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Relationships between termite (*Macrotermes)* mound distribution, plant diversity and large mammalian herbivory patterns in Gonarezhou National Park, Zimbabwe



A thesis submitted to the Faculty of Science, University of the Witwatersrand, in fulfilment of the academic requirements for the degree of Doctor of Philosophy.

August 2016, Johannesburg

By

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Academic Supervisors:

Prof. Ed Witkowski

Prof. Francesca Parrini

Dr. Andrew B. Davies

Declaration

This submission contains original research undertaken towards a Ph.D. degree in Ecology. The work is my own, and to the best of my knowledge contains no material previously published by another person, except where specifically acknowledged within the body of the text. All sources of information in the text are listed in the references.

Signed:  **Date: 23/08/2016**

Abstract

Termites are widely distributed in tropical and subtropical savanna. They are recognised as major ecosystem engineers through their role in nutrient cycling, decomposition, hydrology and alteration of landscape topography with cascading effects manifesting in ecosystem heterogeneity and productivity up the food chains. In this thesis I addressed the effect of geology on termite species diversity, followed by questioning how the different geologies influence the size and spatial distribution of *Macrotermes* mounds. Furthermore, I explored the effect of termite mounds emanating from different geologies on herbaceous vegetation heterogeneity and finally the effect this heterogeneity has on grazing intensity. Although the diversity of termites has been explored across different environmental gradients such as rainfall, altitude and disturbance, little is known regarding variation in their diversity across landscapes of varying geology. In my quest to understand how varying geology influences the ecology of termites and their functional importance, I sampled granite and basalt for termite diversity using standard transects (100 m x 2 m). I predicted that termite diversity is higher on nutrient-rich geology following the productivity diversity hypothesis. However, both functional and taxonomic diversity were higher on nutrient-poor granite. Twelve species from three subfamilies representing two feeding groups were recorded on granite whereas on basalt only five species from two subfamilies consisting of one feeding group were recorded. Although the influence of *Macrotermes* mounds on ecosystem heterogeneity has been well studied, little is known on how the environment (geology) and other termite colonies influence size and distribution pattern, despite how these interactions could influence ecosystem functioning. Termite mounds were sampled in 1 km^2 plots, four in each geology. Each mound location was recorded using a hand held GPS and structural variables (height and diameter) measured. The data were analysed for spatial distribution of termite mounds using the software Programita. The general distribution pattern of termite mounds (active and inactive mounds combined) was investigated using both the pair correlation function, $g(r)$, and Ripley's $K(r)$ function. Termite mounds were larger and covered a significant proportion of the landscape on granite compared to basalt. Mounds were generally over-dispersed on granite and randomly distributed on basalt. Mounds covered ~ 6% of the landscape on granite compared with only ~ 0.4% on basalt. These results show that the significance of termites varies across geologies, being more important on nutrient-poor geologies because of their size and a more productive spatial pattern displayed here. The majority of studies testing

mound effects on savanna vegetation spatial heterogeneity have been based on single site observations mostly comparing mounds and their paired savanna control plots. Furthermore studies did not consider the spatial effects of mounds with distance into the savanna matrix from mound edge, and this has rarely been tested across landscapes of varying geologies, as well as across mounds of different sizes. Therefore there was a need to explore this in order to broadly understand the functional importance of mounds. I sampled the herbaceous community on and off termite mounds and along distance transects from mounds on nutrient-rich and nutrient-poor geologies. Termite mounds as sources of spatial vegetation heterogeneity was more pronounced on nutrient-poor granite, with larger mounds having greater effect on vegetation composition and diversity than smaller ones. Mounds harboured compositionally different herbaceous plants compared with the savanna matrix on granite whereas there was no difference on basalt. In acknowledging the effect erosion from mounds may have on vegetation heterogeneity, termite mound effect on composition expressed at landscape level based on mound densities recorded in this study was estimated to be 19% of the landscape on granite whereas on basalt, the mounds influenced ~ 0.4% of the landscape. The choice of foraging sites by large herbivores in the landscape is influenced by food quantity, quality, inter and intra-specific competition and predation risk. Termite mounds harbour highly nutritious herbaceous plants compared to the savanna matrix, which makes them preferred foraging sites. Due to very small differences in soil nutrient content between mounds and savanna on basalt, mounds were expected to have little effect on grazing. In line with the set hypothesis termite mounds largely influenced grazing on the nutrient-poor granite and when viewed at landscape scale, based on mound densities and extent of erosion recorded, mounds influenced ~ 28% on granite and only ~ 0.8% on basalt. Overall my study has demonstrated that the significance of termites as ecosystem engineers varies across landscapes of varying geology, being more important on nutrient-poor compared with nutrient-rich geologies.

Key words: basalt, bivariate, diversity, geology, Gonarezhou National Park, granite, grazing, heterogeneity, Ripley's *K* function, savanna, spatial distribution, termite mound, Zimbabwe.

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First and foremost I would like to thank my academic supervisors, Prof Ed. Witkowski, Prof F. Parrini and Dr A.B. Davies for the guidance and support they gave throughout my PhD. You have shown me that where there is a will there is a way, you have also challenged me to learn and think independently which I feel is a huge transformation that will help me meet my carrier goals. I highly appreciate your deep involvement in my work, most importantly giving me feedback in time. To committee members of this PhD, Profs N. Pillay and M. Byrne your contribution during proposal writing is highly appreciated.

I would like to thank the Director General of the Zimbabwe National Parks and Wildlife Management Authority (ZNPWMA) who granted me permission to carry out this research in Gonarezhou National Park (GNP). Vivienne Uys is thanked for assistance in termite specimen identification. I am indebted to the man who helped me with plant identification, Julius Shimbani my life was made easy as I did not carry too many specimens to the National Herbarium. I express gratitude to all the field assistants who participated in data collection, Marco Mudede, Buckley Dzamara, Tongai Musariri, Tafadzwa Tichagwa and Chikomborero Kasawaya.

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Disclaimer

Chapters 2, 3, 4 and 5 are presented as manuscripts for different scientific journals; therefore some repetition of information in some sections, especially the methods is inevitable. Although style and format vary between Chapters, referencing style is consistent throughout the thesis. Figures and tables are imbedded in the text and Supporting Information/Appendices have been placed at the end of each chapter.

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Chapter 1

Chapter 1: Introduction

Project rationale

Ecosystem heterogeneity is the main determinant of species richness, abundance and coexistence of animal and plant assemblages in savannas (Cornell and Lawton, 1992; Tilman and Kareiva, 1997). Heterogeneity is influenced by both biotic and abiotic processes in the ecosystem and heterogeneity can be viewed at different spatial levels (Scholes et al., 2003; Venter et al., 2003), from local to continental. At regional to continental scales, rainfall is the main determinant (Sankaran et al., 2005), whereas at local to landscape scales, fire, herbivory and soils become more important (Asner et al., 2009; Bond et al., 2005). Variation in soils is primarily influenced by the parent rock material (geology) from which the soils were derived. However, ecosystem engineers such as termites, ants and dung beetles are also known to influence soil fertility, but mostly at a local scale (Jones et al., 1994; Seymour et al., 2014). Termites qualify as ecosystem engineers because they enhance decomposition processes, soil water status and control mineralization (Wood and Lee, 1971; Holt and Lepage, 2000; Jones et al., 1994). The genus *Macrotermes* mostly uses subsoil for mound building, and soil from this horizon has high clay content and inorganic nutrients such as Ca, Mg, K and Na (Konaté et al., 1999), but not necessarily N, P and C (Abbadie and Lepage, 1989). Also, termite mounds influence wind movement, local fire regimes and grazing patterns, which can have implications on spatial patterning of resources in natural ecosystems (Davies et al., 2010; Joseph et al., 2013b). Earlier studies on termite mounds are fragmented, focusing on different aspects of termites, for example, species classification (Ahmed(Shiday) et al., 2011; Inward et al., 2007); nest building and foraging activities (Bagine, 1984; Dangerfield and Schuurman, 2000), nutrient cycling (Holt and Coventry, 1990; Konaté et al., 1999; Lepage et al., 1993) and termite-herbivore interactions (Muvengwi et al., 2013; Okullo et al., 2012; Van der Plas et al., 2013). However, little has been done to holistically answer, within the same study, the question of what contributes to termite mounds being nutrient hotspots and how termite mounds contribute to plant species diversity and grazing intensity within the landscape, especially in savannas of variable fire regimes, altitude and temperature. To date there is only one study that has used a holistic approach, looking at the diversity of termites, spatial distribution of mounds and effects mounds have on plant diversity and grazing

patterns, but along a rainfall gradient (Davies, 2013). Another source of variation in savannas with limited comparative studies is geology. The two common geologies in southern Africa are basalt and granite. Basalt is weathered to produce nutrient-rich soil that is basic with a high clay content whereas granite produces coarse-textured, nutrient-poor soils (Grant and Scholes, 2006; Olowolafe, 2002). Granitic landscapes are generally undulating, leading to catenal sequences with seeplines, mid-slopes and crests (Khomo et al., 2011; Levick et al., 2010a), whereas basalt is strikingly flat.

Topography and mound slope influences soil movement from termite mounds, for instance erosion from the mounds will be carried down slope as outwash, which might impact nutrient redistribution around the mound (Arshad, 1982; Gosling et al., 2012). As such, the nutrient rich soil from the mound may increase the termite mound sphere of influence beyond the mound itself, and influence spatial patterns of plants and herbivory (Davies et al., 2014, 2016a, 2016b; Levick et al., 2010b). However, in most studies an experimental plot is placed on the mound and a control plot is randomly placed at a fixed distance in the inter-mound matrix. This may miss the influence of mounds in terms of the spatial pattern of resource distribution and use with distance from the edge of the mound (Sileshi and Arshad, 2012). Also, most studies have focused on diversity of woody species (Holdo and McDowell, 2004; Joseph et al., 2013a; Loveridge and Moe, 2004), although the herbaceous community is key to the abundant grazers within savanna ecosystems. Additionally, only recently has a study been conducted to test the influence of mound size on vegetation diversity (Joseph et al., 2013a). However, this recent study only focused on woody vegetation, although the graminoids and forbs are an integral component of savanna ecosystem functioning.

The extent to which termites contribute to spatial heterogeneity is hinged on the size, number and spatial distribution of the mounds they build per unit area in an ecosystem. The spatial distribution of termite mounds is still an open subject for debate as highlighted by differences in findings from various ecosystems (Davies et al., 2014; Lepage, 1984; Levick et al., 2010; Meyer et al., 1999; Pomeroy, 2005; Schuurman and Dangerfield, 1997). Contrasting results have been found, with mounds in east Africa reportedly having a regular distribution (Darlington, 1982; Kaib et al., 1997; Pomeroy, 2005) while most areas in southern Africa have a random pattern (Schuurman and Dangerfield, 1997; Turner, 2000), with some studies describing a regular distribution at smaller scales (Davies et al., 2014a; Grohmann et al., 2010). Therefore, understanding the spatial placement of termite mounds and their directional

influence on the surrounding matrix can be a key component in predicting habitat utilisation by game animals since mounds can provide both refugia and high quality forage for herbivores (Fleming and Loveridge, 2003; Grant and Scholes, 2006; Mobæk et al., 2005). *Macrotermes* construct large mounds with the potential to influence ecosystem processes. Also, understanding the spatial distribution of *Macrotermes* mounds and herbivory patterns in savannas is important in the management and conservation of the variety of herbivores found, since mound pattern can influence ecosystem structure and function. In addition, information on the distribution of termite mounds is important for conservation and to manage them as nutrient hotspots. Therefore, the main aim of this study was to determine how termite species diversity and spatial distribution of the mounds they build varies between geologies as well as whether termite mounds influence spatial patterns in plant species diversity and large mammals herbivory between geologic substrates in Gonarezhou National Park.

Study site

The study was carried out in the northern section of Gonarezhou National Park (Chipinda Pools area, 360 km^2 in extent and located between, latitude 21^0 15′ 35 and 21^0 21′ 07 S, longitude 31^0 55′ 38 and 31^0 59′ 28 E) (Figure 1.1). Chipinda Pools area was chosen as the study area due to accessibility, availability of termite mounds and the presence of both granitic and basaltic substrates. Granite weathers to produce course textured, poorly buffered, acidic nutrient-poor soils. The granitic landscapes are generally undulating, leading to catenal sequences with seeplines, mid-slopes and crests (Khomo et al., 2011; Levick et al., 2010a). In contrast, basaltic landscapes are strikingly flat, lacking catenal formations and their associated soil and water regimes (Kelly and Walker, 1976). Furthermore, basaltic landscapes are regarded as nutrient-rich compared to granite (Grant and Scholes, 2006; Scholes, 1990), resulting from their soil being formed from rocks rich in basic cations, which when weathered produce fine textured, fertile alkaline soils that are generally black in colour and rich in clays (Olowolafe, 2002). Granite is located in the east of Gonarezhou and has higher tree species diversity than basalt in the west. Common tree species on granite include *Androstachys johnsonii*, *Brachystegia glaucescens*, *Vitex payos*, *Diospyros loureiriana* and *Xeroderris stuhlmannii*. Areas on basalt are covered mostly by *Colophospermum mopane* woodland, with scattered *Combretum apiculatum*. The herbaceous community on basalt is

dominated by the grasses *Aristida rhiniochloa, A. adscensionis and Brachiaria deflexa* while granite consists largely of *Digitaria eriantha, Tragus berteronianus, Urochloa mosambicensis* and *Heteropogon contortus*. Common game species of the park include buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), elephant (*Loxodonta africana*), giraffe (*Giraffa Camelopardalis*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepiciceros*), nyala (*Tragelaphus angasii*), sable (*Hippotragus niger*), warthog (*Phacochoerus africanus*), waterbuck (*Kobus ellipsiprymnus*), wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga burchelli*) (Dunham, 2012). The study area was overlaid with 1 km^2 grids and four were randomly sampled from each geology. Four 1 km^2 grids were randomly chosen in each of the two geologies after overlaying a map of 1 km^2 grids on the GNP geological map, basalt (black squares) and granite (white squares) (Figure 1.2). All data collection was concentrated in these 1 km^2 grids. Accessibility and being at least 3 km from permanent water holes was also considered.

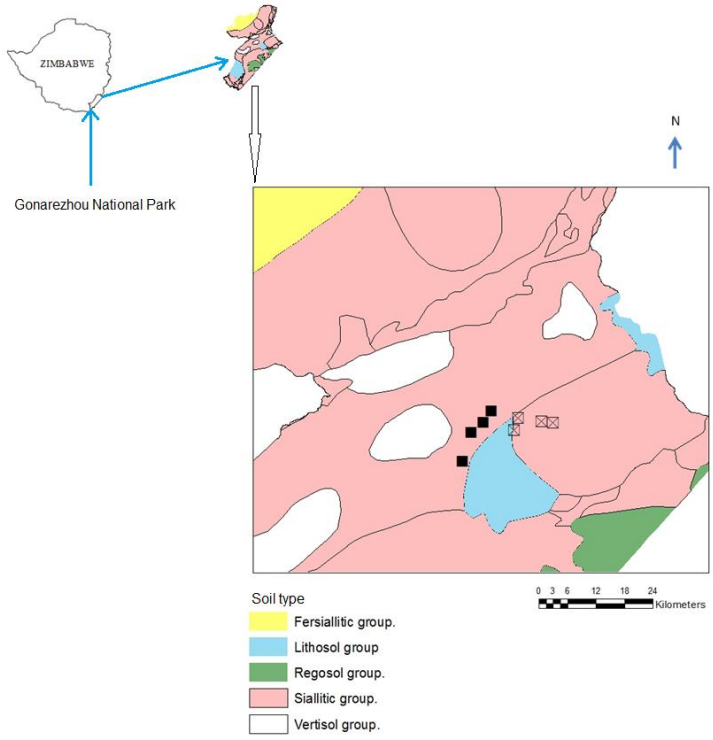


Figure 1.1: Location of Gonarezhou National Park in Zimbabwe together with soil map of Chipinda Pools northern section of the park where the study was carried out, black squares (basalt) and marked squares (granite).

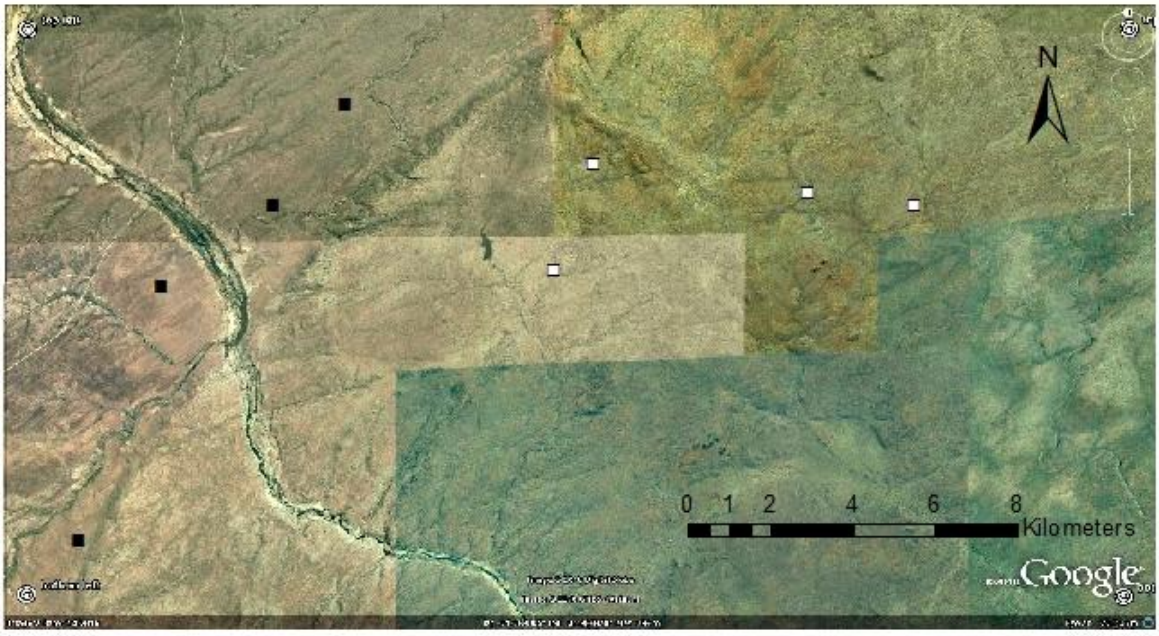


Figure 1.2: Randomly placed 1 km^2 sampling plots in each geological substrate (Black on basalt and white on granite).

Literature review

Termite diversity

Termites belong to the order Blattodea and are found across six of the seven continents with more than 2600 species identified so far (Inward et al., 2007). The highest diversity occurs on the African continent. African termites are classified into five distinct families, Termitidae, Rhinotermitidae, Hodotermitidae, Termopsidae and Kalotermitidae (Eggleton et al., 1994). All five families have been recorded in Zimbabwe (Mitchell, 1980). These families are further subdivided into eleven subfamilies Termitinae, Rhinotermitinae, Hodotermitinae, Kalotermitinae, Coptotermitinae, Macrotermitinae, Apicotermitinae, Nasutitermitinae, Porotermitinae, Stolotermitinae and Termopsinae (Figure 1.3) (Ahmed(Shiday) et al., 2011; Mitchell, 1980; Uys, 2002).

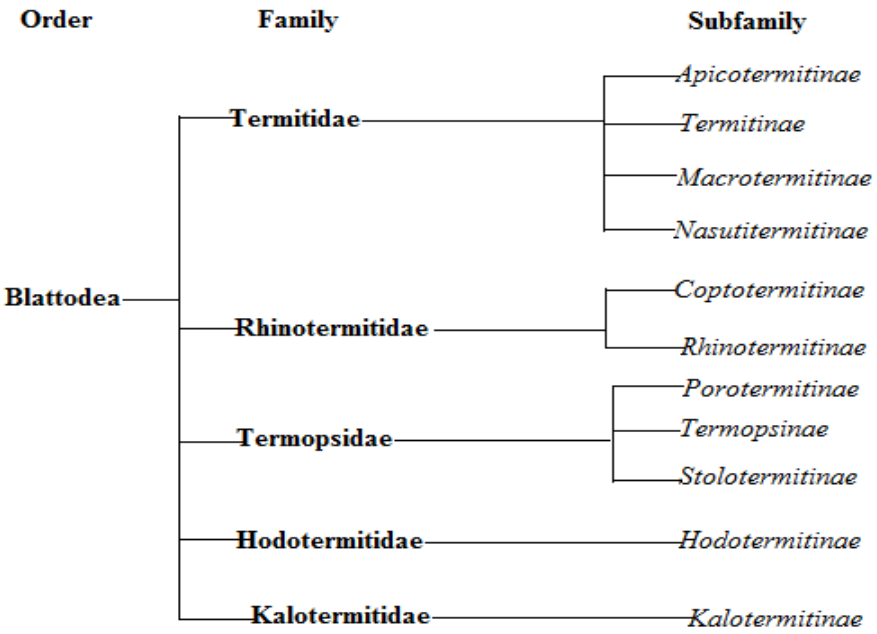


Figure 1.3: Phylogeny showing termite families and subfamilies occurring in Africa following Ahmed(Shiday) et al. (2011).

One hundred and sixty-five species from 54 genera have been identified and described from southern Africa. However, the number of known (classified) African termite species is expected to increase, since there are a large number of unidentified specimens (Uys, 2002). The highest termite species diversity falls under the subfamily Termitinae, while *Odontotermes* is the most diverse genus with 78 species recorded from Africa (Uys, 2002).

Termites can be divided into two major categories, the higher and lower termites. Lower termites generally do not build epigeal conspicuous mound structures like the higher termites do. Lower termites have both flagellated protists and prokaryotes in their digestive system which enable the digestion of lignocelluloses, while higher termites have prokaryotes only and cannot digest cellulose (Collins, 1981; Matsui et al., 2009). Lower termites mainly feed on wood (Ohkuma, 2008), whereas higher termites feed on wood, grass, soil and/or humus and some grow 'fungus gardens' of the species *Termitomyces* spp. in their nests and feed on their fruits (Ohkuma, 2008; Wood, 1991). Different uses of fungal gardens in termite nest are proposed, such as for food and to maintain a suitable humid environment for the delicate larvae (Jouquet et al., 2005; Lüscher, 1951; Sands, 1956; Zoberi, 1979). Although belonging to one apical family (Termitidae), higher termites are the most divergent group and are made up of four subfamilies (Termitinae, Macrotermitinae, Nasutitermitinae and Apicotermitinae). Of the African termites, Rhinotermitidae, Hodotermitidae, Termopsidae and Kalotermitidae

belong to the lower termites while Termitidae belongs to the higher termites (Kambhampati and Eggleton, 2000; Mitchell, 1980). Kalotermitidae live in small colonies within the wood on which they feed. The family Rhinotermitidae comprises mainly subterranean wood eating termites. The family Hodotermitidae, commonly known as the harvester termite feeds mainly on grass (Uys, 2002). Termopsidae is the only family that feeds on decaying wood. Termitinae is commonly regarded as a forest dwelling subfamily; however, some do occur in savannas (Sileshi et al., 2010). Of primary interest in this study is the Macrotermitinae, which is divided into seven genera, *Odontotermes*, *Pseudacantotermes*, *Acanthotermes*, *Allodontotermes*, *Ancistrotermes*, *Microtermes*, and *Macrotermes*. Some genera build conspicuous epigeal mounds, others build low flattened mounds, and some do not build mounds at all. This study mainly focused on *Macrotermes* because they build conspicuous mounds which are easy to see in the landscape and hence may more clearly be defined as ecosystem engineers.

Factors influencing the distribution of termites

The distribution of termites has been studied from several regions on 5 continents: Africa (Sands, 1965), North America (Crist, 1998; Haverty and Nutting, 1976; Haverty et al., 1975), Asia (Matsumota, 1976), South America (Gontijo and Domingos, 1991) and Australia (Wood and Lee, 1971). Nuptial flight is an important termite behavioural characteristic that facilitates perpetuity of termites, ants and some bee species (Leponce et al., 1996; Long et al., 2003; Mitchell, 2008; Neoh and Lee, 2009). Termite species have been shown to synchronise swarming so that they increase the chances of cross breeding (Calleri et al., 2007; Luykx, 1986; Shellman-Reeve, 1999). In termites, alates (sexually mature stage in the termite life cycle) leave the colony to start their own colonies after receiving proper environmental cues, for example temperature, bright sunlight, wind velocity, humidity and atmospheric pressure (Freeland, 1980; Henderson and Delaplane, 1994; Johnson, 1981).

However, depending on the landing spot, several factors have been observed to influence the distribution of termites in the environment, including temperature, soil quality, topography and rainfall (Ackerman et al., 2009; Mitchell, 1980; Pomeroy, 2005, 1977). As such, diversity varies within and between regions. In the desert xeric conditions of North Africa, termite species diversity is low with a richness of less than 15 species while Sub-Saharan Africa has a richness of over 500 species (Ahmed(Shiday) et al., 2011; Sileshi et al., 2010). Eggleton et

al. (1994) modelled the global distribution of termites and found moderate support for a positive relationship between net primary productivity (NPP) and species richness. Considered the importance of rainfall, termite species diversity and abundance has been observed to increase along an increasing rainfall gradient (Buxton, 1981; Davies et al., 2013a; Erpenbach et al., 2013). Assessed along anthropogenic disturbance gradients, termite diversity conspicuously decreased with increased disturbance (Dosso et al., 2010; Eggleton et al., 1997, 1996; Vasconcellos et al., 2010). In studies focusing on altitudinal gradients, it emerged that there was a negative correlation between termite diversity and altitude (Gathorne-Hardy et al., 2002; Palin et al., 2011). When considered along land use gradients, termite diversity was always higher in intact forests compared to anthropogenic uses, for example plantation forests (Attignon et al., 2005; Dosso et al., 2013). To date there are no consensus findings among fire regimes, different results have been presented, with Davies et al. (2012) finding no difference along fire frequency gradient. Abensperg-Traun and Milewski (1995) found diversity, especially of wood feeding termites to be significantly lower on burnt compared to unburnt sites and Dawes-Gromadzki (2007) recorded a significant decline in termite species abundance post fire, but trends in species richness were not clear.

In Zimbabwe, species of *Amitermes* were found to be numerous in the hotter drier parts of the country and absent in the cool moist eastern highlands (Mitchell, 1980). Some common *Amitermes* species such as *A. truncatidens* were dominant in sandy soils whilst *A. unidentatus* was dominant in clay soils of *Colophospermum mopane* woodlands. This shows the importance of soil substrate on species distribution. The distribution of *Macrotermes bellicosus* in Uganda was significantly correlated to temperature, with the species being absent in cooler environments, such as forests and swamps (Pomeroy, 1977). Contrary to Mitchell (1980), Pomeroy (1977) did not observe any relationship between termite distribution and soil or vegetation. This, however, could be attributed to the spatial scale at which the study by Pomeroy (1977) was conducted, since heterogeneity normally increases with an increase in scale (Deblauwe et al., 2008). At a smaller spatial scale, microhabitat variation driven by factors such as woodland canopy gaps, the presence of swampy areas and the location of inactive nests may be important (Schuurman and Dangerfield, 1997). In a later study, Pomeroy et al. (1991) observed *M. michaelseni* distribution to be more predominant at high altitudes and in moister areas compared with *M. subhyalinus*, although there was

substantial overlap. Also, in Zimbabwe, Mitchell (1980) observed *M. michaelseni* and *M. subhyalinus* to occur in the same areas. Similarly, these two species are also sympatric in Kenya (Pomeroy, 1989). In Nigeria, *M. bellicosus* and *M. subhyalinus* distribution was influenced by the drainage of the soil along a toposequence (Kang, 1978).

For mound building termites, soil type can be a major aspect of their distribution (Mitchell, 1980; Wood, 1988). The likely impacts of soil type on termites could be reduced reproduction and survival. Sometimes topography may not only influence distribution, but also termite behaviour. For example, in a study by Pomeroy (2005) at Ruaraka, Kenya, *Odontotermes stercorivorus* produced no mounds on upper slopes of the catena while on bottom slopes they produced sizeable mounds. In two separate studies, the distribution of *Cubitermes* mounds was correlated to grasslands, soil depth and clay content (Mitchell, 1980; Okwakol, 1976). In north eastern Tanganyika (now Tanzania), climate was considered the principal determinant of termite distribution (Kemp, 1955). These different observations indicate that different taxa may have different requirements (biotic and abiotic) for establishment, and therefore this variation in requirements shows the need for case specific studies if meaningful conclusions are to be made for different species across ecosystems (Figure 1.4).

Spatial distribution of mounds

Knowledge of the spatial distribution of organisms is central to an understanding of population dynamics, community interactions and ecosystem functioning (Crist and Wiens, 1996; Gontijo and Domingos, 1991). Spatial patterning of organisms is often linked to outcomes of competition (Pomeroy, 2005, 1989) and predation (Bertram, 1978; Fryxell, 1991). There is also a high likelihood that nutrient and energy flows in ecosystems may be organised by the spatial distribution of key organisms, for example ants and termites. Several studies on the dispersion of termite mounds have been conducted (e.g. Dangerfield et al., 1998; Grohmann et al., 2010; Pomeroy, 2005). The dispersion pattern of termite mounds has been shown to be an important criterion for coalescence of thicket clumps (Bloesch, 2008). In Africa, the spatial distribution of termite mounds has been studied in Botswana (Schuurman and Dangerfield, 1997); Kenya (Pomeroy, 2005); Uganda (Pomeroy, 1977); South Africa (Davies et al., 2014a; Levick et al., 2010; Meyer et al., 1999) and Namibia (Grohmann et al.,

2010). However, little has been done on the spatial distribution of termite mounds in Zimbabwe (Muvengwi et al., 2016).

