rainfall and nutrient gradients.

The percentage of the landscape influenced by *Macrotermes* mounds calculated from the sphere of influence measurements and LiDAR terrain data (Chapters 3 and 4) are informative as to the contribution made by termites to savanna spatial heterogeneity. However, I only measured the influence of *Macrotermes*, while at least another 22 termite genera are present in KNP (Davies et al. 2012). Quantifying the effect and area of influence of these other genera would provide a more comprehensive figure on the overall influence that termites have on savanna heterogeneity. Measuring such influence is, however, fraught with difficulties with respect to sampling methods (see Davies et al. 2013) and estimation of colony sizes and foraging areas, especially for non-mound building species.

The decomposition study of Chapter 5 revealed interesting and important interactions between fire and other savanna dynamics, including the role of termites. Although expected to slow decomposition based on previous studies (Brennan et al. 2009, Silveira et al. 2009), frequent burning lead to contrasting effects, slowing the process in wet savannas, accelerating it in intermediate rainfall sites and having no effect at the driest sites. The contrasting roles of fire were ascribed to effects it has on opening up the vegetation at wetter sites and interactions with fungus-growing termites (including *Macrotermes*) at the intermediate site.

These mechanisms are indeed plausible and likely, but need to be clarified through further manipulative experimentation. This includes the use of different mesh-sized litterbags or other appropriate methods (e.g., insect repellents) to exclude invertebrates, thus explicating directly the role of termites and other decomposer invertebrates. Furthermore, the role of photodegradation was not tested in my study, but certainly plays a role in grass decomposition, particularly in dry savanna ecosystems (Austin 2011). Notwithstanding this, the role of fungus-growing termites was implicated in the study and shown to vary with landscape context, accentuating the investigation of this thesis into the functional role of termites across savanna types.

In conclusion, this thesis has demonstrated that termites make significant contributions to savanna functioning, across a range of savanna types. Conservation authorities would do well to consider them when formulating management plans and estimations of ecosystem carrying capacity. For example, areas with higher densities of *Macrotermes* mounds, particularly in nutrient-poor savannas, will have the potential to sustain larger than expected herbivore populations, of both mammals and insects. Furthermore, termite mounds can be useful tools in monitoring exercises because they are likely to show early signs of ecological degradation and over-grazing due to increased levels of utilization. Termites are therefore of great value to rangelands, enhancing overall biodiversity and ecosystem health, and providing multiple benefits to managers of savanna areas.

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