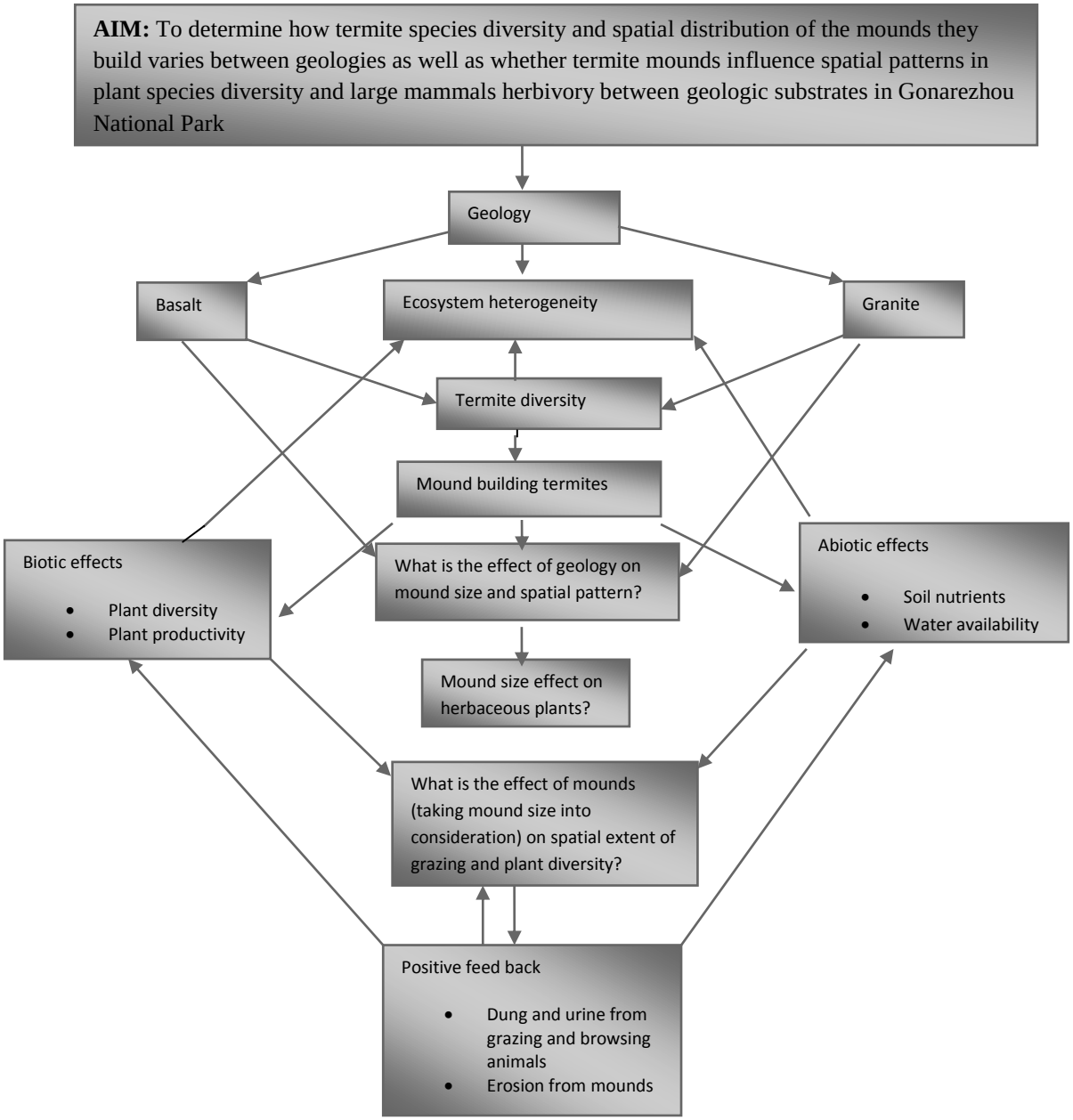


Figure 1.4: A conceptual framework presentation of the main study aim, linked with the gaps in knowledge on how geology influences termite species diversity, mound size and spatial distribution, and the cascading effects on vegetation heterogeneity and grazing. Arrows connect factors and variables from the two geologies.

The extent to which termites contribute to vegetation spatial heterogeneity is dependent on the size and number of mounds they build per unit area in an ecosystem. Therefore understanding the spatial distribution of termite mounds can be a key aspect in managing the savanna ecosystem. Mounds can either be, random, clustered or evenly distributed. Studies on spatial patterning of mounds have yielded different patterns, across ecosystems. For example, in Botswana *Macrotermes* species exhibited a random distribution (Schuurman and Dangerfield, 1997) and in South Africa both regular and clustered distributions were observed (Davies et al., 2014a; Meyer et al., 1999). In Kenya, mounds of species of *Odontotermes* had a regular distribution (Pringle et al., 2010), which was attributed to competition between colonies. In Namibia, *M. michaelseni* had a regular distribution with the exception of newly formed colonies that appeared clustered (Grohmann et al., 2010). In a large, extensive study covering three countries in east Africa, *Trinervitermes* and *Macrotermes* had a regular distribution (Bloesch, 2008). Due to their elevated nutrients, it appears that the spatial distribution of mounds is important in the spatial patterning of vegetation and in its use. In the Kruger National Park, South Africa, the termite mounds sphere of influence, combining the area covered by the mounds and their outwash, was approximated at 20% of the landscape (Levick et al., 2010b). Although it was not estimated to scale, the influence of outwash from mounds through erosion has been acknowledged (Arshad, 1982; Gosling et al., 2012). This may indicate that termite mounds have the potential to influence diversity and herbivory patterns at scales much bigger than their actual sizes.

Mound construction

The termite mound construction process changes the soil physical and chemical status. During mound building, termites produce organo-mineral structures such as crop galleries, crop sheetings and nests (Jouquet et al., 2011). These biogenic structures are a product of intestinal transit, mixed thoroughly with saliva, and they constitute microsites where a number of particular physico-chemical changes occur in the soil (Mora et al., 2003). Also, the origin of construction material can have an important influence on soil nutrient concentrations. Humivores (soil feeding termites) build their mound with their nutrient-rich faeces. In contrast, deeply sampled soil material, mixed with saliva, is used by fungus feeders, and their faeces contribute to mound construction to a limited extent (Fall et al., 2001). However, this difference does not define their relative importance to soil nutrient

enrichment in the ecosystem because both have been observed to have higher soil nutrient concentrations than the reference matrix soil (Brauman, 2000; Fall et al., 2001; Muvengwi et al., 2013).

Termite nests can be subterranean (underground), epigeal (conspicuous), or arboreal (within or attached to the outside of shrubs and trees) (Pomeroy et al., 1991). Mound size can vary from a few centimetres to several metres (Darlington, 1982) and this may be linked to nest age and termite species. During mound building, termites move large quantities of soil, at times from depths below two metres (Pomeroy, 1976). The weight of mounds was observed to range from 100 kg ha^{-1} to 2.4 x 10^6 kg ha^{-1}, with the potential to cover areas ranging from 0.1% to 30% of the surface (Wood, 1988). In a study in northern Kenya, *O. latericius* and *O. boranicus* soil sheetings attached to food surfaces was equivalent to 1059 kg $ha^{-1}yr^{-1}$. In the Sonoran Desert, Arizona, USA, two subterranean species, *Hetrotermes aureus* and *Gnathamitermes perplexus*, together moved approximately 744 kg $ha^{-1}yr^{-1}$ of soil to the surface (Nutting et al., 1987). This increased the clay content of surface soil by 21 kg $ha^{-1}yr^{-1}$. The conspicuous mounds built by the family Termitidae in African savannas are a major source of vegetation heterogeneity (Asner et al., 2009; Levick and Rogers, 2008; Moe et al., 2009; Støen et al., 2013). The variation in quantities of soil moved by different termite species may mean that their influence could be ecosystem specific. All of this may contribute to modifying the soil nutrient status of an ecosystem, hence influencing vegetation dynamics.

After the soil has been moved to the soil surface, the mounds are subjected to different agents of erosion. In the Democratic Republic of Congo, water erosion moved approximately 3 tonnes ha^{-1} yr^{-1} of soil from *Cubitermes* mounds (Aloni and Soyer, 1987). In Australia, rainfall moved 475 kg ha^{-1} yr^{-1} from *A. vitiosus* mounds (Bonell et al., 1986). Lepage (1984) observed a loss of soil from *M. bellicosus* mounds amounting to 9 m^3 ha^{-1} yr^{-1}. Although there are several factors that could influence the quantities of soil moved, such as the amount of rainfall, rainfall intensity and soil type, the above studies confirm that mounds have the potential to redistribute soil nutrients. This could lead to positive feedbacks in the ecosystem through increased plant growth in the area around mounds (Figure 1.4).

Termite foraging

Termites are considered to be detritivores, feeding on a wide range of material in the ecosystem. The termite guild is comprised of four main feeding groups. Feeding group I are termites that feed on dead wood and grass; group II feed on dead wood, grass, leaf litter, and micro-epiphytes; group III on organic rich upper soil layer and group IV is made up of true soil feeders (Donovan et al., 2001; Eggleton et al., 1997; Jones and Eggleton, 2000). Due to their activity and broad feeding patterns, termites have a great potential to influence ecosystem functioning, for example by changing mineral and organic composition of the soil, water infiltration, and plant species diversity (Holt and Lepage, 2000; Joseph et al., 2014; Konaté et al., 1999). Furthermore, some studies have shown how variation in soil community composition can substantially influence decomposition rates (Davies et al., 2013b; Schuurman, 2005). However, there is limited information on how termite species composition varies from a particular geology to another means that the termite diversity in management units with varying geology remains poorly understood, for example in Gonarezhou National Park (GNP).

During foraging termites removed an estimated 835.5 kg ha^{-1} a^{-1} of wood litter (60% of annual wood-fall), and 68.4 kg ha^{-1} a^{-1} of leaf litter, 3% of annual leaf fall, and 24% of total annual litter production (Collins, 1981). In Tsavo National Park (Kenya), termites removed 87 kg ha^{-1} yr^{-1} of animal dung from the surface of soil contributing to a nitrogen turnover of about 12 kg ha^{-1} yr^{-1} (Coe, 1977; Freymann et al., 2008). Fungus growing termites consume 20 to 30% of annual litter fall (Lepage, 1981). *Macrotermes michaelseni* grazed an estimated 270 kg ha-1 yr^{-1}, making it a strong competitor with wild and domestic mammalian herbivores (Buxton, 1981).

Wood feeding, wood-litter feeding, litter feeding and soil feeding species were all found to feed on the dung of different animals. Termites generally feed on items with a higher carbon to nitrogen ratio than their own tissues and the microorganism (symbionts) in their gut balances the ratio either by adding N to the inputs or selectively eliminating C. (Higashi et al., 1992). In a study by Freymann et al. (2008), termites did not show any signs of preference for dung compared with other food items. Termite decomposition of dung was observed to increase during the dry season (Coe, 1977). In the Okavango delta, *M. michaelseni* was shown to prefer wood litter compared to herbivore dung (Dangerfield and Schuurman, 2000). However, preference of termites can also be influenced by the spatio-temporal and

heterogeneous distribution of dung in the ecosystem. In addition, physical factors such as soil bulk density and texture, and spatial location of food items can have an influence on the food choices of termites (Eggleton et al., 1997).

Rouland et al. (2003) in the Sahelo-Sudanese savanna found that litter quality had an influence on the foraging of four sympatric species of termites. *Odontotermes nilensis* foraged preferentially on millet canes and *Acacia* leaves, *M. subhyalinus* preferred either millet cane or and ground millet. *Ancistrotermes guineensis* selected millet canes or *Combretum* wood, and *Microtermes* species foraged more on dead wood. Although cattle dung has a high C:N ratio, termites were observed to prefer maize straw which had lower C:N ratios (Freymann et al., 2008). Decomposition is an important process for soil fertility through its effects on both humification and mineralisation.

Nutrient cycling

Many organisms impact the ecosystems in which they occur. This phenomenon has led to the postulation of ecosystem engineering (Dangerfield et al., 1998). Organisms which play a part in ecosystem engineering are sometimes referred to as keystone species and examples include dung beetles, elephants, beavers and termites. Soil organisms determine soil fertility since they influence aeration, decomposition, nutrient levels and water management (Ackerman et al., 2009; Dangerfield et al., 1998). Termites qualify as ecosystem engineers because they modulate the availability of resources like food and water for other species such as plants and animals (Konaté et al., 1999). Termite activities often results in the formation of sheetings, galleries, nests and mounds that generally redistribute minerals and improve water infiltration (Bagine, 1984; Nutting et al., 1987; Wood, 1988). During construction of mounds, termites use topsoil or subsoil cementing it with saliva. *Macrotermes* use subsoil for mound building, and soil from this horizon has more inorganic nutrients and higher clay content (Table 1.1 and 1.2) (Jouquet et al., 2002a). The increased clay content of termite mounds leads to greater cation exchange capacity, which aids nutrient retention in the soil (Adekayode and Ogunkoya, 2009; Jiménez et al., 2008, 2006). Due to their modification of soil physical and chemical properties, termite mounds may be viewed as nutrient hotspots (Table 1.1 and 1.2) (Holdo and McDowell, 2004; Jouquet et al., 2002b; Konaté et al., 1999). In several studies, *Macrotermes* mounds were observed to contain high levels of Mg, Ca, K, and Na as

compared to the inter-mound matrix (Brossard et al., 2007; Dangerfield et al., 1998; Holdo and McDowell, 2004). However, this is not always true for soil organic C and N (Abbadie and Lepage, 1989; Glaser et al., 2001; Okullo and Moe, 2012).

In Côte d'Ivoire, termites improved soil nitrogen mineralisation, but not soil organic carbon (Abbadie and Lepage, 1989). Elsewhere, *Cubitermes niokoloensis* (soil feeding termites) mounds had C and N concentrations at least five times that of the off mound control soil, whilst *M. bellicosus* (a fungus growing termite) had similar or slightly less soil nutrient content than the surroundings (Fall et al., 2001). In a different study, mound soil had significantly higher amounts of C, N and P (López-Hernández, 2001) than the surrounding soil. The various differences between studies may be due to differences in termite species and soil conditions.

Moreover, during foraging termites gather large quantities of litter in their nests, depleting the surrounding environment of its source of humus (Vasconcellos and Moura, 2010). This litter is thoroughly digested such that the end products are of little value in terms of nutrient addition (Pomeroy, 1977). These fungus growing termites consume their own dead and excreta, further restricting nutrient cycling outside the mound, at least until the colony dies (Pomeroy, 1976). In an extensive study covering ultisols in Nigeria, *Macrotermes* mounds had no elevated nutrients compared to adjacent soils (Maduakor et al., 1995). However, in a recent commentary, O'Connor (2013) highlighted the importance of local environmental context when assessing ecological interactions of biotic and abiotic components of an ecosystem. It is likely that mounds located on nutrient-rich soils might not have a large impact on soil nutrients to give a distinct difference with the inter-mound matrix, while in nutrient-poor soil the difference is consequential (Figure 1.4).

Table 1.1: Comparison of elemental concentrations between termite biogenic structures and the surrounding vegetation matrix control soils.

Study area	Genus/species	N %		C %		Na		Mg		K		Ca		Source and units
		Mound/nest	Control	Mound/nest	Control	Mound/nest	control	Mound/nest	Control	Mound/nest	control	Mound/nest	Control	
USA, Temperate	*Heterotermes*	0.43	0.3	1.7	0.7	10.1	1.7	3.4	0.9	17.7	6.4	18.0	4.3	(Nutting et al., 1987) (ppm)
USA, Temperate	*Gnathamitermes*	0.03	0.3	1.0	0.7	7.0	1.7	1.7	0.9	8.0	6.4	10.1	4.3	(Nutting et al., 1987) (ppm)
Kenya, Tropical	*Macrotermes michaelseni*	0.10	0.14	0.91	1.62	0.3	0.1	3.4	2.0	2.7	2.0	15.5	8.1	(Arshad, 1982) (me/100g)
Kenya, tropical	*Odontotermes*	0	0	0.52	0.07	1.50	1.90	7.10	8.80	3.90	2.60	58.7	56.0	(Bagine, 1984) (me/100g)
Brazil, Tropical	-	0.25	0.19	4.38	3.29	-	-	7	7	33.3	24.1	25.6	35	(Ackerman et al., 2007) (mg/kg)
Nigeria, Tropical	*Macrotermes*	-	-	0.65	0.99	0.06	0.08	0.74	1.14	0.28	0.48	2.69	3.65	(Kang, 1978) (me/100g)
Nigeria, Tropical	*Macrotermes*	-	-	0.48	1.60	0.08	0.08	0.77	1.03	0.23	0.59	2.67	3.99	(Kang, 1978) (me/100g)
Zimbabwe, Tropical	*Macrotermes*	-	-	-	-	6	2	284	111	199	68	2973	315	(Holdo and McDowell, 2004) (mg/kg)
Zimbabwe, Tropical	*Macrotermes*	-	-	-	-	96.04	5.18	393.30	74.02	229.83	66.05	4300.40	402.19	(Joseph et al., 2013a) (mg/kg)
USA, Temperate	*Formica canadensis*	-	-	-	-	-	-	-	-	322	215	-	-	(Culver and Beattie, 1983) (mg/kg)
Venezuela, Tropical	*Nasutitermes ephratae*	0.73	0.21	9.3	2.5	-	-	-	-	-	-	-	-	(López-Hernández, 2001)
Senegal, Tropical	*Ancistrotermes guineensis*	0.05	0.07	0.61	0.79	-	-	-	-	-	-	-	-	(Mora et al., 2003)
Senegal, Tropical	*Odontotermes nilensis*	0.05	0.07	0.60	0.79	-	-	-	-	-	-	-	-	(Mora et al., 2003)
Senegal, Tropical	*Cubitermes niokoloensis*	0.26	0.04	2.8	0.57	-	-	-	-	-	-	-	-	(Ndiaye et al., 2004a)
Senegal, Tropical	*Macrotermes subhyalinus*	0.06	0.04	1.06	0.58	-	-	-	-	-	-	-	-	(Ndiaye et al., 2004b)
Senegal, Tropical	*Odontotermes nilensis*	0.05	0.04	0.88	0.58	-	-	-	-	-	-	-	-	(Ndiaye et al., 2004b)
Tropical	*Cubitermes severus*	0.29	0.14	2.5	1.5	-	-	-	-	-	-	-	-	(Wood, 1988)
Tropical	*Cubitermes oculatus*	0.50	0.06	1.7	0.8	-	-	-	-	-	-	-	-	(Wood, 1988)

For Arshad, 1982 mounds have been compared with the furthest distance sampled. Joseph et al. (2012) matrix soil was compared with the largest mounds.

Table 1.2: Comparison of soil physical properties between biogenic structures produced by termites and the surrounding vegetation matrix control soils.

Genus/species	Soil type	Coarse Sand % or sand		Fine sand %		Coarse Silt % or silt		Fine silt		Clay %		Source
		Mound/nest	Control	Mound/nest	Control	Mound/nest	Control	Mound/nest	Control	Mound/nest	Control	
	Dystrophic	0.07	0.06	0.02	0.02	0.2	0.17	-	-	0.72	0.76	(Ackerman et al., 2007)
Macrotermes	Oxic paleustalf	56	73	-	-	9	8	-	-	35	19	(Kang, 1978)
Macrotermes	Quartzipsamment	70	80	-	-	7	11	-	-	23	9	(Kang, 1978)
Cubitermes niokoloensis	Lixisol	9.6-9.0[b]	66.1	10.7-9.8[b]	17.6	24.9-28.8[b]	6.8	27.1-25.4[b]	3.6	23.7-22.8[b]	5.8	(Fall et al., 2001)
Macrotermes bellicosus	Lixisol	10.5-32.7[b]	48.5	18.5-19.5[b]	21.0	10.8-8.8[b]	9.7	8.7-5.3[b]	8.3	48.5-31.8[b]	13.1	(Fall et al., 2001)
Ancistrotermes guineensis		34.03	38.37-36.47[a]	31.17	29.9-27.3[a]	11.6	15.03-10.1[a]	3.67	4.43-2.9[a]	19.53	12.27-23.23[a]	(Mora et al., 2003)
Odontotermes nilensis		41.97	38.37-36.47[a]	30.63	29.9-27.3[a]	12.0	15.03-10.1[a]	3.47	4.43-2.9[a]	12.1	12.7-23.23[a]	(Mora et al., 2003)
Heterotermes aureus	Alluvium	75.6	74.8	-	-	20.8	23.7	-	-	3.6	1.5	(Nutting et al., 1987)
Gnathamitermes perplexus	Alluvium	76.8	74.8	-	-	19.6	23.7	-	-	3.6	1.5	(Nutting et al., 1987)
Odontotermes	Sandy loam to saline clay	66	48	-	-	14	40	-	-	20	12	(Bagine, 1984)

a: denotes values for samples taken at 0-20 cm and 21-40 cm respectively. b: denotes values obtained from the internal and external walls of the termites mound respectively

Plant species diversity

Conspicuous epigeal termite mounds are a common feature of arid and semi-arid savannas and key in creating spatial heterogeneity in soil and vegetation (Sileshi and Arshad, 2012; Sileshi et al., 2010). Elevated soil nutrients in termite mounds create distinct heterogeneous patches in an otherwise uniform landscape (Fox-Dobbs et al., 2010; Sileshi et al., 2010). For example, Moe et al. (2009) and Kirchmair et al. (2012) recorded higher plant species diversity on termite mounds compared to off mound control plots. In the miombo woodlands of central Zimbabwe, Loveridge and Moe (2004) observed a similar trend in plant species diversity on and off termite mounds.

In most studies termite mounds have been shown to contain unique plant species diversity compared with the surrounding woodland matrix (Table 1.3). Termite mounds influence ecosystem heterogeneity, for example the density of trees and shrubs has been found to be higher than the surrounding matrix in several studies (Jouquet et al., 2005; Loveridge and Moe, 2004; Moe et al., 2009; Traoré et al., 2008). The increased plant species diversity on mounds could be attributed to the improved soil chemical and physical properties of mound soil (Table 1.1 and 1.2). Termite mounds may also have improved soil water content, important for plant growth (Konaté et al., 1999; Mando et al., 1996). The avifauna nesting on large trees on old termite mounds (Joseph et al., 2011) may drop seed in their droppings through endozoochory, which can be an important source of propagules leading to high diversity on mounds (Joseph et al., 2013a). Their droppings can also improve the fertility of the mounds. Some bird species such as Tui Parakeets (*Brotogeris sanctithomae*), Cobalt-winged Parakeets (*B. cyanoptrea*) and Black-tailed Trogon (*Trogon melanurus*) were found to nest in arboreal termite mounds (Brightsmith, 2000), which might further improve the fertility of such mounds. In a different study, some *Acacia drepanolobium* trees were observed to have high foliar nitrogen close to termite mounds and even fruiting was significantly higher close to termite mounds than further away (Brody et al., 2010). This is probably due to increased levels of soil nutrients, which are important in fruiting, contained in the outwash from the mounds (Arshad, 1982). The increased spatial use of termite mounds by herbivores mammals and birds that might deposit faecal matter with seed (Grant and Scholes, 2006; Mobæk et al., 2005) may be important in the overall alpha biodiversity of a

site. As such, termite activity may influence spatial heterogeneity in vegetation composition, structure and diversity, which in turn can influence herbivory patterns.

Table 1.3: The number of unique species of woody and herbaceous plants that were observed on termite mounds compared to the total at a study site from some selected studies.

Location	Mean rainfall (mm)	Soil type	Woody/herbaceous	Number of exclusive plant species on termitaria	Total number for the study site	Source
Hwange: Zimbabwe	650	Kalahari sands	Woody	3	-	(Holdo and McDowell, 2004)
Loita Plains: Kenya	508-1016	vertisol	Herbaceous	6	65	Glover et al., 1964
Hluhluwe-iMfolozi park: South Africa	720-950	Basalt	Woody	23	67	Van der Plas et al., 2013
Lake Mburo National Park: Uganda	800	Histosols, vertisols, ferrasols, leptosols	Woody	11	42	Moe et al., 2009
Tiogo State Forest: Burkina Faso	631-1056	Lixisols	Woody	14	61	Traoré et al., 2008
Kijiado: Kenya	400-600	Chromic Luvisol	Herbaceous	1	9	Arshad, 1982
Sampeto: Benin	1000		Woody	6	54	Kirchmair et al., 2012

Hydrology

Soil water availability is one of the key characteristic of savanna ecosystems (Scholes, 1990; Skarpe, 1992). *Macrotermes* colonies extensively modify the hydrology of arid soils, turning their nests into a massive water-gathering system that enables them to survive in arid conditions (Konaté et al., 1999; Turner, 2006). Termites can dig deeper than 50 m in search of water (Wood, 1988). Foraging excursions of termites comprise a dense network of underground galleries that can extend up to 70 m from the nest creating an extensive network of macropores that promotes the infiltration of water into the soil (Darlington, 1982; Turner, 2006). However, the impact of macropores on runoff can be influenced by their density, for example a significant decline in runoff and increased infiltration rate was realised when

macropore density reached at least 30 m^{-2} (Léonard et al., 2004; Léonard and Rajot, 2001). Termites also produce calcite saucer-shaped depressions in the lower sections of the nest and water from the surroundings can drain into these depressions (Turner, 2006). This increases the amount of water that is available to termites, which they can use to maintain nest moisture and make rapid nest repairs, especially during the dry season (Wood, 1988). Water is transported in the termite crop (a sack shaped foregut part of the termite digestive system) in the form of salivary glue, which they use in mound building. Horizontal and vertical movement of soil by termites increases soil porosity and since the soil will have faecal carton and increased clay, it retains water better than the parent soil (Konaté et al., 1999; Wood, 1988). This results in termite mounds having more moisture than the surrounding woodland matrix environment. The improved moisture has the potential to increase the vegetation growth period on termite mounds (Scholes, 1990) and, coupled with elevated soil nutrients, plant species palatability may be improved.

Seasonal shading of leaves by vegetation has been observed to be highly correlated to availability. Comparing similar woody species on termite mounds and the woodland vegetation matrix, Konaté et al. (1999) observed early shedding of leaves by trees in the woodland matrix. Several studies have singled out termite mounds as occupied by vegetation greener than the surrounding vegetation matrix and sometimes by evergreen woody species (Arshad, 1982; Brody et al., 2010; Konaté et al., 1999; Van der Plas et al., 2013). Although vegetation establishment and palatability are highly influenced by soil substrate, moisture forms the link between them (Scholes, 1990). Water loving plants were observed to occupy termite mounds and to possess broad leaves (Van der Plas et al., 2013).

Establishment of vegetation at the base of termite mounds has been linked to the high density of foraging holes here (Bonachela et al., 2015). Also, the high herbaceous biomass at the base of the mound can facilitate infiltration (Arshad, 1982), thereby improving conditions for plant growth (Figure 1.5). Sampling down the profile of termite mounds and the matrix control sites for any given soil water potential, soil water ratio was higher for mound soil than control soil (Konaté et al., 1999). In the Chihuahuan desert, subterranean termites greatly enhanced water infiltration rates (88.4 ± 5.6 mm h^{-1}) into the soil compared with areas that had no termites (51.3 ± 6.8 mm h^{-1}) but similar perennial vegetation cover (Elkins et al., 1986). Maintenance of high soil water content by termites within and near their nest structures could

greatly influence the growth patterns of vegetation in the ecosystem. The ripple effect could be observed on the level of grazing on termite mounds compared to the savanna matrix (Figure 1.4).

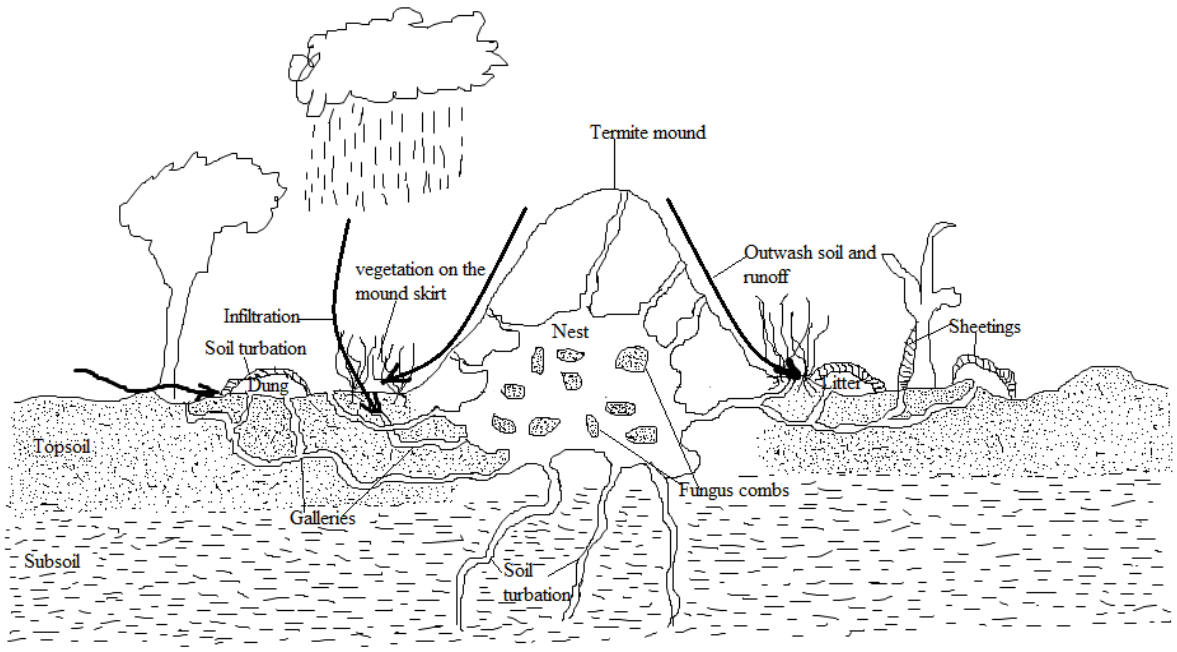


Figure 1.5: Diagrammatic representation of how *Macrotermes* mounds improve water infiltration into the soil adapted from Grohmann (2010).

Large mammal herbivory

Mammalian herbivore distribution is normally influenced by forage quality and quantity (Fryxell, 1991; McNaughton and Georgiadis, 1986), although other factors like predation pressure and competition can also be important (Riginos and Grace, 2008; Valeix et al., 2009).

In tropical and sub-tropical ecosystems, epigeal termite mounds have been shown to influence the distribution of ungulates (e.g. Freymann et al., 2010; Mobæk et al., 2005). (Mobæk et al. (2005) found bushbuck (*Tragelaphus scriptus*), impala (*Aepyceros melampus*), waterbuck (*Kobus ellipsiprymnus*), zebra (*Equus burchelli*), warthog (*Phacochoerus africanus)* and topi (*Damaliscus lunatus*) to graze close to termite mounds. In a similar study, steenbok (*Raphicerus campestris*), eland (*Taurotragus oryx*), Grant's gazelle (*Nanger granti*), zebra, cattle (*Bos taurus*) and buffalo (*Syncerus caffer*) dung density decreased significantly with distance from termite mounds (Brody et al., 2010). Megaherbivores such as

elephants have also been shown to feed on rich patches of termite mounds in the Kalahari sands of western Zimbabwe (Holdo and McDowell, 2004). In central and eastern Zimbabwe, black rhino were observed to selectively feed more on vegetation on termite mounds than in the savanna matrix (Loveridge and Moe, 2004; Muvengwi et al., 2013).

Although several studies on large mammal herbivory found utilization of termite mound vegetation to be higher relative to the surrounding matrix vegetation (Brody et al., 2010; Loveridge and Moe, 2004; Mobæk et al., 2005; Muvengwi et al., 2014), some studies have disputed this phenomena after recording no difference in herbivore preference (Muvengwi et al., 2013; Van der Plas et al., 2013). These contrasting findings are attributed to marked difference in soil nutrients in some of the studies, whereas there were fewer differences in soil nutrients between mounds and matrix soils in others, hence the need to examine termite mound effects across sites of varying environmental context (O'Connor, 2013).

Foraging animals select foraging patches at different spatial scales (Bailey et al., 1996; Cromsigt et al., 2009). Mounds on the savanna vary in size, a characteristic that has a significant effect on vegetation heterogeneity (Joseph et al., 2013a). Larger mounds host a highly different suite of plants compared to the savanna, while small mounds are not different from the savanna (Joseph et al., 2013a). Furthermore, large foraging patches with high quality forage attract grazing and/or browsing animals more compared with smaller ones (Cromsigt and Olff, 2006; Pretorius et al., 2011). In a study comparing herbivory on mopane by elephant on fertilised experimental plots and unfertilized plots, a significant difference in the extent of vegetation utilization was obtained at the scale of 100 m^2 which was higher on fertilized plots but not at the 4 m^2 scale (Pretorius et al., 2011). This difference could be attributed to the spatial scale at which a nutrient hotspot can influence feeding of a large herbivore like an elephant. However, the effects of termite mound size on grazing patterns, including across environmental gradients such as geology, have not been addressed (Figure 1.4).

Thesis objectives and structure

My main aim was to evaluate the effect of geology (and therefore nutrient status and/or environmental context) on termite related aspects of savanna ecology. From the Introduction Chapter above, I move to Chapter 2 as my first data chapter, looking at how the diversity of termite species varies between two geologies (granite and basalt). After establishing the species occurring in the two geologies (Chapter 2), focus in Chapter 3 is on the epigeous *Macrotermes* mounds. Mound density, size and spatial distribution are compared between the two geologies. Building on Chapter 3, focus in Chapter 4 is on how the mounds influence vegetation heterogeneity across landscapes emanating from different geologies. In Chapter 5, spatial and temporal effects of mounds on grazing intensity are investigated. Chapter 6 is a synthesis of the study, starting with conclusions and recommendations and finally the implications of my findings for conservation.

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Chapter 2

Chapter 2: Termite Diversity is higher in Landscapes with Lower Productivity

Abstract

Termites are recognised as soil ecosystem engineers in the tropics and sub-tropics, making the understanding of their distribution and population biology a priority. However, there is a poor understanding of the links, if any, between termite species diversity and landscape-level heterogeneity, such as differences in soil properties. We compared the diversity of termites between two soils of differing geological provenance (basalt and granite), and consequently contrasting nutrient status, but subject to a similar climatic envelope in a dry Zimbabwean savanna. We found basaltic soils to be more nutrient-rich than granitic soils, with higher amounts of exchangeable Ca and Mg, total N and available P. However, despite this higher soil nutrient status on basalts, functional and taxonomic termite diversity was higher on granites, although termite abundance was similar between the geological substrata. Termite assemblages differed between the substrata, with very little overlap. We conclude that termite diversity is highly influenced by soil productivity, with nutrient poor soils having higher levels of diversity due to reduced competitive exclusion.

Key words: feeding groups; geology; productivity-diversity hypothesis; semi-arid savanna; soil fertility; species density; Zimbabwe

Introduction

Understanding variation in species diversity across and between landscapes is of paramount importance for ecosystem management and the implementation of conservation measures. Landscape productivity is known to influence diversity, and usually a hump-back shaped (unimodal) relationship is observed between productivity and species richness, with an increase at low productivity but a decrease in species richness at very high productivity with evidence suggesting that an increase in productivity leads to an increase in diversity (the "productivity-diversity hypothesis", Tilman 1982). Support for this hypothesis comes from a number of studies across different ecosystems and taxa (e.g. Tilman *et al.* 2001, Cardinale *et al.* 2009, Cusens *et al.* 2012). However, although empirical evidence exists in support of this hypothesis, other studies have disputed the existence of a positive correlation between productivity and diversity. For example, there was a negative relationship between biomass production and grass diversity in England (Silvertown, 1980), rodent diversity decreased with an increase in productivity in a wide ranging study in North America (Owen, 1988), and diatom species diversity decreased with increasing productivity in an aquatic experiment (Yount, 1956). In an extensive review, 41-44 percent of the studies examined showed a unimodal pattern between species richness and productivity of vascular plants, and no dominant pattern was observed for animals (Mittelbach *et al.* 2001). Higher productivity may imply more available resources for the different organisms. However, some studies which are against the productivity diversity hypothesis would argue that as the environment becomes more productive, competitive exclusion becomes more important hence monopoly by a few species (Grime, 1973).This observation shows that more research is still needed before generalizations can be made. We therefore took the opportunity to test the productivity diversity hypothesis using termites which are widely distributed in the savanna.

Termites (Blattodea: Termitoidae) are frequently important organisms in tropical and subtropical ecosystems. They not only constitute a large proportion of animal biomass in these systems (Moe et al., 2009), but also act as ecosystem engineers (Jones *et al.* 1994, Dangerfield *et al.* 1998, Jouquet *et al.* 2011), altering the mineral and organic composition of soils, influencing water infiltration and drainage (Scholes 1990, Mando *et al.* 1996), and playing important roles in decomposition processes (Collins, 1981; Schuurman, 2005), there by influencing nutrient cycling (Holt and Coventry, 1990; Konaté et al., 1999). Through such

activities, termites contribute substantially to landscape heterogeneity. Larger termite mounds harbour distinct communities of woody and herbaceous vegetation compared to the inter-mound matrix (Moe *et al.* 2009, Davies *et al.* 2016, Davies *et al.* 2014a), increasing landscape diversity (Joseph et al., 2014), and, together with a preponderance of green and nutrient-rich vegetation (Sileshi et al., 2010), often positively influence patch utilization by mammalian herbivores (Mobæk *et al.* 2005, Brody *et al.* 2010, Muvengwi *et al.* 2014, but see Muvengwi *et al.* 2013, Van der Plas *et al.* 2013 for exceptions to this general pattern).

Termite species diversity has been shown to change along numerous environmental gradients: increasing as mean annual rainfall increases in the savanna (Buxton 1981, Davies *et al.* 2015), while conspicuously decreasing with increased levels of anthropogenic disturbance in tropical forests (Eggleton *et al.* 1996, 1997, Dosso *et al.* 2010)**.** Termite diversity is always higher in intact forests compared to more disturbed anthropogenic land use areas, such as plantations (Attignon et al., 2005; Dosso et al., 2013). Sharp decreases in termite diversity have also been reported with increasing altitude (Gathorne-Hardy et al., 2001; Palin et al., 2011). As yet, there is a lack of consensus on the influence of fire (see Davies *et al.* 2010 for a review), with some studies finding no effect of long-term fire regimes (e.g. Davies *et al.* 2012), and others recording a decline in termite abundance immediately following fire (e.g. Dawes-Gromadzki 2007). Although geological variation has been shown to have an effect on vegetation heterogeneity (Venter *et al.* 2003), little is known about the landscape and point-scale relationships between termites and soil properties (Jones et al., 2010). Indeed, there is little information on how termite species composition varies in areas with different geologies (but see Wild 1975, Jones *et al.* 2010), resulting in a poor understanding of how termite diversity differs across landscapes. Where geology has been considered, the focus has been on the density and spatial distribution of mounds built by *Macrotermes* (Meyer *et al.* 1999, Davies *et al.* 2014b), excluding the majority of taxonomic and functional termite groups that do not build conspicuous mounds. To date, very little is known regarding how variation in geological substrate influences overall termite species diversity in savannas, especially at the landscape scale (but see Wild 1975).

Soil nutrient status has frequently been used as a surrogate of ecosystem productivity (Chapin III *et al.* 1986, Fridley 2001) and is known to strongly influence floral and faunal distribution and diversity (Scholes & Walker 1993, Archer 1995, Giller 1996, Ettema & Wardle 2002).

This is further supported by the notion that the link between productivity and diversity lies in the fertility of the soil (Cowling et al., 1994; Scholes, 1990), which in turn is primarily influenced by the parent rock material from which the soils were derived (Bell, 1982). In southern Africa, basaltic landscapes are generally regarded as nutrient rich and granite as nutrient poor (Grant and Scholes, 2006; Scholes, 1990). Granitic landscapes also have a lower clay content compared to basaltic ones (Olowolafe, 2002). Termites, being consumers of organic matter, are expected to respond to landscape productivity and in particular soil nutrients since they live in the soil and several groups actively feed off it (Donovan *et al.* 2001). Termites also require clay for nest construction (Levick *et al.* 2010a, Jouquet *et al.* 2002, 2004), and may possibly be absent in very sandy soils (Levick *et al.* 2010a). However, too much clay can cause soil to become water logged and prone to cracking, becoming unconducive to termite nesting or activity (Dawes-Gromadzki & Spain 2003, Dibog *et al.* 1998**)** and resulting in an absence of termites (Levick *et al.* 2010a, Meyer *et al.* 1999). Therefore, in this study we ask how geological variation affects termite diversity.

Here, we compare variation in termite species diversity between two geological substrates of differing soil nutrition, granite and basalt, in a semi-arid African savanna. We first assessed soil nutrient concentrations (and hence fertility) on both substrata, and then compared termite species density, abundance, composition and activity levels between the two substrata. Differences in soil nutrients were used as a surrogate for ecosystem productivity. We expected basalt to have higher fertility than granite and therefore, based on the productivity-diversity hypothesis, we expected higher termite species diversity on the basaltic substratum.

Methods

Study site

The study was conducted on two geological substrata (basalt and granite) in the 5000 km^2 Gonarezhou National Park (GNP), in the south eastern lowveld (low altitude) of Zimbabwe (21^0 00′ - 22^0 15′ S, 30^0 15′ - 32^0 31′ E). The study area lies in a semi-arid savanna ecosystem with an average annual rainfall of 466 mm. Sampling plots were located in relatively close proximity, resulting in rainfall between them being similar (Figure 1.2). Mean monthly maximum temperatures range between 26 ^{0}C in July and 30 ^{0}C in January, whereas mean monthly minimum temperature ranges between 9 ^{0}C in June and 24 ^{0}C in January (Gandiwa et al., 2011). GNP experiences three distinct seasons, hot wet (November to March), hot dry

(August to October) and cool dry (April to July). Fire return period across the entire study site was two years (E. Gandiwa, pers. comm.).

Areas on basalt are dominated by *Colophospermum mopane* woodland, with scattered *Combretum apiculatum*. The granitic areas have a mixture of tree species, including *Androstachys johnsonii*, *Brachystegia glaucescens*, *Vitex payos*, *Diospyros loureiriana* and *Xeroderris stuhlmannii*. The herbaceous community on basalt is dominated by *Aristida rhiniochloa, A. adscensionis and Brachiaria deflexa,* while granite consists largely of *Digitaria eriantha*, *Tragus berteronianus*, *Urochloa mosambicensis* and *Heteropogon contortus*. All sampling was carried out in four randomly marked 100 ha (1x1 km) grid cells on each geological substratum, spaced between 3 km and 12 km apart.

Soil sampling and analysis

A total of six soil cores of 6 cm diameter and 10 cm depth were randomly collected from each of the four 100 ha grid cells located on each geological substratum. Soil sampling was conducted at least 16 m away from any termite mound to avoid termite influence on soil nutrition (Levick *et al.* 2010b, Gosling *et al.* 2012, Davies *et al.* 2014a). The samples from each 100 ha grid cell were bulked into one sample for laboratory analysis. Therefore, a total of four samples were analysed for nutrient concentrations, pH and texture for each geological substratum.

Soils were assayed for total N, Resin-extractable P, pH, texture (sand (0.02 - 0.2 mm), silt (0.02 - 0.002 mm) and clay (< 0.002 mm), as well as exchangeable Ca, Mg, Na and K at the Department of Research and Specialist Services, Chemistry and Soil Research Institute in Harare, Zimbabwe. Soil samples were air dried at room temperature before analysis. Soil texture and pH were obtained using the hydrometer and $CaCl_2$ method respectively (Okalebo et al., 2002; Thomas, 1996). Exchangeable bases were extracted using the aqua regia digestion method (Anderson and Ingram, 1993). The resulting compound was then dissolved in concentrated HCl and filtered. The solution was diluted with distilled water. Using a spectrophotometer, total Ca and Mg were determined at 0.460 nm and 0.595 nm, respectively, and flame emission was used for K and Na. Total N was determined using the Kjeldahl method (Okalebo et al., 2002). Plant available phosphorus was determined using the molybdenum-blue calorimetric method (Sibbesen, 1978).

Termite sampling

Termites were sampled between November 2013 and February 2014, the period of highest termite activity in southern African savannas (Davies *et al.* 2015) using two methods, active searching along transects and cellulose baits. A single transect, 100 m long and 2 m wide (following Jones & Eggleton 2000), was laid in each 100hagrid cell, starting at the centre of the grid and running north. Each transect was divided into 20 contiguous plots of 10 m^2 (5 × 2 m) (following Dosso *et al.* 2010, Davies *et al.* 2013). To standardize sampling effort, one person spent 30 minutes sampling through a single plot. In all plots, termites were hand-searched from all available microhabitats, including logs, litter, stumps, twigs, nests, runways, sheeting, fallen branches and grasses (Davies et al., 2013; Jones, 2000; Jones and Eggleton, 2000). Trees were searched up to a height of 2 m above ground level. The surface of the soil was also sampled by excavating 12 random samples per plot, each 12 x 12 cm surface area to a depth of 10 cm (Jones and Eggleton, 2000). Excavated soil was hand-sorted *in-situ*. Total encounters of each species present along transect sections was used as a surrogate for relative abundance (following Davies *et al.* 2003a). Termite soldiers were removed and placed in vials containing 70 percent ethanol for later identification. When soldiers were unavailable, workers were collected.

Eighteen cellulose baits consisting of toilet rolls (110 mm diameter and 100 mm long, 350 sheet single-ply, unscented) were placed in a six metre by three metre grid at the centre of each 100 ha grid cell. All baits were buried 2 cm below the surface (Davies et al., 2013; Dawes-Gromadzki, 2003) and checked after 14, 28, and 56 days. At each sampling interval, six different baits were randomly selected for inspection and replaced. The replaced baits were re-examined during each subsequent visit (28 and 56 days) for species collection only (Dawes-Gromadzki, 2003). Bait attack by termites was identified by the presence of termites or gallery material and signs of termite feeding where bait material had been removed. The proportion of baits attacked at each census was recorded as well as the frequency of termite attack. Intensity of bait attack by termites was estimated following Dawes-Gromadzki (2003) using a six point scale: 0 = no attack, 1 = 1-24 percent of bait consumed, 2 = 25-49 percent, 3 = 50-74 percent, 4 = 75-99 percent and 5 = 100 percent consumed, or replaced by gallery and/or faecal carton material.

Termite identification

Termites were identified at the University of Pretoria, and the Plant Protection Research Institute, Agricultural Research Council, Pretoria, South Africa. Specimens were identified to species level, using the soldier castes when available. Where species identification was not possible (*e.g.*, for *Odontotermes*), samples were identified to morphospecies. When soldier castes were unavailable, worker castes were identified to the genus level (*e.g.*, *Microtermes*, *Macrotermes*, *Microcerotermes*). The identified species were categorised into four taxonomic and feeding groups. Group I comprises the lower termites which feed on dead wood and grass. Groups II to IV comprises the order Termitidae; group II feed on grass, dead wood leaf litter and micro-epiphytes; group III feed on soil organic matter in the upper layer of the profile and group IV feed on mineral soil (Donovan et al., 2001).Termite voucher specimens are housed at the University of the Witwatersrand, Johannesburg, South Africa.

Data analysis

We tested for differences in soil nutrients, texture and pH by comparing soil samples from the two geologies using independent Student's *t*-tests. Percentage data were arcsine square root transformed before analysis.

Termite species sampling completeness was assessed by constructing sample-based and individual-based species accumulation curves using the *Biodiversity* package in R. Measures of termite community diversity on each geological substratum were computed using EstimateS (Colwell, 2013). Hill's numbers and evenness values, Fisher's α, Simpson's index and Shannon Wiener index were calculated. Differences in species density and termite encounters between geologies sampled by active searching were assessed using independent Student's *t* tests, after confirming that the data were normally distributed. Correlation between termite species richness and measured soil nutrients, pH and texture were assessed using Spearman rank correlation tests for each geological landscape (four blocks). Correlation strength was interpreted as strong, moderate and weak for $\rho \geq 0.7$, $0.4 \leq \rho < 0.7$ and $\rho < 0.4$, respectively (Evans, 1996).

Variation in termite species composition between the two geologies at the species level was tested using Analysis of Similarity (ANOSIM). ANOSIM computes a test statistic (R_{ANOSIM}) ranging from -1 to 1, with 1 indicating greater dissimilarity between groups (Magurran, 2004). In order to visualise variations in termite assemblage composition between the two

geological substrata, non-metric multidimensional scaling (nMDS) was applied separately to active searching and cellulose bait data. These were iterated fifty times in order to achieve a global optimum (Clarke & Warwick 2001). Fisher's exact tests of independence were used to test for differences in both functional (feeding groups) and taxonomic composition (at the subfamily level) of the termite species between the two geologies.

Patterns observed in bait attack intensity, bait attack frequency and accumulated number of termite species at baits were statistically inferred using mixed effects models. Since we were interested in the influence of location (basalt or granite) on termite activity on baits, time and grid cell were incorporated as random factors, with time nested within grid cell. All analyses were carried out in either EstimateS (Colwell, 2013) or R software v 2.15.1 (R Foundation for Statistical Computing, Vienna, AT). All values are given as mean ± SE.

Results

Soil characteristics

Soil texture was not significantly different between basalt and granite (Table 2.1). Basaltic landscape had significantly higher pH (6.1 ± 0.1) compared to granite (5.2 ± 0.2, Table 1), and had larger amounts of exchangeable Ca and Mg, total N and available P by factors of 1.7, 2.4, 1.4, and 1.8, respectively (Table 2.1). The concentrations of Na, total mineral N and K did not differ significantly between the two landscapes (Table 2.1). Basalt had a significantly higher sum of exchangeable bases, Ca, Mg, Na and K (S-value) by a factor of 1.8 (Table 2.1).

Table 2.1: Comparisons of soil nutrient concentrations, pH and texture (mean ± SE) between the two geological substrates, granite and basalt. Significant P values in bold type, d.f.= 6 throughout.

	Geology			
Variable	Basalt	Granite	t-value	p value
Sand (%)	58.0 ± 2.0	62.3 ± 2.84	-1.2	0.274
Silt (%)	28.5 ± 2.3	23.3 ± 1.8	1.8	0.128
Clay (%)	13.5 ± 1.4	13.3± 1.3	0.1	0.916
pH	6.1 ± 0.1	5.2 ± 0.2	5.2	**0.004**
Total N (g/kg)	1.0 ± 0.1	0.7 ± 0.1	2.7	**0.042**
Mineral N (mg/kg)	23.0 ± 3.9	12.8 ± 1.4	2.5	0.070
P (mg/kg)	12.8 ± 1.0	7.0 ± 1.2	3.4	**0.019**

Ca (me. %)	2.8 ± 0.2	1.7 ± 0.2	3.7	**0.010**
Mg (me. %)	1.2 ± 0.1	0.5 ± 0.1	4.3	**0.006**
Na (me. %)	0.1 ± 0.01	0.06 ± 0.02	0.1	0.916
K (me. %)	0.3 ± 0.05	0.2 ± 0.09	0.3	0.745
S-value (me. %)	4.4 ± 0.3	2.5 ± 0.3	4.2	**0.006**

S-value is the sum of exchangeable bases (Ca, Mg, Na and K) Cowling & Witkowski (1994)

Sampling adequacy, species diversity and abundance

All termite species sampled belong to one family, Termitidae and three subfamilies (Macrotermitinae, Termitinae and Nasutitermitinae, Table 2S1). Species accumulation curves indicated that the sampling was adequate on both substrates (12 species on granite and five species on basalt, Fig. 2.1). The rate of finding new species beyond two plots was generally low considering that only one species was added from plot 3-4 and 2-4 on granite and basalt, respectively (Fig. 2.1A). There were 375 termite encounters (relative abundance, *sensu* Jones & Eggleton 2000), for a total of 15 species on both geological substrates combined, although they only shared three species. One termite species that was missed by both baiting and active searching, but known to occur at the study site, was *Hodotermes mossambicus*. This species was seen on the ground in some sections of the study site on cloudy days in October 2013, but not retrieved from the soil or by dissecting dead wood.

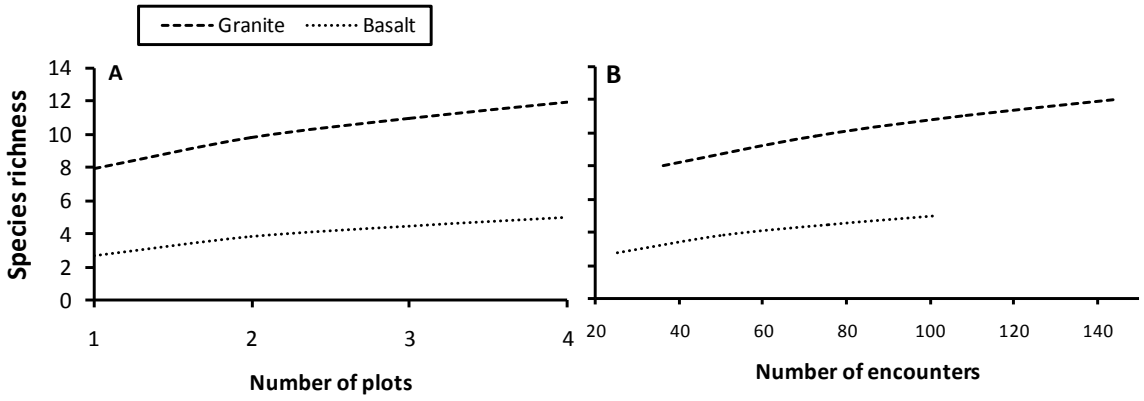


Figure 2.1: Cumulative termite species richness based on (A) sampled plots and (B) number of encounters on each of the two geological types, granite and basalt from the active searching method. Each plot was measuring 100 x 2 m (200 m^2).

Although basalt had similar termite abundance (number of encounters) to granite (185 vs. 190), assemblages on basalt were dominated by one genus, *Microtermes*, which comprised 80 percent of the total encounters (Table 2S1). Active searching, which targets all feeding

groups, showed that geology had a significant effect (t = 12.01, df = 4.97, P< 0.0001) on termite species density, with basalt having 2.25 ± 0.25 and granite 8.00 ± 0.82 species per sampling transect. Furthermore, for baiting data, geological substrate had a significant influence (Z = 2.14, P = 0.03) on the mean number of termite species per grid of baits (Fig 2.2C). Shannon Wiener, Simpson and Fisher's α diversity indices showed that termite diversity was higher on granite than basalt (Table 2.2).

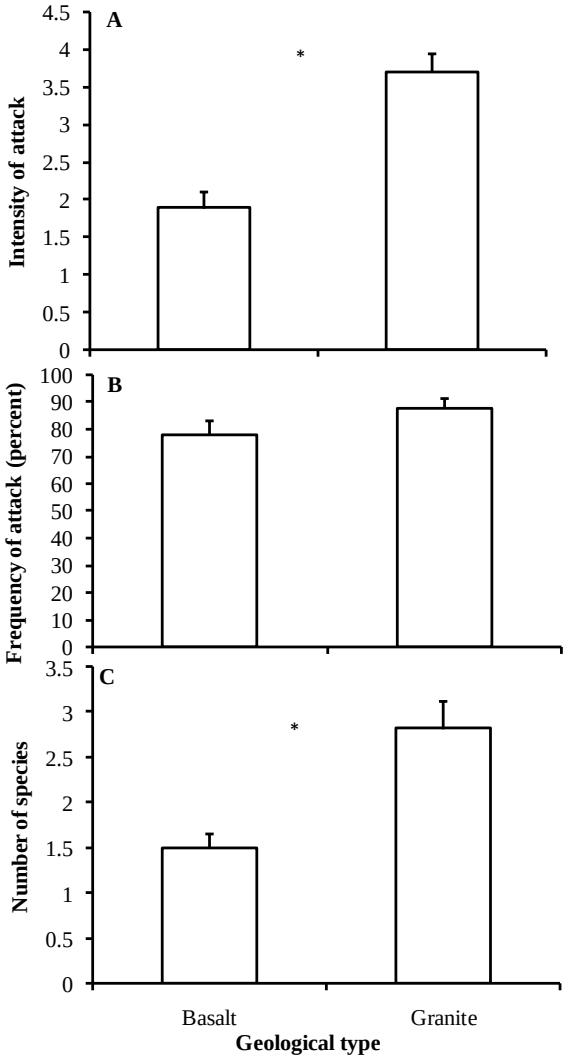


Figure 2.2: Mean (± SE) (A) bait attack intensity, (B) bait attack frequency and (C) number of termites recorded at cellulose baits on the two geological substrates, granite and basalt, after 56 days. An asterisk denotes significant differences between geologies.

Species evenness (E1 and E5) was higher on granite compared to basalt for the searching method, whereas the opposite was true for baiting. Hill's numbers showed that the number of species that are abundant (N_1), very abundant (N_2) and most abundant (N_∞) were higher on

granite for both searching and baiting methods (Table 2.2), with Hill's numbers (N_2 and N_∞) clearly indicating that basalt was dominated by one species. Geology had no effect on the numbers of termite encounters per sampling transect (t = -2.00, df = 5.06, P = 0.101). Basalt had 25.25 ± 2.93 encounters and granite 36.25 ± 4.64 encounters.

Table 2.2: Comparison of selected measures of diversity between basalt and granite from two methods, searching and baiting in Gonarezhou National Park.

	Searching		**Baiting**	
Index	**Basalt**	**Granite**	**Basalt**	**Granite**
Total encounters	101	145	84	45
Species richness	5	12	2	8
Shannon (H′)	0.50	1.94	0.62	1.64
Simpson (-ln λ)	0.26	1.64	0.56	1.49
Fisher's α	1.10	3.10	0.37	2.83
Evenness E1 (Shannon J′) (H'/H'_{max})[a]	0.31	0.78	0.89	0.81
Evenness E5 (N2-1/N1-1)	0.46	0.70	0.87	0.79
Hill's N1 ($e^{H'}$)	1.65	6.96	1.86	5.37
Hill's N2 (1/ λ)	1.30	5.17	1.75	4.45
Hill's N_∞ (N/N_{max})[b]	1.15	2.96	1.45	2.14

[a] H'_{max}= ln S (maximum value of the Shannon index)

[b] N_{max} = (the number of individuals of the most abundant species)

Assemblage composition

Termite community composition was significantly different between basalt and granite substrates for both sampling methods (ANOSIM: Global R= 1, P = 0.035 and Global R = 1, P = 0.025 for active searching and cellulose baits, respectively), and samples from each substrate were clumped together on the nMDS ordination (Fig. 2.3). Termite species richness

in the three subfamilies was not associated with geology (P = 0.075, Fig. 2.4A), whereas the proportion of encounters (abundance) was significantly associated with geology (P = 0.0003, Fig. 2.4B), with more encounters of Macrotermitinae, but fewer of Termitinae and Nasutitermitinae on basalt (Fig. 2.4B).

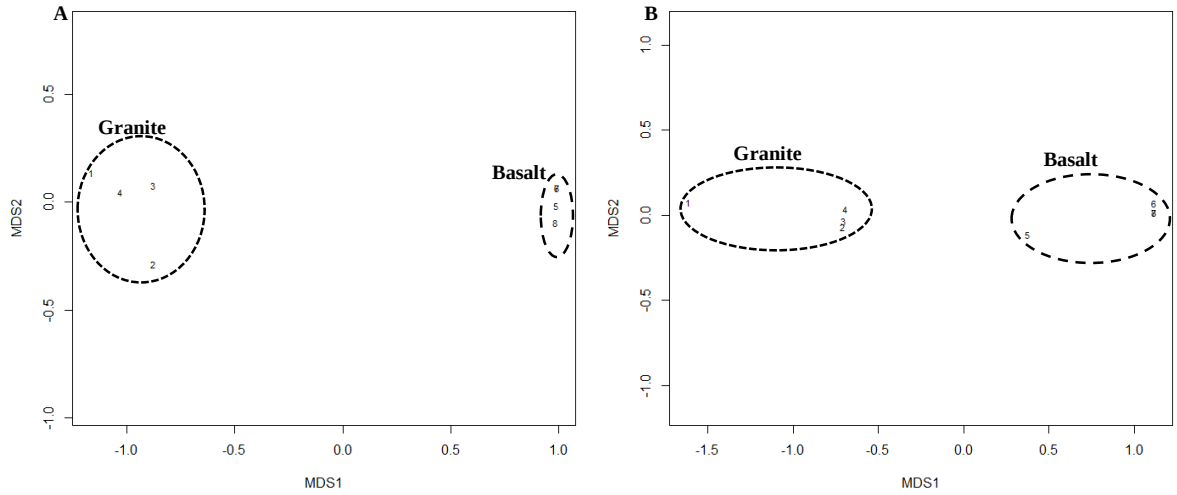


FIGURE 2.3. Non-metric multi-dimensional scaling (nMDS) ordination of abundance of termite species for (A) active searching and (B) cellulose baits on the two geological substrates, granite and basalt. Numbers 1-4 represent sampling grid cells on granite, while 5-8 represent grid cells on basalt.

Overall, termite functional diversity was low, with only two feeding groups recorded, groups II and IV, with feeding group IV unique to granite. Feeding group species composition was independent of geology (P = 0.075, Fig. 2.4C), however, the proportion of species encounters in the two feeding groups was dependent of geology (P = 0.0003, Fig. 2.4D).

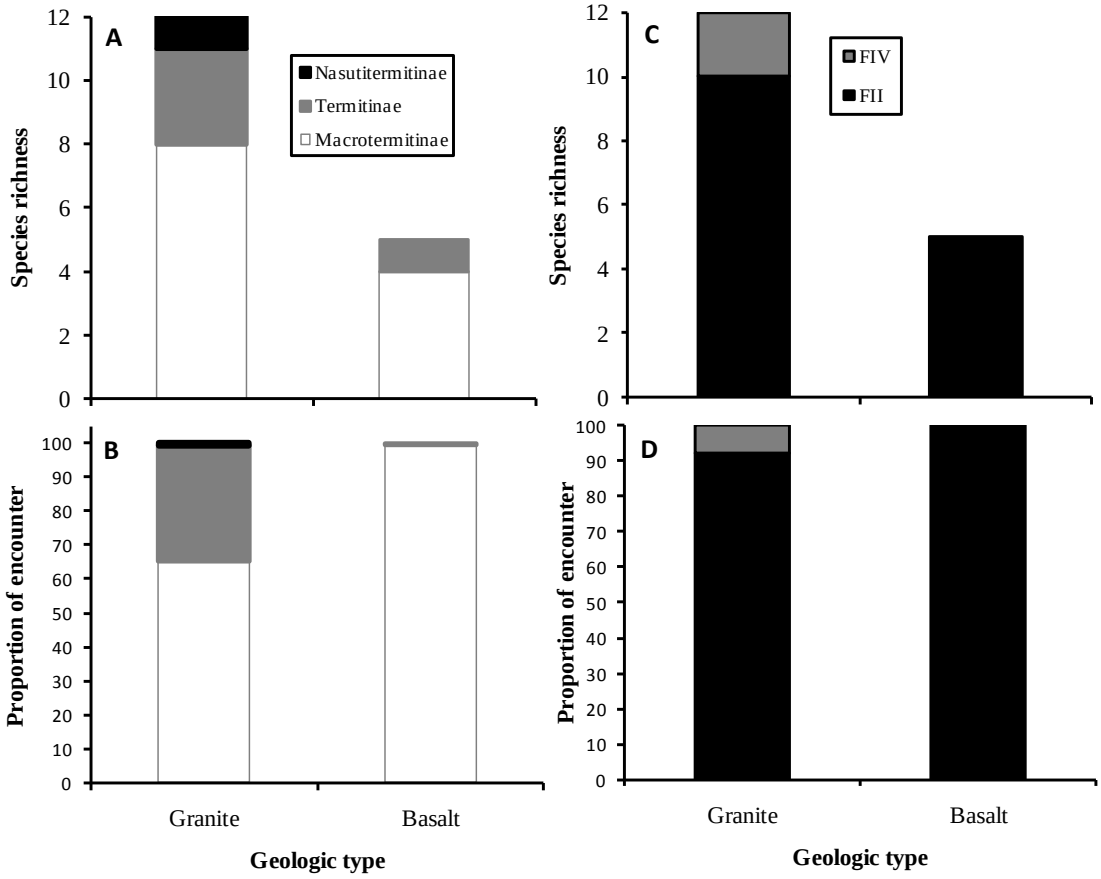


Figure 2.4. Taxonomic and functional composition of termites from the two geological substrates, granite and basalt. (A) and (B) represent species richness and encounters of subfamilies, respectively, while (C) and (D) show species richness and encounters of feeding groups, respectively. Values are pooled over all the four transects from each geology, each transect = 100 x 2 m (200 m^2).

Frequency and intensity of bait attack

Bait attack intensity varied significantly ($Z = 4.51$, $P < 0.0001$) between the two geologies, being higher on granite (3.71 ± 0.23) compared to basalt (1.89 ± 0.22) (Fig. 2.2A). However, frequency of bait attack was not significantly different between substrates ($P > 0.05$), although it was higher on granite (87.42 ± 3.61) compared to basalt (77.68 ± 5.54) (Fig. 2.2B).

Discussion

Despite the basalt being more nutrient rich compared to the granite, termite species richness, diversity, evenness and Hill's numbers were higher on granite. Furthermore, species

assemblages were very different between the two geologies. In contrast, the number of termite encounters (abundance) was similar between the two geologies. Although attack frequency at baits was similar between geologies, attack intensity was higher on granite.

Species diversity and abundance

Our findings suggest that in savannas, basaltic landscapes represent areas of high soil productivity (high N, P and S-value), but termite species attain higher richness on granites despite the lower soil nutrient status compared to basalt (Braithwaite et al., 1988). In a different study testing the energy-diversity theory, termite diversity increased with increase in net primary production at a global scale (Eggleton et al., 1994). However, when termite diversity was considered at biogeographical scales, generic richness was highest at the least productive site (Eggleton et al., 1994). As such, it is plausible that scale may override the influence of some environmental factors that influence termite species diversity. According to Tilman (1988, 1994), the resource ratio hypothesis predicts that more species coexist at low levels of resources because organisms perceive the environment as more spatially variable (Tilman, 1994, 1988), thus with more niches, leading to higher species evenness, such as we observed on granite. Therefore, our results do not appear to follow the productivity-diversity hypotheses (Tilman, 1982) as we had expected, but rather confirm observations made on plant species composition, that nutrient-poor environments are more diverse, partly because such environments limit competitive exclusion by a few dominant species as can occur in nutrient-rich environments (Grime 1976**,** Wisheu *et al.* 2000, Crawley *et al.* 2005). Alternatively, termite diversity could have been higher on granite comparing with basalt due to higher plant productivity and diversity on granite (Chapter 4).

The higher Ca, Mg and hence S-values recorded on basalt could have also led to the lower termite species richness and diversity. In a similar study, higher concentrations of Ca and Mg were associated with a species depauperate site (Jones *et al*. 2010). Furthermore, the higher soil pH recorded on basalt may have influenced the observed significant differences in species richness and diversity between geologies. In a study in Borneo, comparing ultramafic and non-ultramafic soils, termites were highly influenced by pH (Jones et al., 2010). It could be that higher pH on basalt excludes many termite species by severely disrupting their gut physiology (Jones et al., 2010). Although clay content was not significantly different between the geologies, even slight differences can influence termite species abundance and diversity (Pequeno et al., 2015). Although several other factors are known to influence termite species

richness and diversity, such as fire (Davies et al., 2012; Dosso et al., 2010), rainfall (Davies et al., 2015, 2013) and temperature (Mitchell, 1980; Pomeroy, 1976), they did not differ between the plots. Our data strongly suggests that geology was the major driver of the observed patterns. The absence of soil feeders on basalt further contributes to the decrease in termite species diversity on this landscape. Basaltic soils are black in colour due to their high clay content, and likely absorb more heat than the lighter coloured granitic soils, leading to faster desiccation, which can be lethal for these fragile soil feeding groups (Davies et al., 2012; Eggleton et al., 2002). Therefore, geology could indirectly affect diversity via soil climatic conditions and not necessarily via soil nutrition.

Assemblage composition

The termites sampled were dominated by the subfamily Macrotermitinae, regardless of geological substrate (Fig. 2.3A). This is one of the most important termite feeding groups in arid and semi-arid savannas and responsible for about 20 percent of C-mineralization (Aanen and Eggleton, 2005; Songwe et al., 1995). Macrotermitinae are able to process low-quality food in dry environments because of their mutualistic symbiosis with the fungus *Termitomyces* (Aanen and Eggleton, 2005). Macrotermitinae originated in African rainforests together with *Termitomyces* and were able to spread to arid and semi-arid savannas because they can harvest and store food as fungus combs (Collins 1981, Aanen *et al.* 2002, Aanen & Eggleton 2005). Furthermore, Macrotermitinae create environments with buffered temperature and humidity required for full growth of *Termitomyces*, which has enhanced their ability to colonise these dry savannas (Aanen and Eggleton, 2005).

Termite species composition was almost entirely different between the two geological substrata. However, *Microtermes* was the most prevalent spp. on both geologies, and is generally the most dominant termite species in African savannas (Collins, 1981)**.** This high encounter with *Microtermes* in both landscapes could be further explained by them often being secondary inhabitants of mounds constructed by other genera.

Frequency and intensity of attack

The higher bait attack intensity on granite, but similar frequency of attack in the two landscapes could result from two possible causes. First, the higher species richness of wood feeding termites at baits on granite compared to basalt, and second, baits on basalt were mostly colonised by *Microtermes* spp., whereas on granite, other genera, such as

Odontotermes spp. and *Ancistrotermes latinotus*, were also common. Considering the body size-food quantity requirement principle (Illius and Gordon, 1992), *Microtermes* are the smallest of the sampled Macrotermitinae, and therefore expected to take longer to consume a bait. In support of this, higher quantities of dead wood were recorded on the basaltic landscape (J. Muvengwi, unpubl. data), suggesting that cellulose decomposition is slower on this substrate, possibly due to the higher proportion of *Microtermes* present compared to granite. Sampling of *Cubitermes* spp., a Group IV soil-feeder**,** at two baits on granite, was probably a chance event. Davies *et al.* (2013) suggested that the presence of *Promirotermes* spp., another soil feeder, at baits was due to this termite feeding on soil brought into the baits by other wood feeding termites, a likely occurrence for *Cubitermes* here.

We show here that soil macro-fauna (termite) species and functional diversity is higher on nutrient-poor soils, which also have more even species distributions. This confirms theory that at nutrient-rich sites a few competitively-dominant species act to exclude other species and reduce overall diversity, and contradicts the classic productivity diversity hypothesis. The application of this theory is further complicated by the fact that termite abundance was equal across sites - i.e. that productivity was not necessarily higher on the more nutrient-rich site. However, these theories were developed for plant communities and there are two reasons why the basaltic soils might actually be less favourable for termites than granitic soils: they have higher pH and darker (therefore hotter) soils. Thus an alternative hypothesis is that the reduced species diversity on the basalts is due to there being fewer termite species which can tolerate these environmental conditions. Active experimentation is required to distinguish between these two alternative explanations

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Supporting information

TABLE 2S1: Number of termite species encounters from both active searching and baiting at the two geological substrates (basalt and granite) in Gonarezhou National Park, Zimbabwe. The morphospecies were separated using size, *Odontotermes* sp. *1* being the largest and *Odontotermes* sp. *3* being the smallest.

Termite species	Basalt		Granite		Feeding Group
	Active searching	Baiting	Active searching	baiting	
Termitidae					
Macrotermitinae					
Odontotermes sp. *1*	-	-	8	4	II

Odontotermes sp. *2*	-	-	9	7	II
Odontotermes sp. *3*	-	-	9	1	II
Ancistrotermes latinotus	-	-	18	21	II
Allodontermes rhodesiensis	1	-	-	-	II
Macrotermes sp.	9	26	3	1	II
Macrotermes falciger	-	-	2	-	II
Macrotermes subhyalinus	-	-	2	-	II
Macrotermes ukuzii	2	-	-	-	II
Microtermes sp.	88	58	31	8	II
Termitinae					
Cubitermes sp.	-	-	12	2	IV
Lepidotermes sp.	-	-	1	-	IV
Microcerotermes sp.			49	1	II
Amitermes sp.	1	-	-	-	II
Nasutitermitinae					
Trinervitermes sp.	-	-	1	-	II
Total encounters	101	84	145	45	
Total species	5	2	12	8	
Total encounter active searching and baiting	185		190		

Chapter 3

Chapter 3: **Geological substrate influences the spatial distribution and structure of termite mounds in an African savanna**

Abstract

Although the contribution of termite mounds to ecosystem heterogeneity is well studied, the influence the environment and other termite colonies have on mound spatial patterning and structure is still poorly understood, despite the profound implications these dynamics can have on ecosystems. Here, we mapped the distribution and size of both active and inactive *Macrotermes* mounds in eight 1 km^2 plots on granite and basalt geologies in a Zimbabwean savanna. Although mound density was not significantly different between basalt (5.5 ha^{-1}) and granite (6.1 ha^{-1}), the underlying geology influenced termite mound structural attributes and spatial distribution pattern. Mound size distributions differed between the geologies and mounds were 2.6 times taller, 3.9 times wider and had 15 times greater lateral surface area on granite. Subsequently, 6% of the total landscape area was covered by mounds on granite compared to only 0.4% on basalt. On granite, large mounds exhibited significant over-dispersion at scales below 30 m, and small mounds were clustered around large ones. In contrast, random patterning was present on basalt. Over-dispersion of large mounds on granite signifies density dependent thinning. Small mounds clustering around big mounds on granite was not viewed as facilitation, but rather "budding" of new colonies comprising fully fledged castes less vulnerable to competition. The distribution of inactive mounds also differed between the two substrates, with inactive mounds significantly clustered on granite, but not on basalt, suggesting that colony death on granite may be a consequence of localised events such as water inundation and/or disease rather than larger scale natural processes. Our results demonstrate a powerful influence of geological substrate on mound spatial patterning and structure, suggesting that the importance of termite mounds for ecosystem functioning is more pronounced on nutrient poor granitic substrates than basalts because of the pronounced over-dispersion and much larger mound size here. However, species composition between granite and basalt differs and that different species have different mound characteristics. So, geology may not directly affect mound spatial patterning via chemistry or physics but indirectly via differences in species composition.

Key words: ecosystem heterogeneity, termites, basalt, granite, *Macrotermes,* savanna landscapes, Mark correlation function, nearest neighbour analysis.

Introduction

Spatial heterogeneity is a key facilitator of species richness, creating multiple niches that can be occupied by organisms with different specialisations (Tilman, 1994, 1988) and enabling the coexistence of competing species (Tilman and Kareiva, 1997). Spatial heterogeneity thereby increases biodiversity and helps to maintain ecosystem stability (Bonachela et al., 2015). The actions of some organisms, popularly known as "ecosystem engineers", have profound impacts on the creation of spatial heterogeneity across landscapes (Lawton, 2000; Pickett et al., 2000). For example, nest construction by ants and termites leads to the formation of nutrient-rich patches in otherwise largely uniform landscapes (Jones et al., 1994; Seymour et al., 2014). Not only are these patches themselves important for heterogeneity, but the patterning and spacing between them has also been shown to have profound impacts on ecosystem processes (Bonachela et al., 2015; Pringle et al., 2010). Three spatial distribution patterns are common in nature: random, clustered, and evenly spaced (over-dispersion), and differences in these patterns across landscapes can result in differences in ecosystem productivity, with implications for the abundance, biomass and/or reproductive output of consumers across trophic levels (Pringle et al., 2010).

Macrotermes (Blattodea: Termitoidae) build large conspicuous mounds compared to other termite species in the African savanna ecosystems (Levick et al., 2010a) and contribute to ecosystem heterogeneity by containing elevated levels of soil moisture and nutrients relative to the surrounding savanna matrix (Mando et al. 1996; Seymour et al. 2014). Such alterations in soil properties lead to *Macrotermes* mounds strongly influencing herbaceous and woody plant species diversity and distributions (Holdo and McDowell 2004; Moe et al. 2009), ultimately impacting ecosystem functioning (Joseph et al. 2014) and affecting the foraging habits of herbivores (Mobæk et al., 2005; Muvengwi et al., 2014). Erosion from termite mounds results in their influence extending beyond the mound itself (Arshad, 1982; Gosling et al., 2012), with mound effects influencing as much as 20% of savanna landscapes (Levick et al., 2010b). The dispersion pattern of termite mounds has also been shown to be an important determinant of the scope of their influence, with mound patterning important for the patchy distribution of thicket clumps (Bonachela et al. 2015). Even distribution of termite mounds also results in them having a stronger effect on ecosystem processes because such distribution patterns minimize the average distance from any given point in the landscape to a highly productive termite mound (Pringle et al., 2010).

Although termites are drivers of ecosystem heterogeneity themselves, the environment in which they occur has a strong bearing on colony establishment, distribution and spatial pattern (Davies et al., 2014a). Hydrogeomorphology, mean annual rainfall and woody cover have been shown to have profound effects on the size, density and distribution of *Macrotermes* mounds (Davies et al., 2014a; Levick et al., 2010a; Meyer et al., 1999; Pomeroy, 2005). Although strong geological effects have been detected, for example reduced mound densities on gabbro, the focus of previous studies has been on other environmental attributes such hillslope morphology and usually biased to one dominant geology (Davies et al., 2014a; Meyer et al., 1999), with more investigations of geological effects, based on these preliminary findings, warranted.

Previous studies have shown that mound size has an influence on the level of competition between colonies because it correlates with colony size (Meyer et al. 2000), with overdispersion among large mounds, and clustering among small mounds (Grohmann et al., 2010; Korb and Linsenmair, 2001). However, the role of competition between colonies in shaping mound distributions is not always apparent and could also result from historical precedence and chance events (Schuurman and Dangerfield, 1997). Furthermore, competition can lead to different distribution patterns, random, even or clumped (Pielou, 1960; Ryti and Case, 1992)**.** Therefore**,** further research into mound spatial distributions is necessary.

Granitic landscapes are generally undulating, leading to catenal sequences with seeplines, mid-slopes and crests (Khomo et al., 2011; Levick et al., 2010a). Because of their undulating nature, depending on the amount of annual rainfall, termite mounds are often restricted to crests due to water inundation in the lowlands (Levick et al., 2010a). In contrast, basaltic landscapes are strikingly flat, lacking catenal formations and their associated soil and water regimes (Kelly and Walker, 1976). Furthermore, basaltic landscapes are regarded as nutrient rich compared to granite (Grant and Scholes, 2006; Scholes, 1990), resulting from their soil being formed from rocks rich in basic cations, which when weathered produce fine textured fertile alkaline soils that are generally black in colour and rich in clays (Olowolafe, 2002). In contrast, granites are formed from intrusive magma that takes time to cool beneath the earth's surface, resulting in course textured rocks. This quartz-rich material weathers to produce poorly buffered acidic soils of poor nutrient status and low clay content (Olowolafe, 2002). Clay content is important for termites because they require moderate amounts of clay for nest construction (Levick et al., 2010a), with too little limiting nest construction and too

much causing water inundation, precluding nest construction (Jouquet et al., 2004; Levick et al., 2010a).

Despite the increasingly recognised role of termites and their mounds in shaping ecosystem processes, few studies have examined differences in the spatial distribution of termite mounds between geological substrates, representing vastly different savanna types. Therefore, in this study we ask how differences in geology influence the spatial patterning of *Macrotermes* mounds. This is particularly important in savannas because understanding termite mound distributions will lead to improved understanding of the role they play in structuring savannas at landscape scales. Furthermore, most studies investigating spatial patterning of termite mounds have only applied the nearest neighbour analysis, which mainly detects competition that leads to size reduction (Korb and Linsenmair, 2001; Pomeroy, 2005; Schuurman and Dangerfield, 1997). We hypothesised that (i) the spatial pattern of all mounds (active and inactive) is randomly distributed on basalt and aggregated on granite, because of the greater catenal variation on granite compared to basalt, (ii) overall inter-mound distances are shorter on basalt compared to granite because of the undulating nature of the terrain on granite, with mounds expected to be absent from low-lying areas (Davies et al., 2014a; Levick et al., 2010a), (iii) the death of mounds is a spatially random process at any given point in time on both geological substrates, and (iv) intra-specific competition *via* the exploitation of shared resources leads to a more regular post mortality pattern on both substrates. In this respect, we expected a clumped distribution among small mounds and a regular distribution among large mounds because mound size is closely related to colony size (Korb and Linsenmair, 2001).

Methods

Study area

The study was conducted in the Gonarezhou National Park, Zimbabwe (GNP) (21^0 00′ - 22^0 15′ S, 30^0 15′ - 32^0 31′ E). Mean annual rainfall at the study site averages 466 mm, and mean monthly maximum temperatures range between 26^0C in July and 30^0C in January, whereas mean monthly minimum temperatures range between 9^0C in June and 24^0C in January (Gandiwa et al., 2011). Granite is located in the east and has higher tree species diversity than basalt in the west. Common tree species on granite include *Androstachys johnsonii*, *Brachystegia glaucescens*, *Vitex payos*, *Diospyros loureiriana* and *Xeroderris stuhlmannii*. Areas on basalt are covered mostly by *Colophospermum mopane* woodland, with scattered

Combretum apiculatum. The herbaceous community on basalt is dominated by the grasses *Aristida rhiniochloa, A. adscensionis and Brachiaria deflexa* while granite consists largely of *Digitaria eriantha, Tragus berteronianus, Urochloa mosambicensis* and *Heteropogon contortus*. The common *Macrotermes* mound-building species include *M. subhyalinus, M. ukuzii and M. falciger* (Muvengwi et al. *in review*). Herbaceous biomass production is higher on granite compared with basalt (Chapter 4).

Termite mound sampling and structural variables

Sampling of termite mounds was conducted in October 2013 (end of the dry season) when environmental visibility was high due to reduced tree and grass cover. The study area was divided into 200 100 ha (1x1 km^2) grid cells and from these four sampling plots (each 100 ha) were randomly selected from each geology, basalt ($plot_{B1}$, $plot_{B2}$, $plot_{B3}$ and $plot_{B4}$) and granite ($plot_{G1}$, $plot_{G2}$, $plot_{G3}$ and $plot_{G4}$). Three observers, walking in a straight line and separated by at least 20 m, searched each survey plot simultaneously for *Macrotermes* mounds. The location of each mound was recorded using a handheld GPS unit (Garmin III Plus, with an error of approximately ± 3 m). This GPS error margin was not considered problematic because the average distance between two nearby mounds varied between 32 m and 40 m. In order to increase accuracy, location averaging was used, with an average of 10 positions recorded for each termite mound. Active mounds were identified by fresh signs of termite activity (evidence of recent constructions). When no signs of activity were observed, a hole was drilled into the mound and checked a day after for any repair (Grohmann et al., 2010; Korb and Linsenmair, 2001). If no repairs had occurred, the mound was classified as inactive. Mounds were further divided into large and small, with those having diameters greater than population mean, 2.5 on basalt and 10.8 m granite regarded as large (Fig. 3.A1).

Mound height was estimated by placing a telescopic pole level with the top of the termite mound in each of the four cardinal directions, and measuring the four heights from the ground to the pole (Fig. 3.A2). The longest diameter of the mound (d1) and the diameter perpendicular to d1 (d2) were measured using a tape measure (Fig. 3.A2). The edge of the mound was determined as the zone around the skirt of the termite mound where a change in soil colour was visible or where changes in slope were noticeable and no eroded soil evident (Arshad, 1982). Mounds were modelled as cones in order to calculate surface area, following Muvengwi et al. (2013).

Data analysis

Termite mound structural analysis

Correlation between termite mound height and diameter for both active and inactive mounds was assessed with Spearman rank correlation tests. The size-frequency distributions of mound height and diameter in the two landscapes, basalt and granite, were compared using Kolmogorov-Smirnov two sample tests. In cases where the test statistic was significant ($p < 0.05$), differences in mean values were then compared between geologies using either Wilcoxon Rank Sum tests or an independent t-test, depending on whether the data were normal or non-normal distributed. The area of the landscape covered by mounds was compared between basalt and granite using an independent t-test. Normality was tested prior to analysis using the Shapiro-Wilk test and data were non-normal distributed. All statistical analyses were conducted using R software version 3.1.0 (www.r-project.org). Values are given as mean ± standard error (SE).

Spatial distributions of termite mounds

To determine whether termite mounds were randomly distributed across each landscape, we used pair correlation and Ripley's *K*-functions. All spatial data analyses were performed using the software Programita (Wiegand and Moloney, 2004). Spatial point pattern analyses have the ability to detect strong competitive interactions, which result in the mortality of individual mounds, while subtle interactions with the potential to only reduce mound size may not be detected (Getzin et al., 2006). Alternatively, the nearest neighbour analysis (NN) has the ability to detect slight interactions that can cause size reduction (Getzin et al., 2006). Indeed, NN, a first order statistic, has been widely used in detecting competition between termite colonies in savannas (Korb and Linsenmair, 2001; Meyer et al., 1999; Pomeroy, 2005), and was therefore applied to complement the second order spatial statistics.

The general distribution pattern of termite mounds (active and inactive mounds combined) was investigated using both the pair correlation function, $g(r)$, and Ripley's $K(r)$ function, which use rings and circles, respectively, to determine differences in the intensity of points from an arbitrary point (Wiegand and Moloney, 2004). Rings consider all points lying in the perimeter of the circle from an arbitrary point whereas circles include all points from the arbitrary point to the perimeter of the circle. The $g(r)$ function is non-cumulative, as opposed to the $K(r)$ function, and has the added advantage of being a probability density function, with the interpretation of a neighbourhood density that is more intuitive than the

$K(r)$ cumulative measure (Stoyan and Penttinen, 2000). Furthermore, the $g(r)$ function has the advantage of isolating specific distance classes and can therefore be used to precisely determine spatial scales at which a given null model is violated (Getzin et al., 2006). However, Ripley's $K(r)$ is pertinent in detecting first order effects, those effects that result from the environment rather than from the interaction of organisms under investigation (Wiegand and Moloney, 2004), and was therefore also applied. The univariate pair correlation function, $g(r)$ is related to the derivative of Ripley's $K(r)$ function (Ripley, 1976), and is given by:

$$K(r) = \int_0^r g(r')r'dr' \qquad (1)$$

This function is defined as the expected density of points at a given distance r from an arbitrary point divided by the intensity λ of the pattern (Getzin et al., 2006; Stoyan and Stoyan, 1994). Consequently, the pair correlation function was interpreted as: $g(r) = 1$ random, $g(r) > 1$ aggregated and $g(r) < 1$ regular distribution.

The spatial distribution pattern of active versus inactive mounds was explored using the bivariate pair correlation function, $g_{12}(r)$. The bivariate pair correlation function is defined as the expected density of points of pattern 2 (inactive mounds in this case) within a given distance r of an arbitrary point of pattern1 (active mounds), divided by the intensity λ_2 of pattern 2 (Wiegand and Moloney, 2004).The bivariate $g(r)$ statistic is defined as:

$$g_{12}(r) = \frac{K_{12}(r)}{2\pi r} \qquad (2)$$

We further used the transformed L-function for Ripley's $K(r)$ function, which is pertinent for confirmation of null models (Stoyan and Penttinen, 2000). For a homogeneous Poisson process of complete spatial randomness (CSR), $K(r) = \pi r^2$ and $L(r) = 0$, values of $L(r) > 0$ indicate aggregation up to distance r, whereas $L(r) < 0$ indicates regularity of the pattern up to distance r (Wiegand and Moloney, 2004). The estimation equation is defined as:

$$L(r) = \frac{\sqrt{K(r)}}{\pi} - r \qquad (3)$$

The corresponding second order bivariate estimator for Ripley's *K*-function was also used to determine spatial patterns between active and inactive mounds because it is recommended that a combination of two or more statistical analyses be applied in spatial point pattern analysis (Diggle, 2003; Ripley, 1981), and was defined as:

$$K_{12}(r) = (n_1 n_2)^{-1} |A| \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} I_r(u_{ij}) \qquad (4)$$

Wheren_1 and n_2 are the total number of active and inactive mounds, respectively, that occur in area *A*. u_{ij} represents the distance between the i^{th} focal mound and the j^{th} neighbouring mound. $I_r(u_{ij})$ is an indicator function, being equal to 1 if $u_{ij} \leq r$,or otherwise equal to zero(Gray and He, 2009). w_{ij} corrects for edge effects and is defined as the proportion of the circumference of a circle centred on the i^{th} mound with a radius of u_{ij}, which lies within area *A*. The variance reduction bivariate form of $K_{12}(r)$ was defined as:

$$L_{12}(r) = \frac{\sqrt{K_{12}(r)}}{\pi} - r \quad (5)$$

Significant departure from applicable null models was quantified by 95% confidence limits, determined using the 5thlowest and 5thhighest value of 999 Monte Carlo simulations.

The distribution of inactive mounds in relation to active mounds was investigated using a random labelling model (Bourguignon et al., 2011). Under random labelling, *g*-functions are invariant and therefore $g_{12}(r) = g_{21}(r) = g_{11}(r) = g_{22}(r)$. Any departure from random labelling is evaluated by pair wise differences corresponding to specific biological effects. If g_{21}-$g_{22}(r) < 0$ at radius *r*, then type 2 points (inactive mounds in this case) are more frequent around type 2 points than type 1 points (active mounds) are around type 2 points, hence inactive mounds are positively correlated at radius *r*, which would suggest a strong influence of local conditions (Bourguignon et al., 2011; Getzin et al., 2006). Significant departure from random labelling was quantified using 95% confidence limits, determined using the 5thlowest and 5thhighest value of 999 Monte Carlo simulations.

Density dependent competition

In order to investigate density dependent competition between termite colonies, we applied a "case-control" design commonly used in environmental epidemiology, where disease cases

and controls are drawn from a population at risk (Diggle et al., 2007; Gatrell et al., 1996), with the control pattern accounting for any environmental heterogeneity (Getzin et al., 2008). Only active mounds were considered for this analysis since inactive mounds would not be subject to intra-specific competition. Termite mounds grow in size with age, and size is correlated to nest population (Meyer et al. 2000). Therefore, density dependent thinning might be expected. Small mounds were treated as cases and large mounds as controls, with mounds with diameters greater than the population mean, 2.5 m on basalt and 10.8 m on granite, regarded as large (Fig. 3.A1).The control pattern (large mounds) was used to control for any possible environmental heterogeneity in the distribution of the cases (small mounds), which was the pattern under investigation for detecting the presence of density dependent thinning (Getzin et al., 2008). With the $g(r)$ functions being invariant under random thinning, we expected $g_{12}(r)=g_{21}(r)=g_{11}(r)=g_{22}(r)$ when small mounds surrounded large mounds at the scale r in the same way as large mounds surrounded large mounds, meaning that small and large termite colonies exploit the landscape in a similar way (Getzin et al., 2008). In cases of any additional clustering within the small mounds, independent of large mounds (*e.g.* large areas that may be created by dead mounds that can allow more young colonies to establish), we would expect $g_{21}(r)\text{-}g_{22}(r) \ll 0$. Significant departure from random labelling was quantified using 95% confidence limits, determined using the 5thlowest and 5thhighest value of 999 Monte Carlo simulations.

Mound spatial correlation

A mark correlation function (MCF) was applied to test for significant inter and intra-specific competition between large mounds on each geological substrate. The MCF, $k_{mm}(r)$ was applied only to large active mounds on both basalt and granite because they host foragers that could compete for resources. This function measures the dependence between marks (mound diameter in this case) of two points of the process at distance r. The relationship between the marks is quantified by $f(m_1,m_2)$ where f is defined as $f(m_1,m_2) = m_1 \times m_2$ for quantitative marks (Getzin et al., 2008). If the product of diameters (r length units) of two mounds apart tends to be smaller than the overall marks mean μ, then $k_{mm}(r) < 1$, indicating a negative correlation. If $k_{mm}(r) > 1$, there is a positive correlation between marks, and when $k_{mm}(r) = 1$, marks are independent at scales r (Getzin et al., 2008; Grohmann et al., 2010). Significant departure from an independent mound diameter was quantified using 95% confidence limits, determined using the 5thlowest and 5thhighest value of 999 Monte Carlo simulations.

Nearest neighbour analysis

Density dependent competition between termite colonies (mounds) was assessed using the nearest neighbour analysis (Shackleton, 2002). We established the correlation between the combined diameters of the focal mound and its four nearest neighbours and the sum of the distances of the four nearest neighbours to the same focal mound. A significant positive correlation indicates competition between termite colonies (Shackleton, 2002). Because of the tendency of p-values to be significant when a correlation involves a large sample size, results were interpreted using the coefficient of determination (r^2), which is a robust index of competition in the presence of influential biotic and abiotic factors (Welden et al., 1988). The r^2 also acts as a measure for goodness of fit for the observations. The importance of intra-specific competition was determined using only active mounds, since they host foragers that can compete for resources.

Results

Termite mound structural variables

A total of 2426 termite mounds were sampled on granite and 2182 on basalt. Termite mound height and basal diameter were significantly correlated on both basalt (Spearman rank correlation, $\rho = 0.29$, $p < 0.00001$) and granite ($\rho = 0.83$, $p < 0.00001$). Mound density was not significantly different between granite (6.07 ± 0.50 ha^{-1}) and basalt (5.46 ± 0.69 ha^{-1}) ($t = 0.710$, df = 5.50, $p = 0.507$) at the landscape scale (Fig. 3.1), but the height and diameter size-frequency distributions of the mounds differed between the two geologies (Kolmogorov-Smirnov tests, $D = 0.534$, $p < 0.00001$ and $D = 0.744$, $p < 0.00001$, respectively). Wilcoxon Rank Sum test showed that both height and diameter of mounds were significantly different between the two geologies ($W = 4309219$, $p < 0.00001$ and $W = 4953743$, $p < 0.00001$, respectively). Mounds located on granite were over twice as tall (1.29 ± 0.02 m) than those on basalt (0.49 ± 0.00 m) and almost 4 times larger in diameter (granite: 9.95 ± 0.11 m, basalt: 2.58 ± 0.03 m). When modelled as cones, the 'lateral surface area', of mounds was 15 times larger on granite than on basalt. Active and inactive mounds were significantly different in height and diameter on both geologies (Granite: $W = 749585$, $p < 0.00001$, $W = 758182$, $p < 0.00001$, respectively and Basalt: $W = 513935$, $p < 0.00001$, $W = 328180$, $p < 0.00001$, respectively). Granite had a slightly lower proportion of active mounds (0.76)

comparing with basalt (0.80). On granite, active mounds had larger diameters (10.80 ± 0.12 m) and were taller (1.42 ± 0.02 m) compared to inactive mounds (7.33 ± 0.18 m and 0.90 ± 0.66 m), whereas on basalt, active mounds were taller (0.51 ± 0.01 m) than inactive ones (0.40 ± 0.01 m), but had smaller diameters (2.51 ± 0.03 m) compared to inactive mounds (2.85 ± 0.07 m) (Fig. 1e-h). The proportion of the landscape covered by termite mounds (basal area), was significantly different between granite and basalt (t = 6.181, df = 6, p = 0.001). Mounds covered an area 15 times larger on granite (5.99 ± 0.91%) than on basalt (0.35 ± 0.10%).

Spatial distribution - all mounds

As expected, termite mounds exhibited a regular distribution at small spatial scales (10-30 m) on granite, signifying intense intra-specific competition between colonies at these spatial scales (Table 3.1). Beyond 30 m, the spatial pattern was aggregated. Both the $L(r)$ and $g(r)$ functions generally showed the same distribution patterns, except in $plot_{G4}$ where the $L(r)$ function did not detect over-dispersion at any spatial scale (Table 3.1). On basalt, both the $L(r)$ and $g(r)$ functions detected only two patterns, random and aggregation, with termite colonies having a random distribution at spatial scales less than 30 m and an aggregated pattern above 30 m (Table 3.1). Therefore, there appears to be no competition between colonies on the basaltic landscape at both small and large spatial scales.

Spatial distribution - active and inactive mounds

The bivariate spatial distribution of active versus inactive mounds was random in $plot_{G1}$ and $plot_{G2}$ on granite, random in $plot_{G3}$ at scales ranging between 0 and 60 m and aggregated in $plot_{G4}$ at spatial scales between 20 and 500 m (Table 3.2, Fig. 3.1). On basalt, the interaction between active and inactive mounds was random at small spatial scales and aggregated at larger scales in $plot_{B1,}$ $plot_{B2}$ and $plot_{B4}$, whereas the interaction of active and inactive mounds was regular in $plot_{B3}$ at small (0-30 m) and intermediate (60-150 m) spatial scales (Table 3.2).

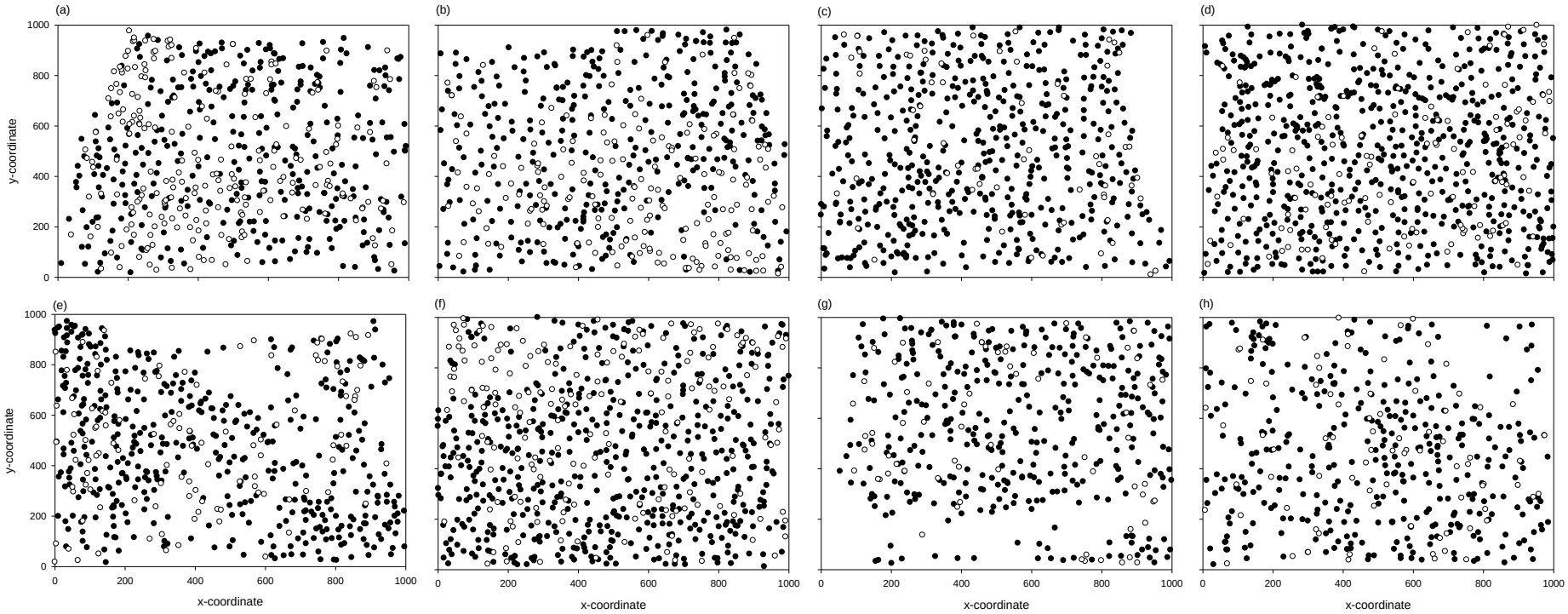


Figure 3.1: Maps of termite mound locations on the different plots on granite (a-d) and basalt (e-h). Black circles represent active mounds and open circles inactive mounds.

Table 3.1: Summary of the univariate ($L(r)$ normal font and $g(r)$) bold font spatial distribution of active and inactive mounds on granite and basalt geological substrates. Values in parentheses indicate the spatial scales at which regular (Re), random (Ra) and Aggregated (Ag) distributions are experienced. $L(r)$ is the transformed function for Ripley's $K(r)$ function and $g(r)$ is the pair correlation function.

Geology/Plot	$L(r)$	$g(r)$
Granite		
$plot_{G1}$	Re(10-30), Ra(0-10), (30-500)	**Re(10-20), Ra(0-10), (20-500)**
$plot_{G2}$	Re(10-30), Ag(70-500), Ra(0-10), (30-70)	**Re(0-30), Ag(40-390), Ra(30-40), (390-500)**
$plot_{G3}$	Re(10-30), Ag(50-410), Ra(0-10), (30-50), (410-500)	**Re(0-20), Ag(40-210), Ra(20-40), (210-500)**
$plot_{G4}$	Ag(60-500), Ra(0-60)	**Re(10-30), Ag(40-200), Ra(0-10), (30-40), (200-500)**
Basalt		
$plot_{B1}$	Ag(50-500), Ra(0-50)	**Ag(30-90), (130-190), (220-260), (270-320), Ra(0-30), (90-130), (90-220), (260-270), (320-500)**
$plot_{B2}$	Ag(30-500), Ra(0-30)	**Ag(30-310), Ra(0-30), (310-500)**
$plot_{B3}$	Ag(80-500), Ra(0-80)	**Ag(30-60), (70-240), Ra(0-30), (60-70), (240-500)**
$plot_{B4}$	Ag(30-500), Ra(0-30)	**Ag(20-250), Ra(0-20), (250-500)**

Table 3.2: Summary of the bivariate ($L_{12}(r)$ normal font and $g_{12}(r)$) bold font spatial pattern indicating the interaction between active and inactive mounds on granite and basalt geological substrates. Values in parentheses indicate the spatial scales at which regular (Re), random (Ra) and Aggregated (Ag) distributions are experienced. $L(r)$ is the transformed function for Ripley's $K(r)$ function and $g(r)$ is the pair correlation function.

Geology/Plot	$L_{12}(r)$	$g_{12}(r)$
Granite		
$plot_{G1}$	Ra(0-500)	**Ra(0-500)**
$plot_{G2}$	Ra(0-500)	**Ra(0-500)**
$plot_{G3}$	Re(10-60), Ra(0-10), (60-500)	**Re(0-40), Ra(40-500)**
$plot_{G4}$	Ag(80-500), Ra(0-80)	**Ag(20-50), (80-340), Ra(0-20), (50-80), (340-500)**
Basalt		
$plot_{B1}$	Ag(60-500), Ra(0-60)	**Ag(30-60), (90-140), (210-250), Ra(0-30), (60-90), (140-210), (250-500)**
$plot_{B2}$	Ag(60-180), Ra(0-60), (180-500)	**Ag(30-90), (120-140), Ra(0-30), (90-120), (140-500)**
$plot_{B3}$	Re(0-30), (60-270), Ra(30-60), (270-500)	**Re(0-30), (60-150), Ra(30-60), (150-500)**
$plot_{B4}$	Ag(80-500), Ra(0-80)	**Ag(40-70), (80-150), (220-330), Ra(0-40), (70-80), (150-220), (330-500)**

Random labelling - inactive mounds

Inactive mounds were clustered in granite plots at small to large spatial scales, ($plot_{G1}$ (0-60 m), $plot_{G2}$ (0-10 m), $plot_{G3}$ (0-370 m) and $plot_{G4}$ (0-190 m)) (Fig. 3.1a-d, Fig. 3.2a-d). On basalt substrate, inactive mounds were generally spatially randomly distributed in three plots

(Fig. 3.2e, f and h), apart from clustered patterns at scales between 20-40 m in $plot_{B2}$ and 60-150 m in $plot_{B3}$ (Fig. 3.2f-g).

Density dependent competition

There was significant clumping of small mounds around large mounds compared to large mounds around large mounds ($g_{12}(r)$-$g_{11}(r) > 0$) at spatial scales between 0-40 m on granitic substrate (Fig. 3.3a-d (inserts) and Fig. 3.1a-d). This indicates that small termite colonies are tolerated around large ones. Interestingly, extra clumping of small mounds independent of large mounds was also detected by the function g_{21}-$g_{22}(r)$ at similarly small spatial scales across all plots (main Fig. 3.3a-d), where small mounds were significantly clustered around small mounds, rather than big mounds around small mounds. This indicates clustering of small mounds, which is independent of big mounds and may signify density dependent competition or some gaps within the habitat where new colonies are taking advantage and establishing themselves. However, in $plot_{G2}$, the g_{21}-$g_{22}(r)$ function significantly differs from the null model of random labelling across all scales (Fig. 3.3b main figure). On basalt, small mounds departed slightly from the null model of random labelling at small spatial scales in $plot_{B1}$ and $plot_{B2}$, with significant clustering of large mounds around large mounds compared to small mounds around large mounds recorded in $plot_{B3}$ between 20 and 80 m (Fig. 3.3e-g inserts). Although there was slight deviation from the null model of random labelling shown by the function $g_{12}(r)$-$g_{11}(r)$, significant clustering of small mounds that was independent of large mounds was confirmed by the function g_{21}-$g_{22}(r)$ at the same spatial scales (main Fig. 3.3e-h).

Mound spatial correlation

The mark correlation function $k_{mm}(r)$ indicated that large mounds on granite were generally negatively correlated at spatial scales between 0 and 40 m across all plots (Fig. 3.4a-d). In $plot_{G4}$, a weak negative correlation was further shown at a scale between 250 and 480 m (Fig. 3.4d). However, there was some significant positive correlation of large mounds between 40-80 m in $plot_{G3}$ on granite (Fig. 3.4c). In $plot_{B1}$ and $plot_{B3}$, significant positive correlations were demonstrated at spatial scales of 50-100 m and 20-60 m, respectively, signifying a lack of competition at these spatial scales (Fig. 3.4e and g). However, a weak marginal negative correlation was experienced across almost all scales in $plot_{B4}$ (Fig. 3.4h).

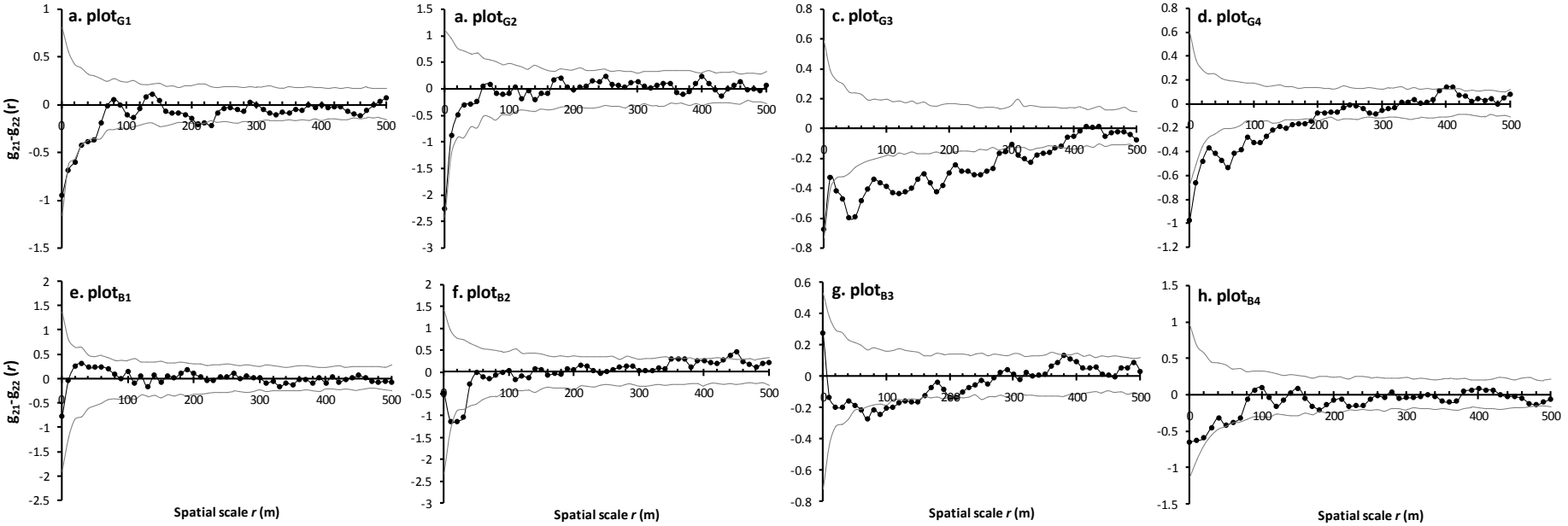


Figure 3.2: Bivariate random labelling (g_{21}-$g_{22}(r)$) used to investigate whether colony death was a random process among mounds in plots located on granite (a-d) and basalt (e-h) geological substrates. Under the null model "random labelling" the observed pattern (dark dotted line), $g_{21}(r)$-$g_{22}(r)$ = 0 (x-axis line), $g_{21}(r)$-$g_{22}(r)$ < 0 would mean that there are more inactive mounds around inactive mounds than active mounds around inactive mounds and $g_{21}(r)$-$g_{22}(r)$ > 0 indicates that there are more active mounds around inactive mounds than inactive mounds around inactive mounds. Significant departure from random labelling was quantified using 95% confidence limits (grey solid lines), determined using the 5th-lowest and 5th-highest value of 999 Monte Carlo simulations.

Nearest neighbour

There was a significant positive correlation between the combined sum of mound diameters of the focal mound and its four nearest neighbours and the sum of the four distances from the focal mound for all the plots on granite and basalt (Fig. 3.5a-d and e-h). On granite, the correlation (*r*) ranged between 0.310 and 0.574, whereas on basalt they were less well correlated (ranged between 0.133 and 0.311). Although this positive correlation between size and distance was confirmed by the nearest neighbour analysis across plots on the two geologies, the intensity of competition was more pronounced on granite (r^2 range: 0.137-0.330) compared to basalt (r^2 range: 0.018-0.097) (Fig. 3.5). However, mean nearest neighbour distance was not significantly different ($t = 0.378$, $df = 3448$, $p = 0.706$) between granite (40.13 ± 0.30 m) and basalt (40.30 ± 0.34 m).

Discussion

Our results demonstrate that geological substrate can have a powerful influence on the spatial distribution and structure of termite mounds, important contributors to savanna spatial heterogeneity. Although mound densities did not differ between the two geologies, granite supported clusters of taller and larger mounds that covered substantially more of the landscape compared to the smaller, more evenly spread mounds on basalt. Furthermore, within the mound aggregations on granite, termite mounds were over-dispersed compared to mounds on basalt that were randomly spaced at similarly fine spatial scales. These contrasting findings suggest that different mechanisms shape mound distribution and structure on the two geologies, with the implications of such differences likely leading to substantial differences in the functional roles performed by termite mounds on each geology, and therefore across savanna landscapes.

The lack of a strong geological effect on mound density is somewhat surprising given that geology has been shown to have a strong influence on mound density elsewhere in Africa, with lower mound densities on geologies with high clay content (gabbro and basalt) (Davies et al., 2014a; Meyer et al., 1999; Mujinya et al., 2014). In our case it could be that the crests on the granite had higher densities, and the bottom lands lower densities, and it averaged out to be similar densities to the basalt. Furthermore, it remains difficult to separate species and geological effects since geology determines termite species composition, and, hence, mound characteristics. However, functionally similar *Odontotermes obesus* had similar nest

densities in ferralsol and vertisol soils (Jouquet et al., 2015), suggesting that geological effects on mound densities can be variable.

Differences in mound characteristics across geologies

Our recorded mound densities (6.1 ha^{-1}on granite and 5.5 ha^{-1}on basalt) were also substantially higher than those recorded in the nearby Kruger National Park, where densities of 0.46 ha^{-1} (granite and basalt), 0.6-0.7 ha^{-1}(granite) and 0.73 ha^{-1}(granite) were recorded (Meyer et al. 1999, Levick et al. 2010a, Davies et al. 2014a, respectively). These large differences in mound density can be attributed to methodological differences, the spatial scale of the study and the latitudinal position of our study site. Two of the above studies used remote sensing techniques to measure mound densities, which fail to detect mounds below ~0.5 m in height (Davies et al., 2014a; Levick et al., 2010a). Given the comprehensive field surveys employed in our study, the probability of detecting small mounds was likely higher compared with a purely remote sensing study. Alternatively differences termite mound densities between Kruger National Park and GNP could be resulting from differences in general species composition of the two areas leading to a difference in how *Macrotermes* species interact with other species which are not part of the *Macrotermes* group. and Although the high densities of small mounds recorded in our study may be of less ecological significance compared to larger mounds (Joseph et al. 2014, Seymour et al. 2014, Chapter 4), their future potential should not be underestimated because mounds generally increase in size with age (Bourguignon et al., 2011), and it is therefore important to understand their spatial patterns. However, remote sensing enables surveying of much larger areas, yielding important insights into broad scale patterns of larger mounds, and should not be discounted (Davies et al. 2014b, Mujinya et al. 2014).

Also, excluding mounds below 0.5 m in height from our results, mound densities were still much higher on granite (5 ha^{-1}) and basalt (2 ha^{-1}) in our study compared with the previous studies above. Although at very large spatial scales (when remote sensing is used) there is high inclusion of sparsely populated lower catenal sections leading to an overall lower mound density (Davies et al., 2014a), we recorded mounds in all sections of the catena. Rainfall in our study site was markedly lower than parts of Kruger National Park where mounds were absent from low lying regions (Davies et al., 2014a; Levick et al., 2010a). Water inundation might therefore be less of a challenge for mound construction in lowlands, as also recorded in low rainfall regions of northern Kruger National Park (Levick et al.,

2010a), enabling termite colonies to establish closer to drainage lines and resulting in higher mound densities compared to areas with higher rainfall. Our recorded mound densities are comparable to studies from further north in Africa, which used similar field-based methods (Lepage, 1984; Pomeroy, 1977; Trapnell et al., 1976). Termite diversity decreases with latitude (Eggleton, 2000), and Gonarezhou is warmer than Kruger National Park, potentially providing better conditions for termite colony growth and establishment, and therefore a higher mound density can be expected in Gonarezhou.

Mound height (2.6 times), diameter (3.9 times) and lateral surface area when modelled as a cone (15 times) were significantly larger on granite compared to basalt, demonstrating a strong influence of geology on mound construction. The swelling and shrinking characteristics of clays on basalt make them unstable, limiting nest size due to increased degradation of mounds (Jouquet et al., 2015). Differences in mound height and diameter on the two geologies could also be influenced by the *Macrotermes* species present on each substrate. Mounds on basalt were built primarily by *M. ukuzii*, whereas on granite they were mostly built by *M. subhyalinus* and *M. falciger*. *Macrotermes ukuzii* are small in body size and generally build mounds that are rarely taller than 0.5 m (Mitchell, 1980). Active mounds had larger dimensions (height and diameter) compared to inactive mounds on granite. Inactive mounds are not maintained and will erode without repair, leading to a decrease in size (Korb and Linsenmair, 2001), which is exacerbated on the steeper catenal slopes found on granite (Khomo et al., 2011). Interestingly, although active mounds on basalt were taller, they were smaller in diameter than inactive mounds. In similar ways to granite, differences in height can be attributed to continuous erosion of inactive mounds without repair, whereas the larger diameters of the inactive mounds could be a consequence of continuous accumulation of eroded soil (‘hillock’) around the mound skirt given the strikingly flat terrain on basalt (Jouquet et al., 2015).

Mechanisms of spatial pattern

Competition (evidenced by over-dispersion) was generally recorded at small spatial scales on granite, whilst no such competitively induced patterning was detected on basalt at any spatial scale (Figure 3.2). This was further confirmed by the NN analysis (Figure 3.5), where competition was more pronounced on granite even though mean NN distance was not significantly different between the geologies. Termite mounds on basalt are significantly

smaller (in height and diameter) than on granite, meaning they support smaller *Macrotermes* colonies (Meyer et al., 2000), which most likely forage over smaller areas and may explain the lack of clear competition on basalt. Another plausible mechanism is that basalts are strikingly uniform, which may mean that colonies can randomly occupy any space.

In contrast, environmental heterogeneity on granites, due to catenal sequencing, leads to the concentration of mounds on crests (Davies et al., 2014a), possibly intensifying both inter and intra-specific competition between colonies due to limited space and resources (Korb and Linsenmair, 2001; Pomeroy, 2005). Macrotermes species generally utilize the same food resources such as plants and fungus in their nests. Experiments with worker and soldier castes showed that both inter and intra-specific competition exists in some species of *Macrotermes* (*M. bellicosus* and *M. subhyalinus*) with intra-specific competition being more evident (Jmhasly and Leuthold, 1999). Agonism behaviour was also evident in many termite species (see review by Thorne and Haverty 1991), indicating that competition between termite colonies could be the major mechanism shaping colony patterns. However, we are cautious in our interpretations of mechanisms here because more than just a single mechanism can lead to an observed pattern. Competition, for example, can lead to different distribution patterns such as random, clustered and overdispersion (Levings and Adams, 1984; Pielou, 1960; Ryti and Case, 1992).

Ecosystem consequences of spatial pattern across geologies

When patterns of mound distributions are considered, termite mounds will be of particular significance to ecosystem functioning on granite because of the over-dispersion found at small spatial scales (0-30 m) here. Such over-dispersion has a greater positive effect on the abundance, biomass and reproductive output of consumers across trophic levels than if mounds were randomly distributed (Pringle et al., 2010). Coupled with their large size, mounds become even more important as generators of spatial heterogeneity on granites because these landscapes are nutrient poor compared with basalts, making termite mounds here likely more important because of stronger differences between mound and matrix soil nutrients (Grant and Scholes 2006).

Inactive mounds displayed different distribution patterns in relation to active mounds on the two geologies: random spacing on basalt compared to clustering on granite.

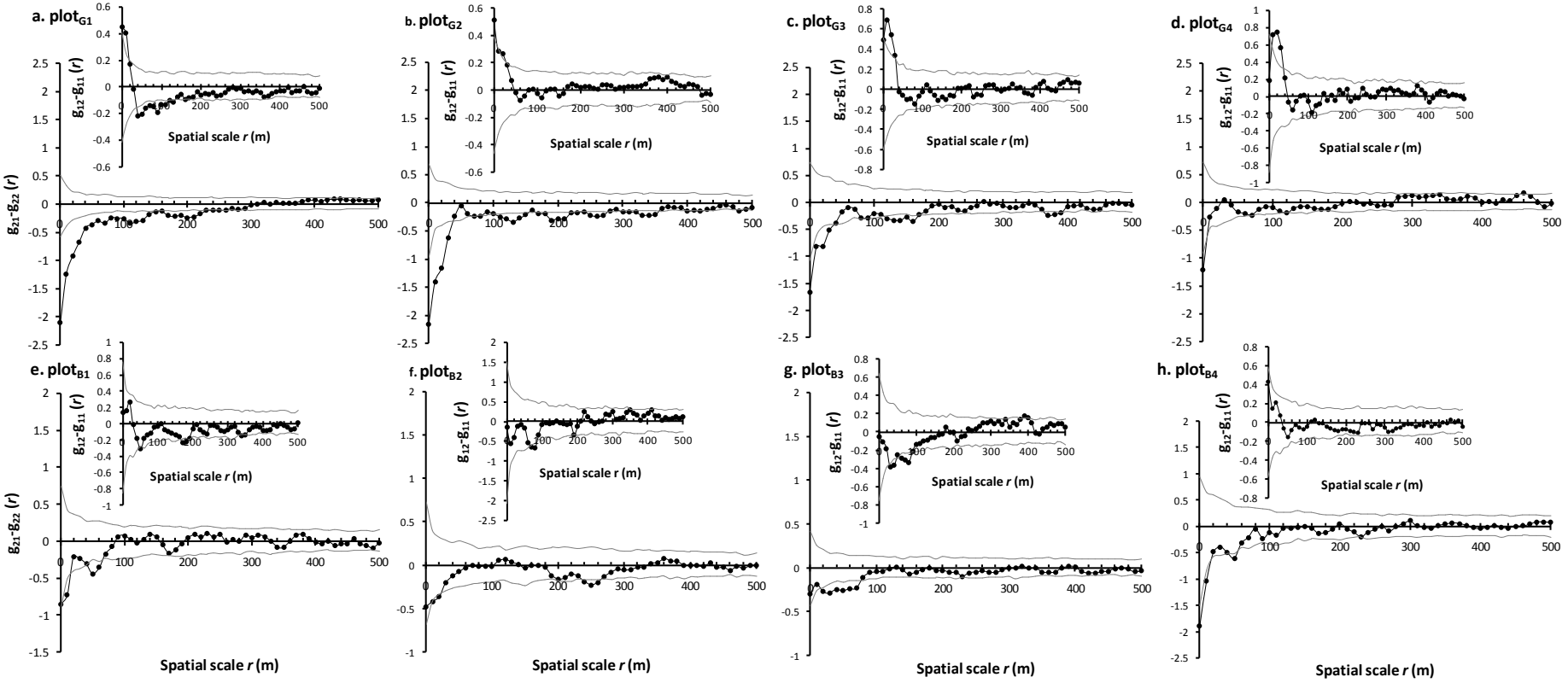


Figure 3.3: Spatial distributions of large and small mounds analyzed with a case-control technique. The large mounds represent the control pattern (pattern 1) and the small mounds represent the cases (pattern 2). The small insert figures ($g_{12}(r)$-$g_{11}(r)$ figure above the main figures a-h) evaluates whether the distribution pattern of small mounds (pattern 2) around large mounds is similar to the pattern of large mounds around large mounds. Then, $g_{21}(r)$-$g_{22}(r)$ evaluates if there is additional clustering of small mounds around small mounds that is independent of the spatial pattern of large mounds. The dark dotted line represents the observed pattern and the grey lines 95% confidence limits.

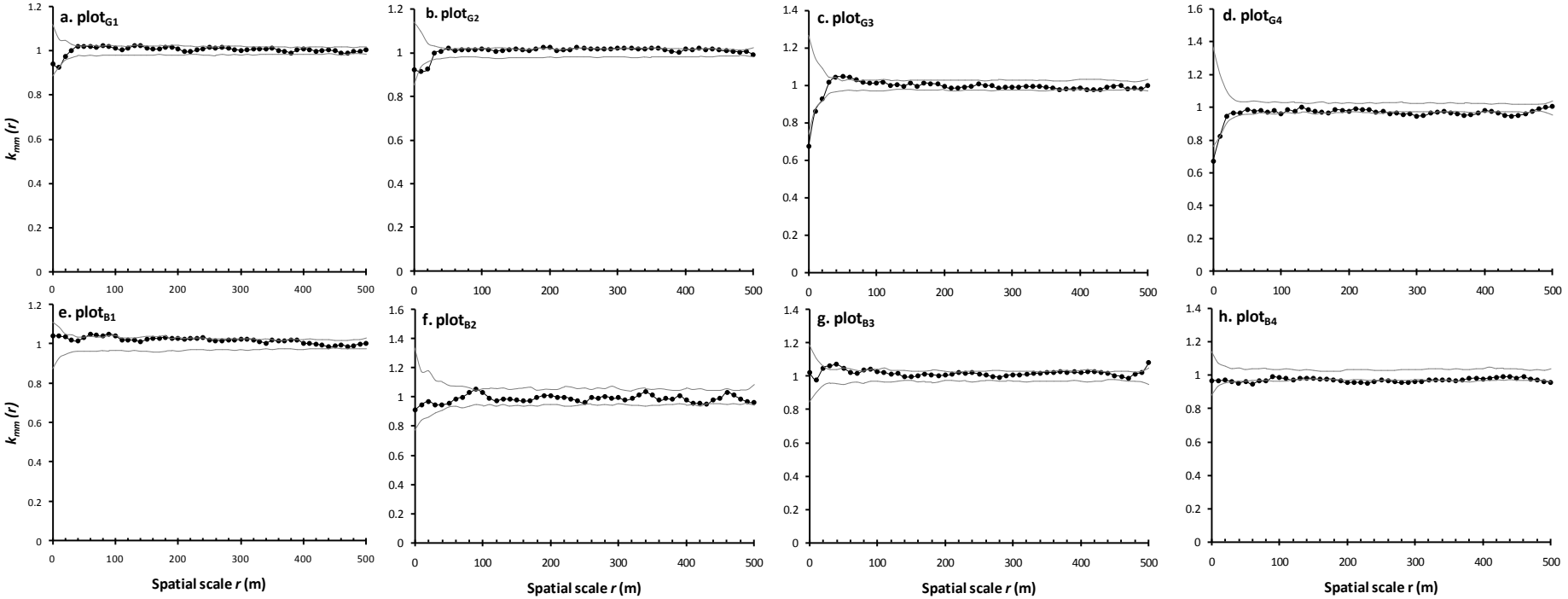


Figure 3.4: The mark correlation function $k_{mm}(r)$ for large mounds on granite (a-d) and basalt (e-h), with diameters greater than 9 and 2.5 m, respectively. Marks are treated independently, positively or negatively correlated at distance r if $k_{mm}(r) = 1$, $k_{mm}(r) > 1$ or $k_{mm}(r) < 1$, respectively. A negative correlation is considered significant if $k_{mm}(r)$ (dark dotted line) falls below the 95% confidence limits (grey lines).

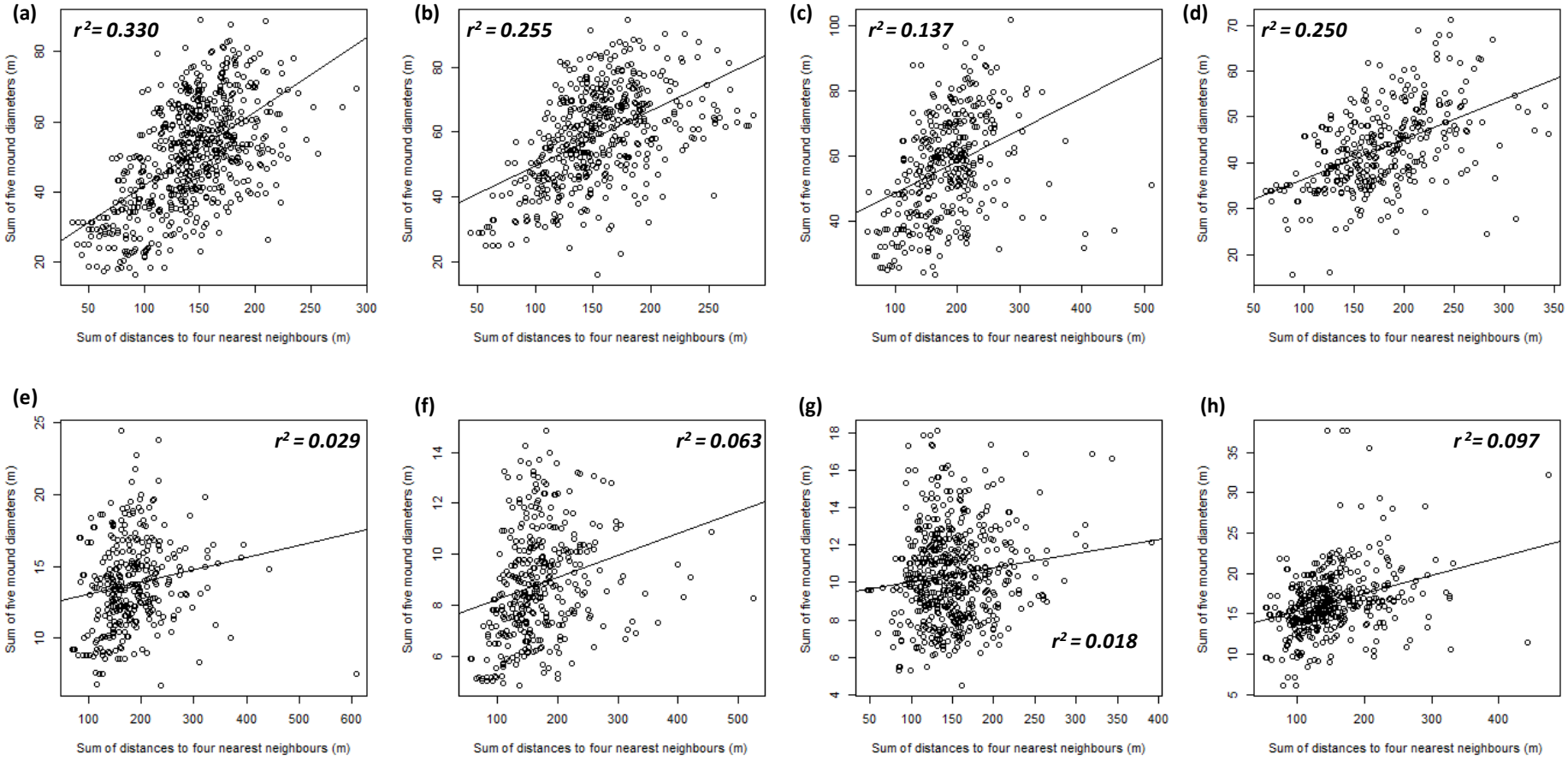


Figure 3.5: Nearest neighbour analysis showing the correlation between the sum of the distances to the four nearest mounds from the focal mound and the sum of the mound diameters of the focal mound and its four nearest neighbours on granite (a-d) and basalt (e-h). The dark line represents the slope of the regression line when the two variables have been converted to z-scores.

The clustering observed on granite suggests the influence of some local factor, such as disease or water inundation on bottom slopes (Bourguignon et al., 2011; Levick et al., 2010a). Another possible explanation for clustering of inactive mounds on granite is the extensive digging and feeding on termites by aardvark (*Orycteropus afer*) on granite (J. Muvengwi, personnel observations). Although aardvark did attempt to attack mounds on basalt, there were clear signs of failure due to the hardness of the mounds that were built primarily by *M. ukuzii* (J. Muvengwi, personnel observations). Mounds built by *M. ukuzii* have a hard compacted clay surface that is difficult to break compared with other *Macrotermes* species (Mitchell, 1980). Colony death (resulting in inactive mounds) on basalt was likely caused by internal causes such as aging and/or hostile inter- or intra-specific competition.

There were clear signs of density dependent thinning on granite where fewer large mounds existed around other large mounds compared with small mounds around large mounds. This indicates that as mounds grow larger they become over-dispersed, which was also detected by the mark correlation function at small spatial scales (0-40 m). The over-dispersion of large mounds at small spatial scales can be inferred to competition (Alba-Lynn and Detling, 2008). The high density of small mounds around large mounds cannot be interpreted as facilitation because self-thinning was evident, but can rather be attributed to chance events leading to colony establishment by queens and/or small foraging areas required by young, small colonies. Another plausible explanation could be that small mounds are a result of "budded", secondary reproductives forming colonies that are less vulnerable during the first phase of establishment because they have a full complement of castes, or possibly through colony migration, although this is a rare event (Wagner et al., 2013). Additional clumping of small mounds on granite, which is independent of large mounds, could be a result of environmental heterogeneity, where new colonies occupy large areas that were occupied by formally inactive mounds within which young colonies can establish at a particular post-mortality age. On basalt, large and small colonies generally exploited the environment in a similar manner, as reflected by how they were randomly distributed.

In this study we demonstrate how geology influences termite mound structure and spatial patterning. It is clear that the mechanisms that determine the structure and spatial distribution patterns of termite mounds are closely related to geology across savanna landscapes. Therefore, the functional roles of termite mounds are unlikely to be equal across landscapes. On granite, termite mounds are larger compared with basalt, covering 15 times

greater surface area, which, together with the observed over-dispersion pattern at small spatial scales (0-30 m), suggests that the significance of mounds to ecosystem heterogeneity, productivity and ecosystem engineering is much more pronounced on granitic savannas.

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Appendices

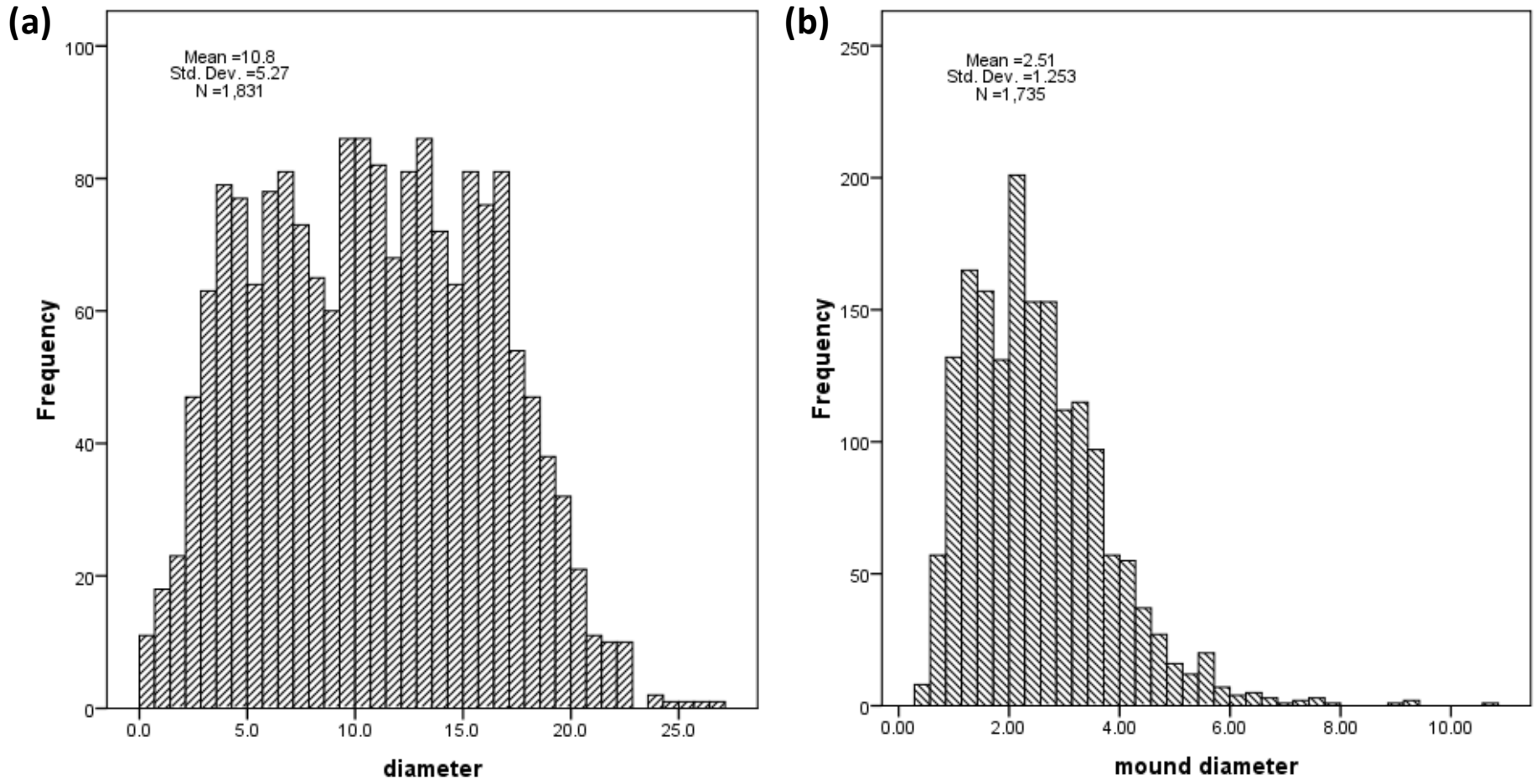


Figure 3.A1: Frequency distribution of active mound diameters on the two geologies, (a) granite and (b) basalt, in Gonarezhou National Park.

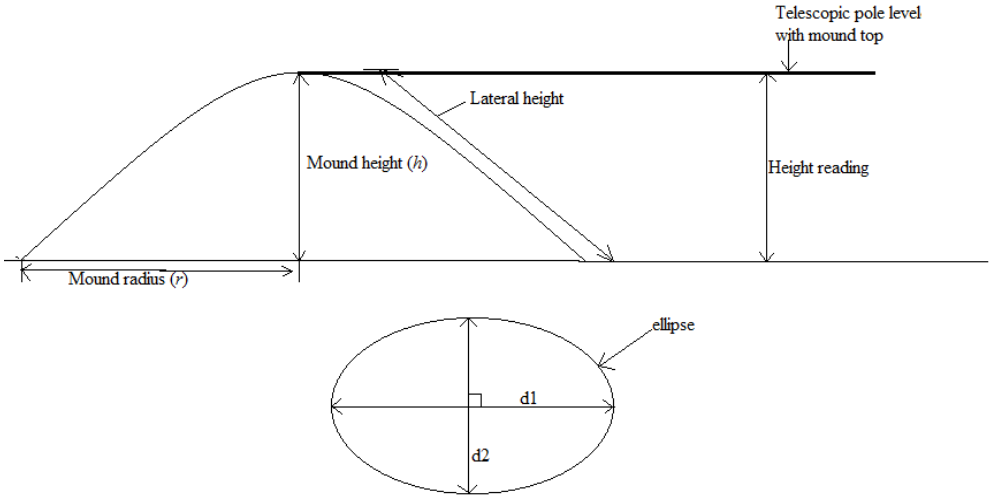


Figure 3.A2: Illustration of how mound height and basal diameter was measured for circular to ellipse termite mounds.

Chapter 4

Chapter 4: **Termite mounds vary in their importance as sources of vegetation heterogeneity across savanna landscapes**

Abstract

Termite mounds are well known to host a suite of unique plants compared to the surrounding savanna matrix. However, most studies testing the significance of mounds for ecosystem heterogeneity have been conducted at single sites. Mound effects on savanna heterogeneity across varying landscapes are less well understood, and how effects might vary across geological types is as yet unknown. In addition, the effect of mound size on savanna herbaceous vegetation has not been previously tested. We studied the effects of termite mounds on vegetation spatial heterogeneity across two geologies (granite and basalt) in Zimbabwe's Gonarezhou National Park, including effects of mound size and the spatial extent of termite influence. Herbaceous vegetation was sampled on mounds and in savanna matrix plots, as well as along distance transects away from mounds. Soil nutrients on mounds and in the savanna matrix were also compared between geologies. Large mounds had higher soil nutrients compared to the savanna matrix on granite, but not on basalt, with mounds therefore acting as nutrient hot-spots on nutrient-poor granite only. Large and medium sized mounds hosted compositionally different grass species to the savanna matrix on granite, but not on basalt. Large mounds on granite also had significantly lower grass and forb species richness compared to the savanna matrix. However, small mounds on granite, as well as all mound size categories on basalt, did not have an effect on grass and forb species richness or assemblage composition, an observation that is attributed to a lack of difference in soil nutrients between mounds and the savanna matrix here. Our study shows that the significance of termite mounds to ecosystem spatial heterogeneity is highly influenced by geology and mound size. Mound effects on herbaceous plant species heterogeneity are more pronounced in dystrophic geologies, but this is dependent on mound size. Future studies on the significance of termite mounds for vegetation heterogeneity should take cognisance of landscape context, such as geology, and mound size when seeking to understand the contribution of termite mounds to ecosystem structure and function.

Key-words: basalt, biomass production, granite, *Macrotermes*, savanna, soil nutrition, spatial extent, species richness

Introduction

Spatial heterogeneity is the main determinant of species richness, abundance and coexistence of plant assemblages (Cornell and Lawton, 1992; Tilman and Kareiva, 1997). Heterogeneity is influenced by both biotic and abiotic processes and can be observed over different spatial scales, from local to continental (Cullum et al., 2016; Scholes and Archer, 1997; Venter et al., 2003). At regional to continental scales, rainfall is the main determinant of heterogeneity (Sankaran et al., 2005), whereas at local to landscape scales, fire, herbivory and soils become more important (Asner et al., 2009; Bond et al., 2005). Within regions falling under one climatic envelope, geological substrate has the greatest influence on heterogeneity (Kruckeberg 1986; Venter *et al.* 2003) and at finer spatial scales, variation in soil nutrients become important.

Soil modification caused by the activities of mound building termites is one such fine-scaled process driving heterogeneity in savanna ecosystems, with strong influences on plant community structure and pattern (Sileshi *et al.* 2010; Jouquet *et al.* 2011). Termites are ecosystem engineers that play important roles in decomposition (Collins, 1981; Holt, 1987; Schuurman, 2005), nutrient cycling (Holt and Coventry, 1988; Konaté et al., 1999) and hydrology (Jones et al., 1994; Mando et al., 1996; Turner, 2006), with cascading effects on savanna vegetation heterogeneity. Recent studies from African savannas have found termite mounds to harbour different woody species (Davies et al., 2016a; Joseph et al., 2013a) and higher woody species richness (Traoré *et al.* 2008; Moe, Mobæk & Narmo 2009; Erpenbach *et al.* 2013) compared to the savanna matrix. Similarly, forb species richness is higher on termite mounds compared to the savanna matrix, although few studies have been conducted (Moe et al., 2009; Okullo and Moe, 2012). In contrast, some studies have found no difference in grass species richness between mounds and the matrix (Moe et al., 2009; Okullo and Moe, 2012), while others have observed higher grass species richness in the savanna matrix compared to mounds (Arshad, 1982; Davies et al., 2014). Similarly, while several studies on large mammal herbivory found utilization of termite mound vegetation to be higher relative to the surrounding matrix vegetation (Loveridge & Moe 2004; Mobæk, Narmo & Moe 2005; Brody *et al.* 2010; Muvengwi *et al.* 2014), some have recorded no difference in herbivore preference (Muvengwi et al., 2013; Van der Plas et al., 2013). Such contrasting findings are likely a result of differing soil nutrient levels in the surrounding matrix that result in termite mound soils differing in their contrast to matrix soils, and demonstrate the need to examine

termite mound effects across sites that incorporate varying environmental context (O'Connor 2013).

Differences related to geological substrate have important implications for savanna heterogeneity, including the abundance, diversity and distribution of both plants and animals (Naiman et al., 2003; Venter et al., 2003). Basalt and granite are two of the most prevalent geologies in southern African savannas and display marked differences. Basaltic geology is rich in clays and basic cations, and when weathered produce fine textured fertile alkaline soils that are relatively nutrient-rich (Olowolafe, 2002), as opposed to granite where the rock weathers to produce nutrient-poor soils (Venter et al., 2003). However, to-date no studies investigating the effect of termite mounds on savanna vegetation heterogeneity across landscapes with varying geology exist, making broad landscape level conclusions of mound effects problematic. Previous studies have found mound effects to vary along rainfall gradients, with the importance of mounds as drivers of savanna heterogeneity increasing with increasing rainfall, likely because increased leaching in wetter savannas makes them relatively nutrient-poor compared to drier areas, leading to larger contrasts in soil nutrients between mounds and matrix soils (Davies et al., 2014; Erpenbach et al., 2013). Because geology has similarly strong effects on soil nutrients, it is likely that termite mounds on opposing geological substrates will also have varying effects on vegetation heterogeneity. Such potential variation requires investigation before a generalised understanding of termite mounds as generators of savanna ecosystem heterogeneity can be realised.

Furthermore, the majority of studies focusing on termite mounds effects on savanna vegetation have only sampled large mounds (e.g. Holdo & McDowell 2004; Loveridge & Moe 2004; Davies *et al.* 2014), resulting in the effect of smaller, younger mounds being poorly understood. However, understanding the effect of small mounds on ecosystem heterogeneity could be useful for determining size thresholds at which mounds become important, as well as for understanding termite mound dynamics more broadly. A single study that has considered mound size found that larger mounds had a greater impact on woody species composition and richness compared to smaller mounds (Joseph *et al.* 2013a), which likely results from increased soil nutrient concentrations on large mounds relative to smaller ones (Seymour et al., 2014). However, no study has investigated changes in herbaceous vegetation in response to mound size. Moreover, termite mound effects on savanna trees (Levick *et al.* 2010; Davies *et al.* 2016a) and herbaceous vegetation (Arshad,

1982; Davies et al., 2014; Gosling et al., 2012) operate at scales larger than the size of individual mounds, making investigation of the spatial extent of termite influences important. Although as yet untested across geologies and mound sizes, erosion from mounds (and thus their sphere of influence) is likely to be less influential on fertile soils because of smaller differences in soil nutrition between mounds and the matrix here.

In order to test the effects of *Macrotermes* mounds on savanna vegetation heterogeneity across landscapes of varying geologies, we sampled vegetation growing on and around mounds located on basalt and granite geologies in Gonarezhou National Park, Zimbabwe. The specific objectives of the study were to: (i) determine how grass and forb species richness, cover and community assemblages differ between termite mounds of varying sizes and the savanna matrix on granite and basalt geologies, and (ii) determine the spatial extent of mound influence on grass and forb species composition in relation to mound size. In order to understand any observed patterns, soil nutrients between mounds and the savanna matrix were compared on each geology. We hypothesized that mounds located on landscapes emanating from nutrient-poor geologies (granite) would be more important for savanna vegetation heterogeneity, whereas no effect on nutrient-rich landscapes was expected. Since mound soil nutrients are related to mound size (Joseph et al., 2013a; Seymour et al., 2014), we predicted that larger mounds would have a stronger effect on savanna vegetation heterogeneity, particularly on nutrient-poor geology, whereas mound size might be inconsequential on nutrient-rich basalt due to fewer differences in soil nutrients between mounds and the savanna matrix here. Similarly, we predicted that mound size would have an effect on the spatial extent to which mounds influence vegetation spatial heterogeneity on nutrient-poor geologies, but not on nutrient-rich geologies.

Methods

Study area

The study was conducted in Gonarezhou National Park (21^0 00′ - 22^0 15′ S, 30^0 15′ - 32^0 31′ E) in south eastern Zimbabwe. Two adjacent geological substrata (basalt and granite), located within similar climatic conditions were sampled. Granite lies to the east and basalt to the west. The average rainfall for the study site is 466 mm, and does not vary between the two substrata. Mean monthly maximum temperatures range between 26 ^{0}C in July and 30 ^{0}C in January, whereas mean monthly minimum temperature ranges between 9 ^{0}C in June and 24

^{0}C in January (Gandiwa et al., 2011). Fire return period across the entire study site was two years (E. Gandiwa, pers. comm.). The common *Macrotermes* mound-building species on granite include *M. subhyalinus* and *M. falciger* and on basalt *M. ukuzii* (Muvengwi J. unpublished data.)

Areas on basalt are dominated by *Colophospermum mopane* woodland, with scattered *Combretum apiculatum* and *Terminalia prunioides* trees. The granitic areas have a mixture of tree species, including *Androstachys johnsonii, Brachystegia glaucescens, Vitex payos, Diospyros loureiriana* and *Xeroderris stuhlmannii*. The herbaceous community on basalt is dominated by *Aristida rhiniochloa, A. adscensionis, Brachiaria deflexa, Seddera suffruticosa* and *Indigofera sp*. whereas granite consists largely of *Digitaria eriantha, Tragus berteronianus, Urochloa mosambicensis, Heteropogon contortus, Indigofera astragalina* and *Chamaecrista mimosoides*.

Study design

Soil sampling and analyses

Within each of the two geologies, mounds were mapped in same plots that were used in chapter 2 and chapter 3. The height and diameter of each mound was measured. For each mound, lateral surface area was calculated following procedures in Muvengwi et al. (2013), and placed into one of three size categories (large, medium and small). Because of distinct mound size differences (Muvengwi J. unpublished data.), size categories differed between the two geologies. Mounds were classified as small when < 10 m^2 on granite *vs.* < 6 m^2 on basalt, medium when between 10-30 m^2 on granite *vs.* 6-10 m^2 on basalt, and large when > 30 m^2 on granite *vs*. > 10 m^2 on basalt (following Joseph *et al.* 2013a). Mounds in each size category were arranged in order of size from the smallest to the largest, and random numbers were generated against each mound and then the mounds were further sorted according to the size of the random numbers and the first three were considered for sampling. Size categories were different between the two geologies because there were no mounds > 30 m^2 on basalt. Three large mounds (granite: >30 m^2 and basalt: > 10 m^2) were randomly selected in each of the four 1 km^2 plots in each geological substrate. Two soil cores (6 cm diameter) to a depth of 15 cm were collected from opposite sides of the mound and bulked, to represent mound soil nutrient concentrations, pH and texture (Mills et al., 2009; Seymour et al., 2014). In total, six

soil samples were collected from mounds in each 1 km^2 plot and bulked into one sample for analysis. A similar procedure was repeated for the corresponding savanna matrix control plots, 16 m away from the edge of the sampled mound to avoid mound effects (Levick *et al.* 2010, Gosling *et al.* 2012, Davies *et al.* 2014). Therefore, in each geological substratum a total of eight samples were analysed for nutrient concentration, pH and texture, four from mounds and four from savanna matrix control plots.

Soils were assayed for total N, mineral N, resin-extractable P, pH, texture (sand (0.02 - 0.2 mm), silt (0.02 - 0.002 mm) and clay (< 0.002 mm), as well as exchangeable Ca, Mg, Na and K, at the Department of Research and Specialist Services, Chemistry and Soil Research Institute in Harare, Zimbabwe. Soil samples were air dried at room temperature before analysis. Soil texture and pH were obtained using the hydrometer and $CaCl_2$ method, respectively (Thomas 1996). Exchangeable bases were extracted using the aqua regia digestion method (Anderson and Ingram, 1993). The resulting compound was then dissolved in concentrated HCl and filtered. The solution was diluted with distilled water. Using a spectrophotometer, total Ca and Mg were determined at 0.460 nm and 0.595 nm, respectively, and flame emission was used for K and Na. Total N was determined using the Kjeldahl method (Okalebo et al., 2002). Plant available P was determined using the molybdenum-blue calorimetric method (Sibbesen, 1978).

Herbaceous vegetation sampling

A total of 72 termite mounds, classified as large, medium and small according to lateral surface area, were sampled for herbaceous plants (grasses and forbs) on both granitic and basaltic substrata in February of 2014 (wet season). In each 1 km^2 plot, three termite mounds were randomly sampled from each of three size categories. A similar sized savanna matrix control plot for each termite mound was placed 16 m from the edge of the mound in a randomly chosen compass direction and on a slope along the same contour line as the mound (*see* Fig. 4S1 in supporting information). A different random compass direction was chosen if the matrix control plot fell within 16 m from any other termite mound in the vicinity.

Mounds were divided into quarters for vegetation sampling. Grass and forb species present in each quarter were identified and their percentage basal cover visually estimated. A similar procedure was repeated in the savanna matrix plot. To assess the spatial extent of the mound's effects, transects were marked from the edge of each sampled mound in the four

cardinal directions and 1 m^2 quadrats were placed at 1 m, 2 m, 4 m, 8 m and 16 m intervals (following Davies et al. 2014).

Herbaceous standing biomass was estimated by dropping a disc pasture meter made up of a long central aluminium rod and a disc plate with a diameter of 36.2 cm. The central aluminium rod is marked in millimetres. The weight of the disc plate is 1.5 kg, and was always dropped from a standard height of 60 cm above the ground in order to measure the compressed height. Biomass was then calculated using the following equation from Trollope (1990):

$$\left(\sqrt{X}\ \mathrm{x}\ 2260\right) - 3019 = \mathrm{kg.\,ha^{-1}}$$

where *X* is the disc height reading in cm obtained from the disc pasture meter. Although this biomass estimation has been calibrated for the Kruger National Park, it was considered suitable for Gonarezhou National Park because the vegetation, rainfall and geology are very similar.

Statistical analyses

Soil variables between mounds and the savanna matrix were compared using paired *t* tests for each geology separately. Sampling adequacy of grasses and forbs on termite mounds and savanna matrix plots was assessed by constructing sample-based rarefaction curves of species richness estimators (Gotelli and Colwell, 2001), including Sobs (Mao Tau), incident-based richness estimator (ICE Mean), Michaelis Menten (MM) Means (1 run), Jack 2 Mean and Chao 2 Mean using EstimateS software (Fig. 4S2). Thereafter, data were tested for normality using Shapiro Wilk test and all percentage data were arcsine square root transformed before analysis. In order to compare species richness for grasses and forbs across different mound size categories, a two-way analysis of covariance (ANCOVA) was applied, with mound area as a covariate to cater for differences in mound area. Differences in grass and forb cover between the savanna matrix and termite mounds were analysed using two-way analysis of variance (ANOVA). Herbaceous biomass was compared across the three mound size categories using a Kruskal Wallis test, while biomass between mounds and the savanna matrix was compared using a paired Wilcoxon signed rank test. To control for differences in mound size between the two geologies, we only compared herbaceous variables for large mounds on basalt against those of medium mounds on granite since all these were in the 10-30 m^2 size category. Differences in grass and forb community composition between

treatments (mound and savanna matrix) for each geology was assessed by constructing a Bray-Curtis dissimilarity matrix and a one-way analysis of similarity (ANOSIM), with pair wise comparisons between mound and savanna matrix for the different mound size categories. When interpreting ANOSIM results, *p*-values should be treated somewhat as a function of sampling effort since they may become inaccurate when sample sizes are low (Clarke and Warwick, 2001). For our interpretation of dissimilarity between mound and savanna, only significant ($p < 0.05$) global R values ≥ 0.4 were considered important. Patterns in grass and forb species composition were visually displayed using non-metric multi-dimensional scaling (nMDS) ordinations. All these analyses were performed separately for each geology.

Grass and forb species characteristic of mounds and savanna matrix plots from each geology were identified using the indicator value (IndVal) method (Dufrêne & Legendre 1997). This technique assesses specificity (uniqueness to a particular habitat) and fidelity (frequency of occurrence in that habitat) of a species to a particular habitat (McGeoch et al., 2002). Species that were significant indicators for a particular site (granite mound, granite savanna, basalt mound and basalt savanna) were considered indicative of that site, however, only those species with significant indicator values $\geq 60\%$ were classified as true indicators (Davies et al., 2014).

Changes in species richness along distance transects were assessed using one-way ANCOVA, with area treated as a covariate. Area was included as a covariate in order to cater for differences in mound and transect quadrat areas. Changes in forb and grass cover with distance along transects was analyzed using one-way ANOVA for each mound size category after pooling data from the four quadrats in each cardinal direction (*see* Davies *et al*. 2014), and changes in biomass were assessed using a Kruskal Wallis test. Variation in grass and forb species composition with distance from mounds was assessed using one-way ANOSIMs applied after construction of Bray-Curtis dissimilarity matrices, with a visual display of the patterns constructed using nMDS ordinations. Pairwise ANOSIM comparisons were made between the mound (as reference) and each distance category (pooled across directions) to detect the extent of mound influence (following Davies *et al.* 2014). As above, assemblages were considered dissimilar when their R value ≥ 0.4 and significant ($p < 0.05$).

Results

Soil nutrition comparison

Large termite mounds on granite had higher levels of mineral and total nitrogen compared to the savanna matrix (Table 4.1). However, termite mounds had significantly lower ($p < 0.05$) sand content but higher silt content compared to matrix plots on both geologies. In contrast, clay content was significantly higher on mounds compared to savanna matrix only on granite (Table 4.1). Matrix plots had significantly lower pH compared to termite mounds on both geologies. On both geologies, mounds had more than twice the concentration of Ca, while the amount of Mg, Na and K was not significantly different between mounds and the matrix.

Table 4.1: Comparison of (mean ± SE) soil variables between mounds and the savanna matrix on the two geologies (basalt and granite). Different superscript letters (a, b) indicate significant differences between mounds and savanna matrix plots (paired *t* test, $p < 0.05$).

	Granite		Basalt	
Variable	Mound	Matrix	Mound	Matrix
Sand %	46.75 ± 2.95^a	62.25 ± 2.84^b	47.50 ± 3.07^a	58.00 ± 2.00^b
Silt %	29.25 ± 1.49^a	23.25 ± 1.80^b	35.50 ± 2.72^a	27.75 ± 2.59^b
Clay %	24.00 ± 1.08^a	13.25 ± 1.31^b	17.50 ± 1.66^a	13.5 ± 1.44^a
pH	7.25 ± 0.13^a	5.15 ± 0.15^b	7.03 ± 0.23^a	6.05 ± 0.09^b
Mineral N (mg/kg)	31.75 ± 1.49^a	12.75 ± 1.38^b	21.25 ± 2.32^a	23.0 ± 3.85^a
Total N (g/kg)	1.9 ± 0.22^a	0.73 ± 0.09^b	1.45 ± 0.17^a	1.0 ± 0.05^a
P (mg/kg)	8.5 ± 1.04^a	6.5 ± 1.56^a	10.0 ± 1.47^a	12.75 ± 1.03^a
Ca (me %)	5.07 ± 0.25^a	1.67 ± 0.22^b	6.50 ± 0.95^a	2.83 ± 0.22^b
Mg (me %)	0.56 ± 0.10^a	0.51 ± 0.13^a	1.06 ± 0.12^a	1.23 ± 0.10^a
Na (me %)	0.11 ± 0.03^a	0.06 ± 0.02^a	0.08 ± 0.01^a	0.06 ± 0.01^a
K (me %)	0.19 ± 0.06^a	0.25 ± 0.09^a	0.14 ± 0.02^a	0.29 ± 0.05^a

Herbaceous vegetation on mounds and in the savanna matrix

In most cases, sampling was generally adequate across all mound size categories for both grasses and forbs species richness in the two geologies (granite and basalt) and this is reflected by the asymptotic nature of the different species richness curves that were

constructed from the different estimators of species richness (Fig. 4S2). Mound size and plot location (mound *vs.* savanna matrix) had a significant effect on grass species richness on granite ($F_{2,65}$ = 12.73, P < 0.0001, $F_{1,65}$ = 7.18, P = 0.0093, respectively; Fig. 4.1a). The interaction between mound size and plot location was not significant ($F_{2,65}$ = 1.82, P = 0.17). The savanna matrix had higher grass species richness than mounds for large mounds (Fig. 4.1a), and large mounds had significantly higher species richness than both small (P < 0.05) and medium sized mounds (P < 0.05). On basalt, mound size also had a significant effect on grass species richness ($F_{2,65}$ = 12.84, P < 0.0001, Fig. 4.1b), whereas plot location did not ($F_{1,65}$ = 2.82, P = 0.0533, Fig. 4.1b). The interaction between mound size and plot location was not significant ($F_{2,65}$ = 0.787, P = 0.46).

For forbs, both mound size and plot location had a significant effect on species richness on granite ($F_{2,65}$ = 6.642, P = 0.0028, $F_{1,65}$ = 13.66, P = 0.0005, respectively), and the interaction between them was significant ($F_{2,65}$ = 3.213, P = 0.046), with the savanna matrix having significantly higher forb richness than mounds for the large size category (Fig. 4.1c). Large mounds had significantly higher forb species richness compared to small and medium mounds (Fig. 4.1c). On basalt, mound size, but not plot location, had a significant influence on forb species richness ($F_{2,65}$ = 4.52, P = 0.015, $F_{1,65}$ = 0.31, P = 0.72, respectively, Fig. 4.1d). Large mounds had significantly higher forb richness than medium sized mounds (Fig. 4.1d). On granite, mound size ($F_{2,66}$ = 16.96, P < 0.00001) and plot location ($F_{1,66}$ = 2.78, P = 0.01) had a significant effect on grass cover (Fig. 4.2a). The interaction between size and location was not significant ($F_{2,66}$ = 3.21, P = 0.047). Only large mounds had significantly higher grass cover compared to the savanna matrix (Fig. 4.2a). Furthermore, large mounds had significantly higher cover compared to medium and small mounds (Fig. 4.2a). On basalt, grass cover did not differ significantly between mound size categories ($F_{2,66}$ = 1.15, P = 0.324), nor between mounds and the savanna matrix ($F_{1,66}$ = 3.16, P = 0.080). The interaction between mound size and plot location was also not significant ($F_{2,66}$ = 1.01, P = 0.37). Forb cover on granite was significantly influenced by mound size ($F_{2,66}$ = 3.303, P = 0.043) and plot location ($F_{1,66}$ = *15.18*, P = 0.0002). Cover was marginally higher for large mounds compared to small ones (Fig. 4.2c). The interaction between size category and plot location was not significant ($F_{2,66}$ = 2.706, P = 0.074).

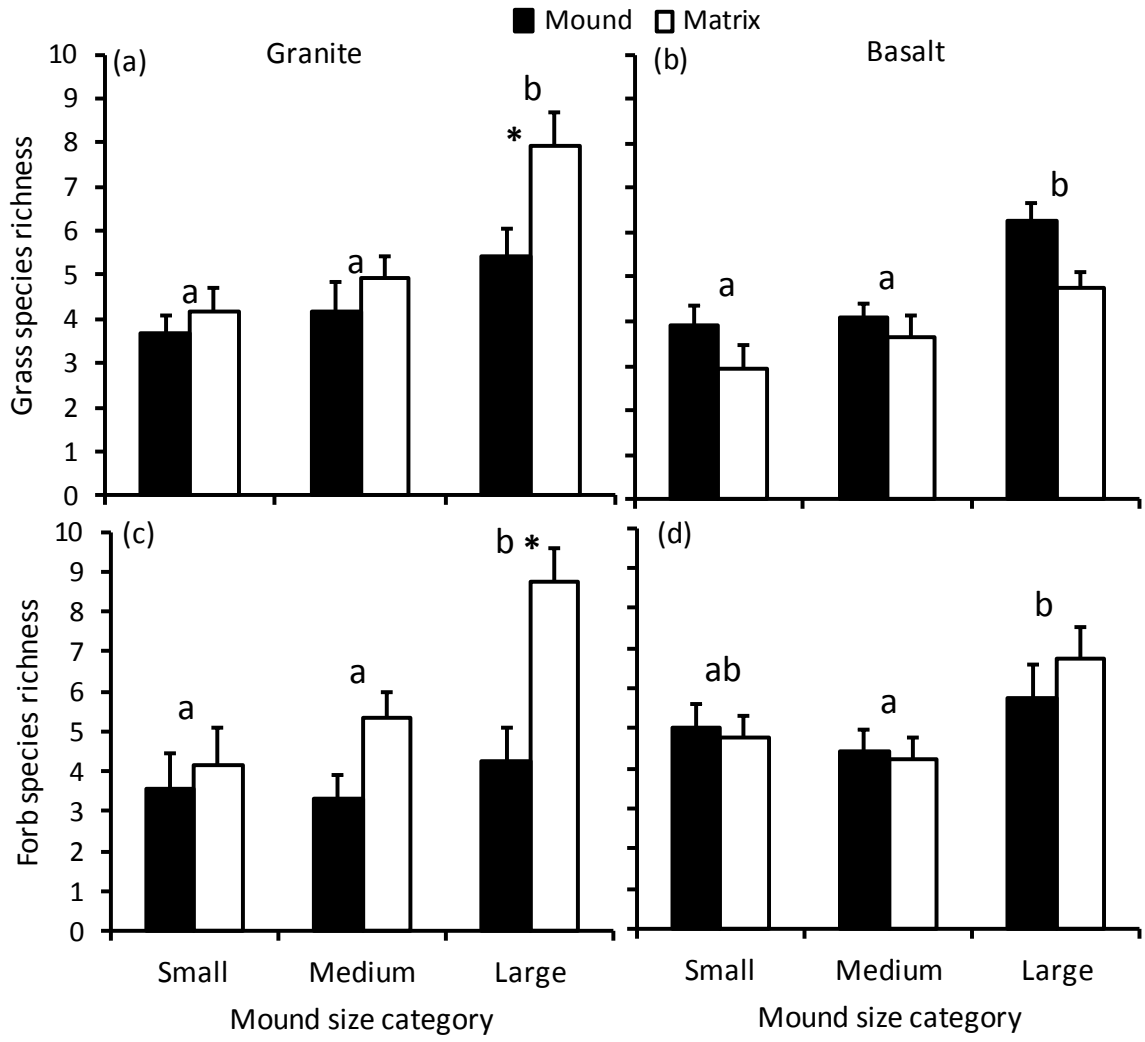


Fig. 4.1: Grass and forb species richness on mounds and in the savanna matrix for (a) granite grasses, (b) basalt grasses, (c) granite forbs and (d) basalt forbs, surveyed across mound size categories. Size categories with different letters are significantly different from each other (Tukey HSD, $P < 0.05$) and asterisks denote significant difference between mound and savanna matrix plots (paired *t* test, $P < 0.05$).

Forb cover was significantly higher in the savanna matrix only for large mounds (Fig. 4.2c). On basalt, mound size ($F_{2,66} = 0.31$, $P = 0.73$) and plot location ($F_{1,66} = 0.005$, $P = 0.95$) had no significant influence on forb cover, (Fig. 4.2d), nor did their interaction ($F_{2,66} = 0.12$, $P = 0.89$). Mound size had a significant influence (Kruskal Wallis test: $\chi^2 = 6.99$, $df = 2$, $p = 0.030$) on standing herbaceous biomass on granite (Fig. 4.3a), increasing with increasing mound size. The pairwise Wilcoxon signed rank test showed that large mounds produced significantly more biomass compared to small mounds (Fig. 4.3a). Large and medium

mounds supported significantly more biomass compared to the savanna matrix (paired Wilcoxon signed rank test: $V = 2938.5$, $p = 0.015$; $V = 2570.5$, $p = 0.0026$, respectively; Fig. 4.3a). On basalt, mound size also had a significant influence on biomass ($\chi^2 = 59.98$, $df = 2$, $p < 0.0001$). Large mounds supported significantly more biomass than medium and small mounds ($p < 0.0001$). Biomass was generally similar between mounds and the savanna matrix on basalt, apart from medium mounds that supported higher biomass compared to the savanna matrix ($V = 2685.5$, $p = 0.0025$).

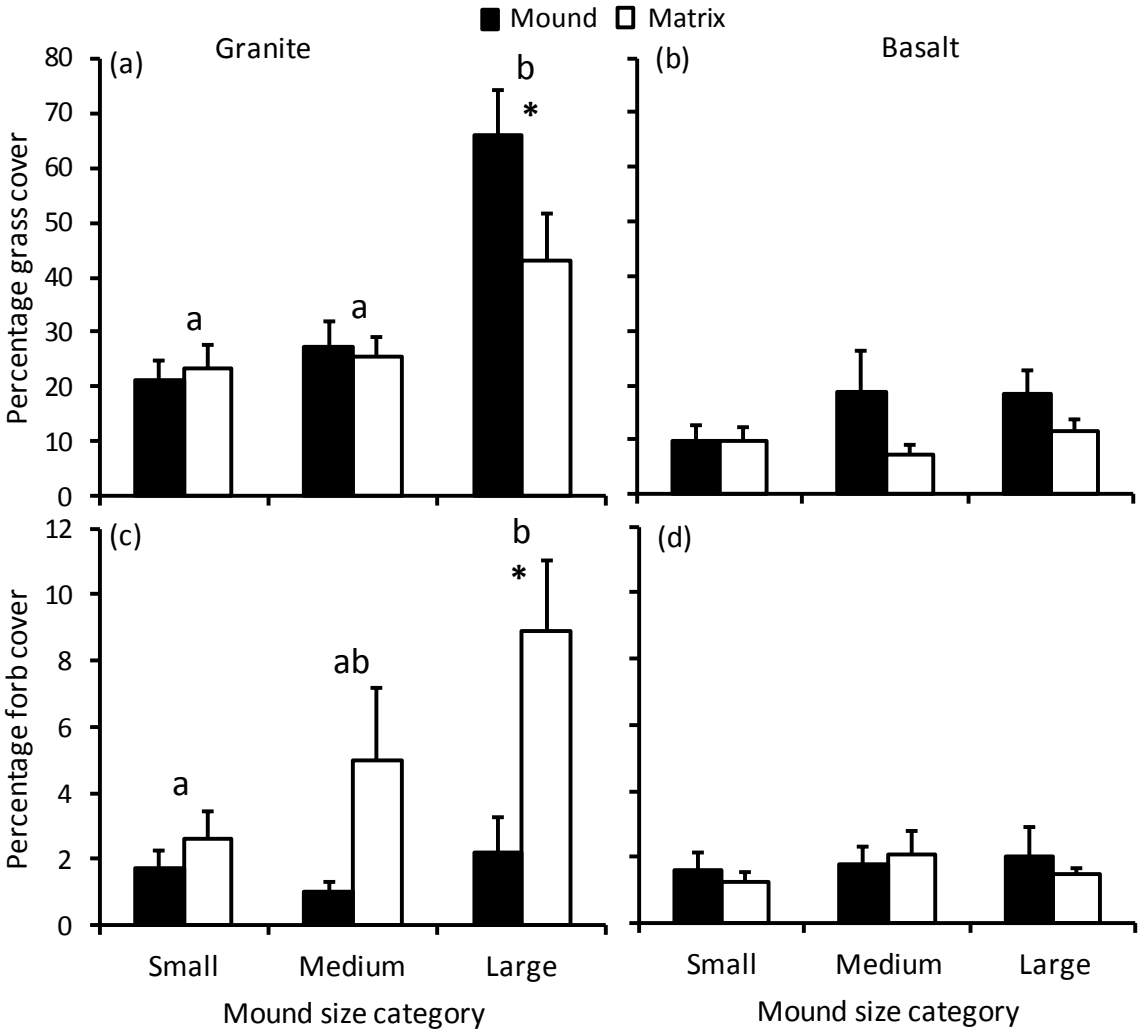


Fig. 4.2: Grass cover on (a) granite and (b) basalt, and forb cover on (c) granite and (d) basalt. Mound size categories with different letters are significantly different from each other (Tukey HSD, $P < 0.05$) and asterisks denote significant difference between mound and savanna matrix plots (paired t test, $P < 0.05$).

Mounds had a greater effect on grass species composition on granite than they did on basalt, and mound size was of consequence on granite, but not basalt (Table 4.2, Fig. 4.4a). On granite, larger mounds clustered together in the nMDS, indicating that they harbour a different suite of species (Fig. 4.4a). Forb species composition was highly dissimilar between mounds and the savanna matrix for large mounds on granite only (Table 4.2, Fig. 4.4b). On basalt, mound size and plot location had no effect on grass and forb species composition, with all mounds clustered together regardless of size in the nMDS (Table 4.2, Fig. 4.4).

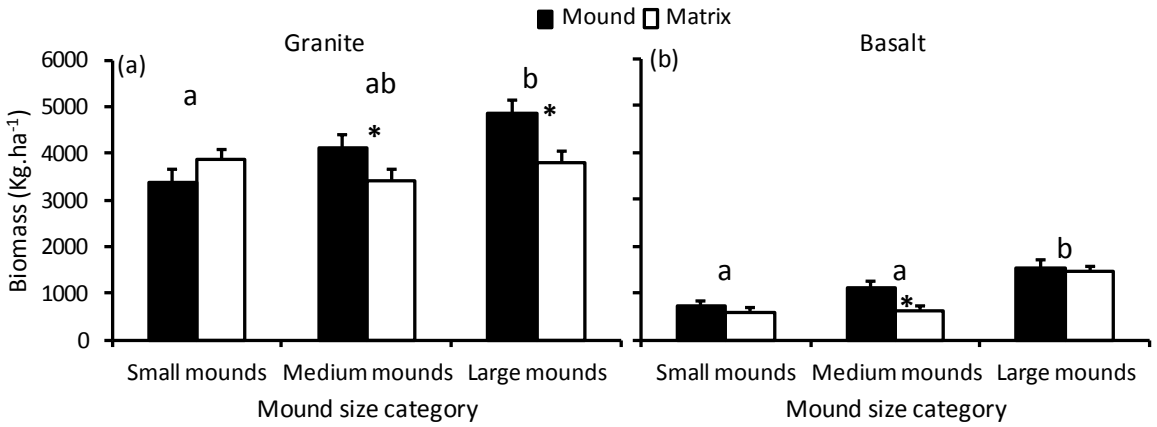


Fig. 4.3: Standing biomass between mounds and the savanna matrix on (a) granite and (b) basalt across mound size categories. Mound size categories with different letters are significantly different from each other (Wilcoxon signed rank test, $p < 0.05$) and asterisks denote significant differences between mound and savanna matrix plots (paired Wilcoxon signed rank test, $p < 0.05$).

Nineteen grass species had significant indicator values across the four sites, of which eight had indicator values greater than 60% (Table 4.3). Of these eight species, mounds and the savanna matrix on granite contained three indicator species each, whereas mounds and the matrix had one species each on basalt (Table 4.3). *Urochloa mosambicensis* had the highest indicator value for mounds on granite, whereas on basalt *Brachiaria deflexa* was an indicator species (Table 4.3, Fig 4S3a,b). The top indicator grass species on granite and basalt for the savanna matrix were *Digitaria eriantha* (84.5%) and *Aristida rhiniochloa* (67.7%), respectively. A total of 22 forb species had significant indicator values across sites, however, only three species had indicator values > 60%, all of which were characteristic of the savanna

matrix on granite (Table 4S1, Fig 4S3c). No forb species had significant indicator values on granite or basalt mounds, or in the savanna matrix on basalt (Table 4S1, Fig 4S3d).

Herbaceous assemblages with distance from mounds

Distance from termite mound had no significant effect ($P > 0.05$) on grass or forb species richness on either geology, across mound size categories (Figs 4S4, 4S5). However, mound distance had a significant influence on grass cover for both large ($F_{5,66} = 14.1$, $P < 0.0001$) and medium ($F_{5,66} = 5.365$, $P = 0.0003$) mounds on granite, but not for small mounds ($F_{5,66} = 1.269$, $P = 0.288$, Fig. 4S6c).

Table 4.2: One-way analysis of similarity (ANOSIM) of grass and forb species assemblages between mounds and the savanna matrix, as well as across mound size categories on granite and basalt substrate. The *R* statistic is a measure of similarity of assemblages, where values closer to 1 reflect higher dissimilarity. Values in bold are those with an *R* statistic ≥ 0.4.

	Grasses	*P* value	Forbs	*P* value
Global *R*	**0.468**	**0.001**	0.327	0.001
Granite small mounds vs savanna matrix	0.332	0.001	0.077	0.174
Granite medium mounds vs savanna matrix	**0.419**	**0.001**	0.324	0.001
Granite large mounds vs savanna matrix	**0.610**	**0.001**	**0.481**	**0.001**
Basalt small mounds vs savanna matrix	0.062	0.189	0.234	0.003
Basalt medium mounds vs savanna matrix	0.083	0.136	0.155	0.022
Basalt large mounds vs savanna matrix	0.131	0.054	0.217	0.004
Granite small mounds vs granite medium mounds	0.026	0.249	0.038	0.252
Granite small mounds vs granite large mounds	0.295	0.002	0.226	0.006
Granite medium mounds vs granite large mounds	0.094	0.063	0.08	0.095
Basalt small mounds vs basalt medium mounds	-0.056	0.828	0.112	0.045
Basalt small mounds vs basalt large mounds	0.101	0.060	0.027	0.316
Basalt medium mounds vs basalt large mounds	0.036	0.218	0.011	0.388

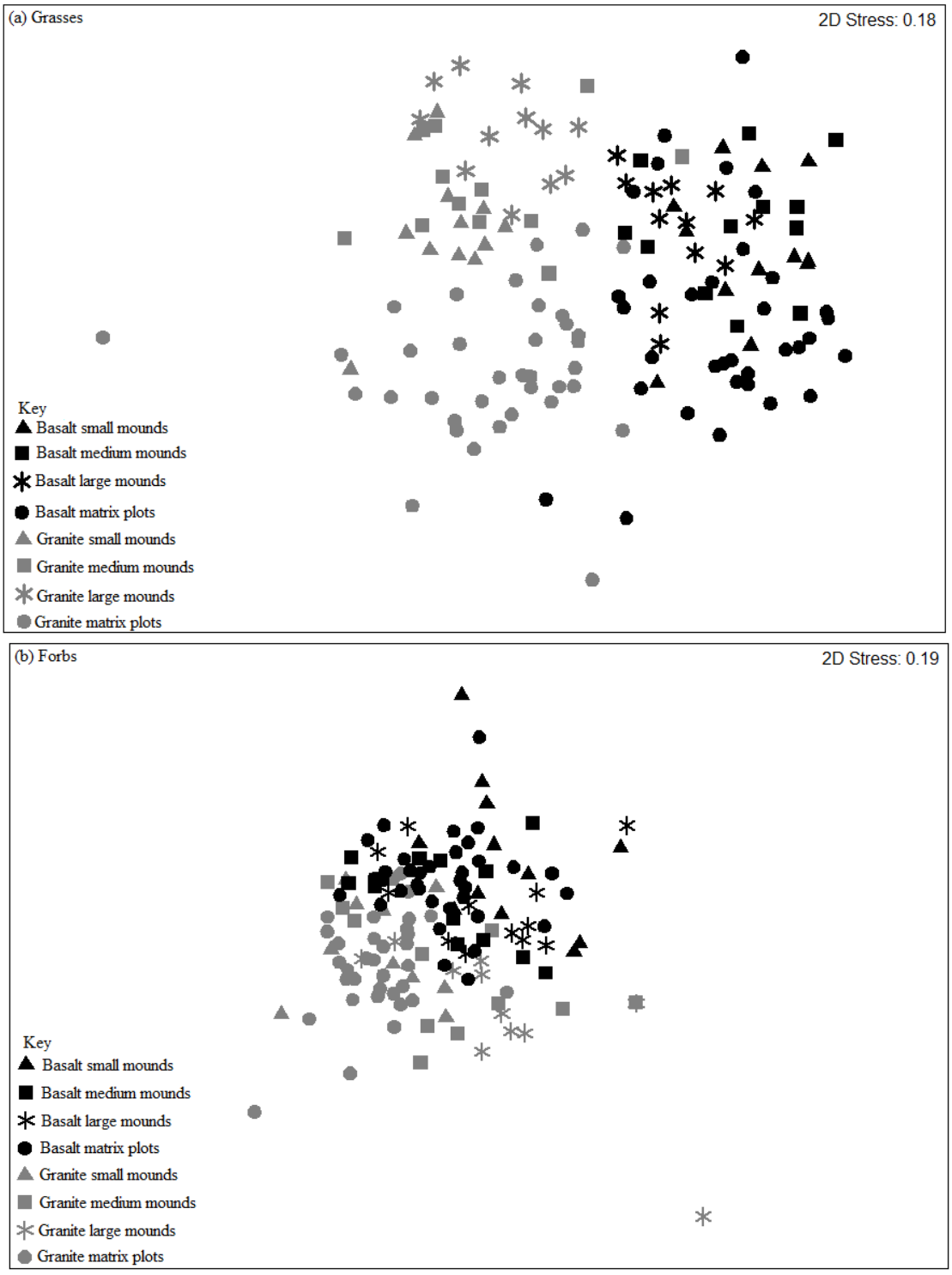


Fig. 4.4: Non-metric multi-dimensional scaling (nMDS) ordination of (a) grass and (b) forb assemblages on mounds of different size categories and the adjacent savanna matrix on granite and basalt substrate.

Table 4.3: Characteristic grass species with significant indicator values (IndVal) for mounds and the savanna matrix on basalt and granite geologies. Indicator values in bold were significant ($P < 0.05$) and scored above 60%, and are therefore regarded as true indicator species for the site. ns denotes that the species was present in a particular habitat, but not significant; - denotes that the species is absent from that particular habitat. Grazing values follow those of Van Oudtshoorn (2014).

Species	Site				
	Granite mounds	Granite savanna	Basalt mounds	Basalt savanna	Grazing value
Urochloa mosambicensis	**91.7**	ns	ns	ns	average
Panicum maximum	**66.8**	ns	ns	-	high
Tragus berteronianus	**63.1**	ns	ns	ns	low
Chloris virgata	52.3	ns	ns	-	average
Brachiaria brizantha	39.0	ns	-	-	average
Digitaria eriantha	ns	**84.5**	ns	ns	high
Melinis repens	ns	**64.5**	ns	ns	low
Heteropogon contortus	ns	**63.3**	ns	ns	average
Aristida congesta	-	50.6	ns	ns	low
Setaria megaphylla	-	44.1	-	-	high
Pogonathria squarossa	-	44.1	-	-	low
Brachiaria nigropedata	ns	44.1	-	-	high
Eragrostis cilianensis	ns	43.4	-	-	low
Sporobolus panicoides	ns	40.2	-	-	low
Brachiaria deflexa	ns	ns	**85.0**	ns	average
Enneapogon cenchroides	ns	ns	59.1	ns	average
Bothriochloa radicans	ns	ns	50.7	ns	low
Aristida rhiniochloa	-	ns	ns	**67.7**	low
Aristida stipitata	-	ns	ns	40.5	low

There was a sharp decline in grass cover between 0 and 1 m from both large and medium mounds, and cover was significantly higher on mounds compared to all other transect distance categories for both large and medium mounds (Fig. 4S6a,b). Similarly, on basalt, distance from mound had a significant influence on grass cover for large and medium mounds (large: $F_{5,56}$ = 4.56, P = 0.0012, medium: $F_{5,66}$ = 3.086, P = 0.0145), but distance from small mounds had no effect ($F_{5,66}$ = 0.258, P = 0.934, Fig. 4S6f). For both large and medium mounds, grass cover was significantly higher on mounds than at any distance along the transects (Fig. 4S6d,e).

Forb cover did not vary with distance from mound on granite for large, medium or small mounds ($F_{5,66}$ = 1.577, P =0.179; $F_{5,66}$ = 1.653, P = 0.158 and $F_{5,66}$ =0.418, P = 0.835, respectively; Fig. 4S7a-c). Similarly, forb cover did not vary with distance from mound for all mound size categories on basalt (large: $F_{5,66}$ = 0.899, P = 0.487; medium: $F_{5,16}$ = 0.762, P =0.58; small: $F_{5,66}$ = 0.692, P = 0.631; Fig. 4S7d-f).

For large mounds, distance had a significant influence on herbaceous standing biomass on both geologies (Kruskal-Wallis test – granite: χ^2 = 23.46, df = 5, P = 0.00028; basalt: χ^2 = 22.79, df = 5, P = 0.00037). Biomass was significantly higher on large mounds compared to distance classes 1, 8 and 16 m on both geologies (Fig. 4S8a,d). Distance from medium mounds had a significant influence on herbaceous biomass on granite (Kruskal-Wallis test: χ^2 = 32.67, df = 5, P < 0.0001), with significantly higher biomass on mounds compared to all distance classes off mounds (Fig. 4S8b). However, distance from medium mounds had no effect on standing biomass on basalt (Kruskal-Wallis test: χ^2 = 5.12, df = 5, P = 0.4013) (Fig. 4S8b,e). Distance from small mounds had no significant influence on standing biomass on either granite (Kruskal-Wallis test: χ^2 = 1.922, df = 5, P = 0.8598) or basalt (Kruskal-Wallis test: χ^2 = 4.27, df = 5, P = 0.511) (Fig. 4S8c,d).

Grass species composition along distance transects on granite varied with mound size. A significant difference in species composition compared to the mound occurred at 4 and 8 m for large and medium mounds, respectively (Fig. 4.5b-c). However, grass assemblages did not change with distance away from small mounds (Fig. 4.5a). On basalt, grass assemblages were not different for any distance class, which was reflected in the way the assemblages at different distances were clustered in the nMDS ordinations and the correspondingly small global R values (Fig. 4.5d-f).

Forb community composition was significantly different from that of large mounds at a distance of 4 m from the mound on granite (Fig. 4.6c). For basalt, there was no change in forb community assembly across all mound sizes (Fig. 4.6d-f).

Discussion

Our findings reveal that termite mounds contribute to plant species heterogeneity in semi-arid savannas, corroborating previous studies (Davies et al., 2016a, 2014; Joseph et al., 2014). However, mound effects on herbaceous plant diversity are not uniform across landscapes, but are more pronounced on dystrophic geologies. Furthermore, mound size is of paramount importance in terms of the size of the effect termite mounds have on plant diversity, with mound size effects being more consequential on nutrient-poor geologies. Since termite mounds are larger on granites, they become even more important as generators of savanna heterogeneity on this nutrient-poor geology. Similarly, mounds had higher soil nutrients compared to the savanna matrix on granite, but not on basalt, likely leading to the stronger mound effects on granite where they subsequently act as nutrient hot-spots.

On granite, grass species richness was generally higher in the savanna matrix compared to mounds, an observation consistent with other studies (Arshad, 1982; Davies et al., 2014). More specifically, large mounds had significantly lower grass species richness compared to the matrix, which can be attributed to their higher soil nutrient concentrations compared to smaller mound sizes (Seymour et al., 2014). This suggests that grass species richness attains maxima in the dystrophic savanna matrix where competition for resources does not lead to the dominance of a few species as in nutrient-rich environments (Grime, 1973). Similarly, grass and forb species composition on granite differed markedly between mounds and the savanna matrix, with this difference becoming more pronounced with an increase in mound size. Larger mounds have similarly been shown to display larger differences in terms of woody species composition (Joseph *et al.* 2013a), and such patterns are likely driven by increased soil nutrient concentrations on large mounds relative to smaller ones (Seymour et al. 2014). In contrast to previous savanna studies (Moe et al., 2009; Okullo and Moe, 2012), forbs attained higher species richness in the nutrient-poor granite savanna matrix in similar ways to grasses.

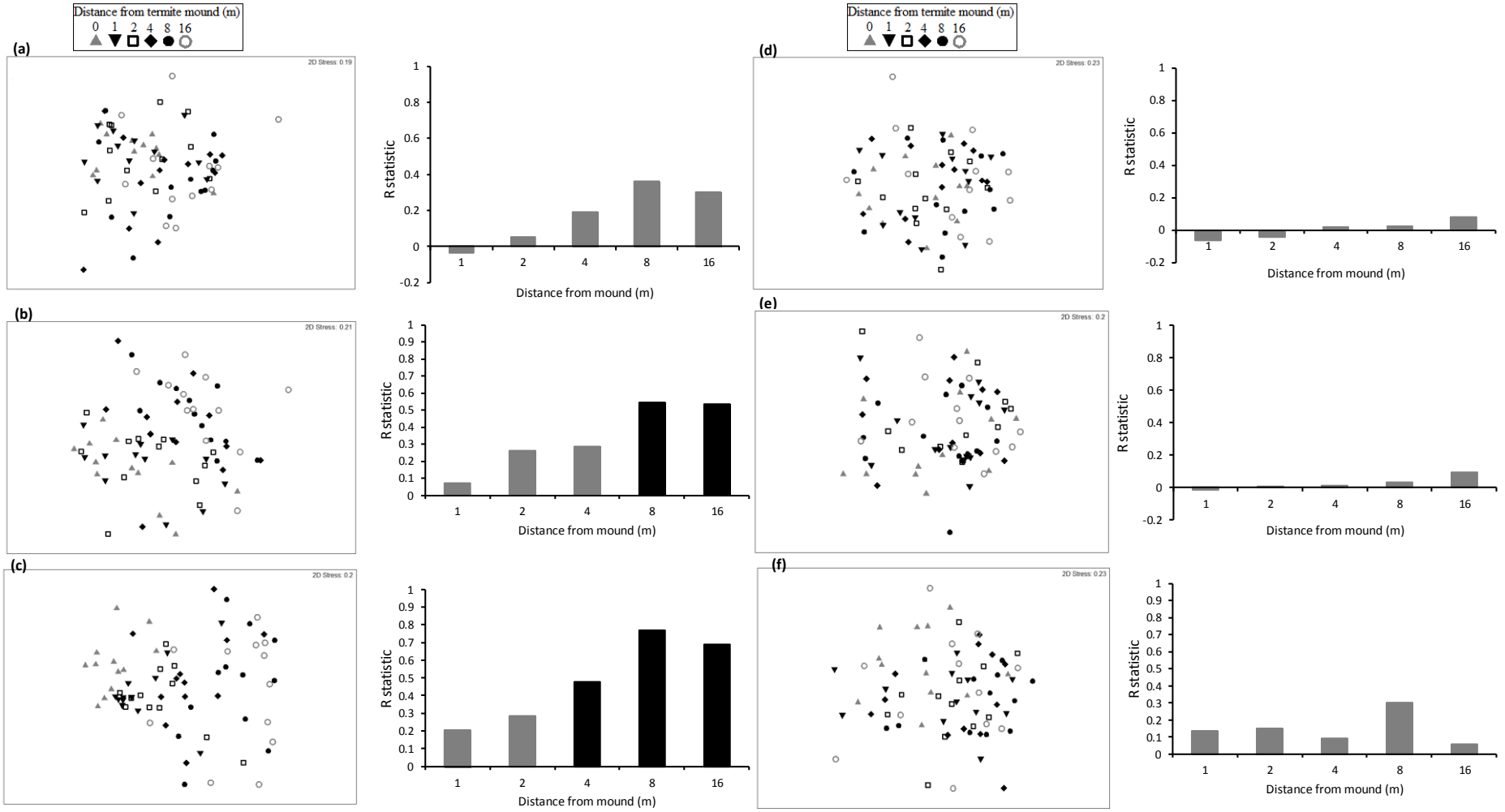


Fig. 4.5: Non-metric multi-dimensional scaling (nMDS) ordinations of grass assemblages along transects of increasing distance from small, medium and large termite mounds at the two geologies, granite (a-c) and basalt (d-f), in order of mound size, respectively. Ordinations are

displayed in the left panel 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 from the mound. Distances with black bars are significantly different from mounds. For our interpretation of the spatial extent around mounds, significant *R* values ≥ 0.4 were considered important.

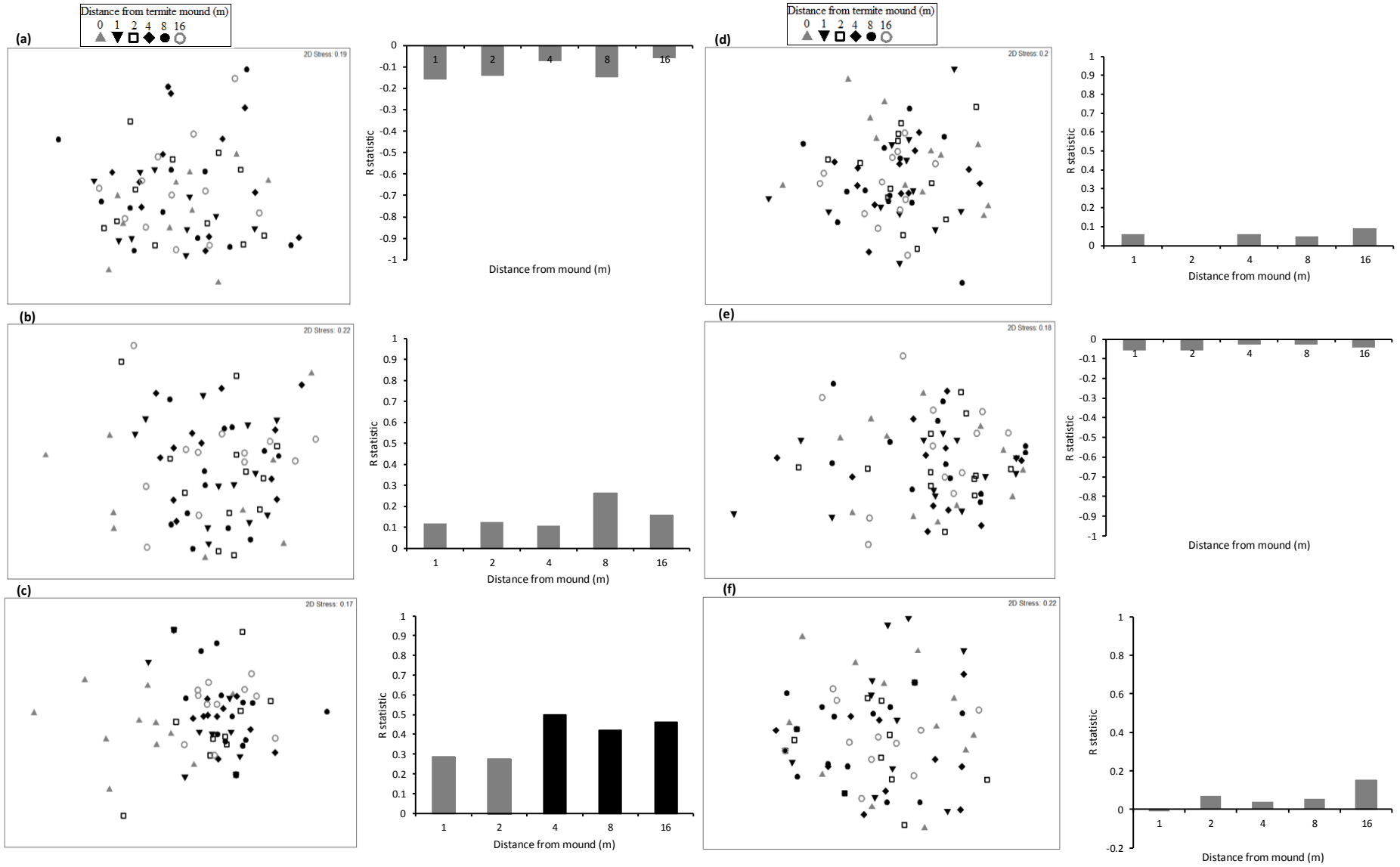

Distance from termite mound (m)
0 1 2 4 8 16
(a)
2D Stress: 0.19
R statistic
Distance from mound (m)
(b)
2D Stress: 0.22
(c)
2D Stress: 0.17
(d)
2D Stress: 0.2
(e)
2D Stress: 0.18
(f)
2D Stress: 0.22

Fig. 4.6: Non-metric multi-dimensional scaling (nMDS) ordinations of forb assemblages along transects of increasing distance from small, medium and large termite mounds at the two geologies, granite (a-c) and basalt (d-f), in order of mound size, respectively. Ordinations are displayed in the left panel 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 from the mound. Distances with black bars are significantly different from mounds. For our interpretation of the spatial extent around mounds, significant *R* values ≥ 0.4 were considered important.

According to the resource ratio hypothesis, spatial variation can increase species co-existence beyond what one would be expected from competition alone, leading to higher species richness, as observed in the granite savanna matrix in our study (Tilman, 1988, 1994).

Mounds on basalt differed little to the savanna matrix in terms of soil nutrients, and these areas concomitantly displayed no difference in grass and forb richness or species composition across all mound size categories. These findings support our hypothesis that mounds are not as important for savanna heterogeneity on nutrient-rich geologies compared to nutrient-poor areas because of their similarity in soil nutrients to the savanna matrix, closely following findings for mammalian herbivory (Muvengwi et al., 2013; Van der Plas et al., 2013) and vegetation patterns across rainfall gradients (Davies et al., 2014; Erpenbach et al., 2013), and demonstrating that the functional role of termite mounds in savanna ecology is dependent on environmental context (O'Connor, 2013). Other factors such as middens, game paths, rubbing posts and herbivory are likely more important drivers of vegetation heterogeneity on such nutrient-rich environments. However, differences in the influence of mounds on the two geologies could be species specific. Also, soil from mounds of different termite species could probably have different effects on plant species growth and development.

Although grass richness was lower on mounds compared to the savanna matrix on granite, grass cover was significantly higher on mounds, especially on large mounds. The greater soil nutrients and moisture, as well as protection from fire likely facilitates plant growth that leads to higher cover on mounds compared to the savanna matrix (Gosling et al., 2012; Joseph et al., 2013b). In contrast, forb cover was higher in the savanna matrix than on mounds. Due to differences in soil nutrients and associated vegetation, there is often higher grazing pressure on mounds relative to the savanna matrix (Mobæk *et al.* 2005; Davies *et al.* 2016a; Chapter

5). Grasses are generally better adapted to handle trampling and defoliation associated with grazing (McNaughton 1984) and cope better under grazing pressure than forbs, increasing in cover under grazing compared with forbs that increase when grazing is suppressed (Rooney, 2009). Grasses can therefore outcompete forbs on mounds and constitute most of the vegetation cover. In support of this notion, there was no difference in forb cover between mounds and the savanna matrix on basalt, which is likely because the lack of variation in soil nutrients between mounds and the savanna matrix here leads to uniform grazing pressure on mounds and in the matrix (Muvengwi J. unpublished data.).

Despite heavier grazing on large mounds, standing plant biomass, which can be used as a surrogate for productivity, increased in the same manner as richness across mound size categories on granite, suggesting a sigmoid curve. This observation is closely related to the hump shaped curve described in many studies on vascular plants (Mittlebach et al., 2001). Competitive exclusion has been observed to intensify with a decrease in the heterogeneity of limiting resources that occurs at highly productive sites, leading to such hump shaped curves (Abrams, 1995). It appears that on granite a threshold for biomass production is attained on medium sized mounds, which we presume to have intermediate nutrient levels between large mounds and the savanna matrix. The lack of difference in soil nutrients between mounds and the savanna matrix on basalt, likely leads to no clear patterns in standing biomass between mounds and the matrix here. However, there was a drop in grass cover from the perimeter of large mounds to a distance of 1 m from mounds on both granite and basalt, possibly due to increased grazing around the perimeter of mounds (Davies et al., 2016b).

In line with our predictions that mound size would have an effect on the extent to which mounds influence vegetation spatial heterogeneity on nutrient-poor geologies, medium and large mounds influenced heterogeneity at distances from the periphery of the mounds on granite. The spatial extent of influence on grass assemblage composition for medium mounds was 8 m compared to 4 m for large mounds. Although the spatial extent of influence of large mounds on forb composition was similar to that for grasses, there was no discernible spatial effect around medium mounds. The spatial effect of mounds on savanna assemblage composition with distance from mounds has been observed along a rainfall gradient (Davies et al., 2014), and is an implication of erosion of nutrient-rich soil from the mounds (Gosling et al., 2012). However, mounds from all size categories on basalt did not have discernible

spatial effects on either forb or grass assemblage composition, an observation similar to patterns observed between mounds and the savanna matrix here.

Of the grass species indicative of mounds on both granite and basalt, *Panicum maximum Urochloa mossambicensis* and *Brachiaria deflexa* are of relatively high grazing quality (Van Oudtshoorn, 2014), suggesting that termite mounds, especially on granite, represent quality forage for herbivores (see also Mobæk *et al.* 2005; Davies *et al.* 2016). Although *Tragus berteronianus*, of poor grazing quality (Van Oudtshoorn, 2014), was also an indicator species on granite mounds, its occurrence can be explained by its tendency of often being the first species to colonise disturbed areas and hard compacted soils, such as those around termite mounds (Van Oudtshoorn, 2014). Few species stood out as indicators for the savanna matrix on granite (*Digitaria eriantha, Heteropogon contortus* and *Melinis repens*) and basalt (*Aristida rhiniochloa*), indicating a more mixed species environment in terms of composition and nutritional value (Van Oudtshoorn, 2014). For forbs, only three species were true indicators in the granite savanna matrix: *Indigofera demissa*, *I. astragalina* and *Chamaecrista mimosoides*, and could probably establish better in the granite savanna matrix compared to mounds because of lower grazing pressure here (Muvengwi J. unpublished data.).

Our results demonstrate that *Macrotermes* mounds alter the spatial distribution of the savanna herbaceous community, increasing ecosystem heterogeneity, but that effects vary across the landscape, being stronger on nutrient-poor geologies. Moreover, compositional differences in plant communities between mounds and the savanna matrix observed on dystrophic landscapes increases their functional diversity (Joseph et al., 2014). Our findings further highlight the growing understanding that termite mound effects are dependent on environmental context and that they are of less consequence in nutrient-rich areas. Although mounds are important components of savanna ecology, even increasing these system's robustness to climate change (Bonachela et al., 2015), we found that only larger mounds influence savanna heterogeneity. However, small mounds do grow into large mounds over time (Bourguignon et al., 2011) and therefore should not be altogether discounted. While studies modelling savanna habitat quality in the immediate term should focus on larger mounds, especially on nutrient poor geologies, smaller mounds should be considered in longer term predictions.

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Appendices

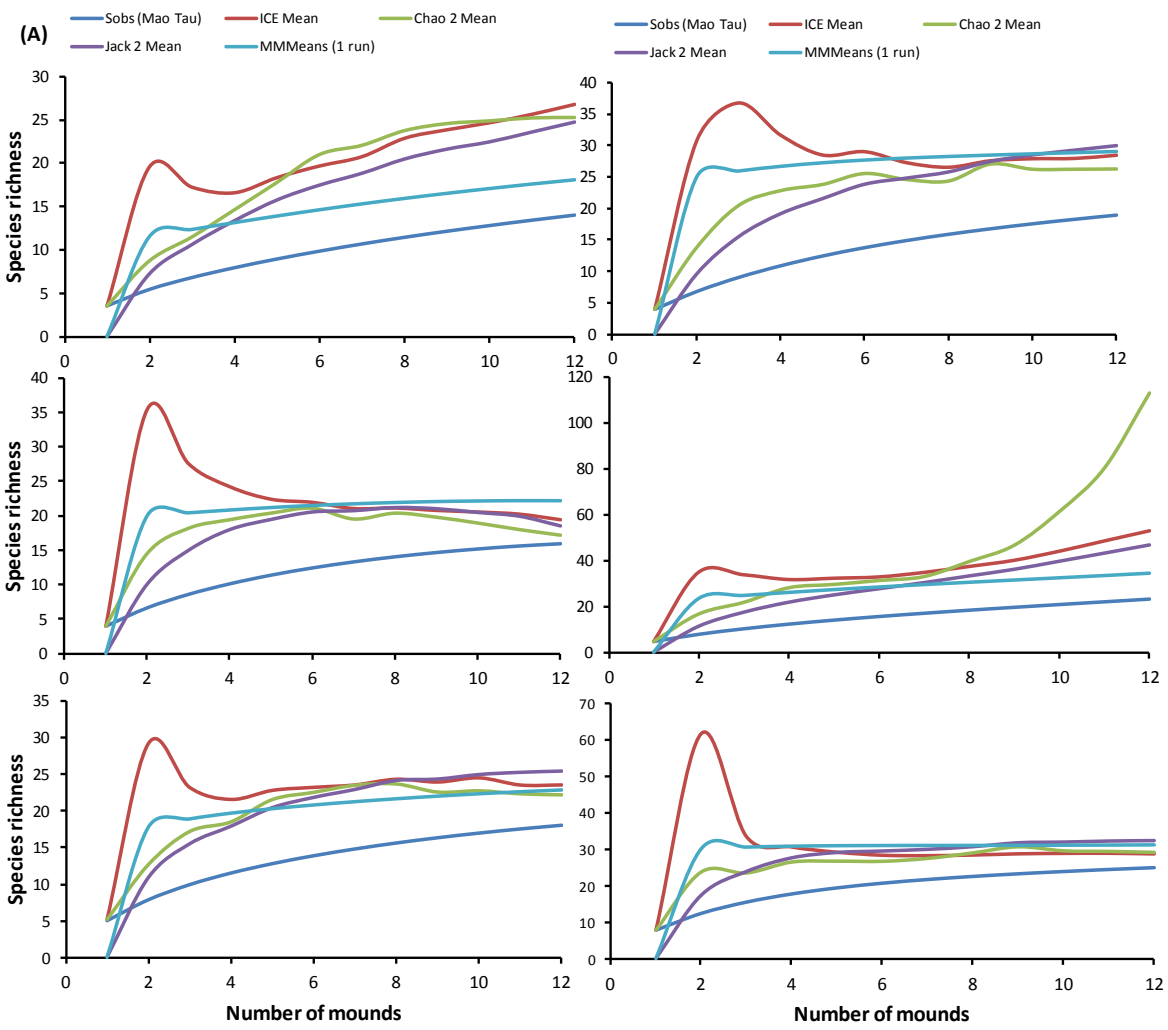
Table 4S1. Characteristic indicator forb species for mounds and the savanna matrix sampled on basalt and granite geologies. Indicator values in bold were significant (P<0.05) and above 60% and regarded as true indicator species for the site. ns denotes that the species is present in a particular habitat, but not significant; - denotes that the species is absent from that particular habitat.

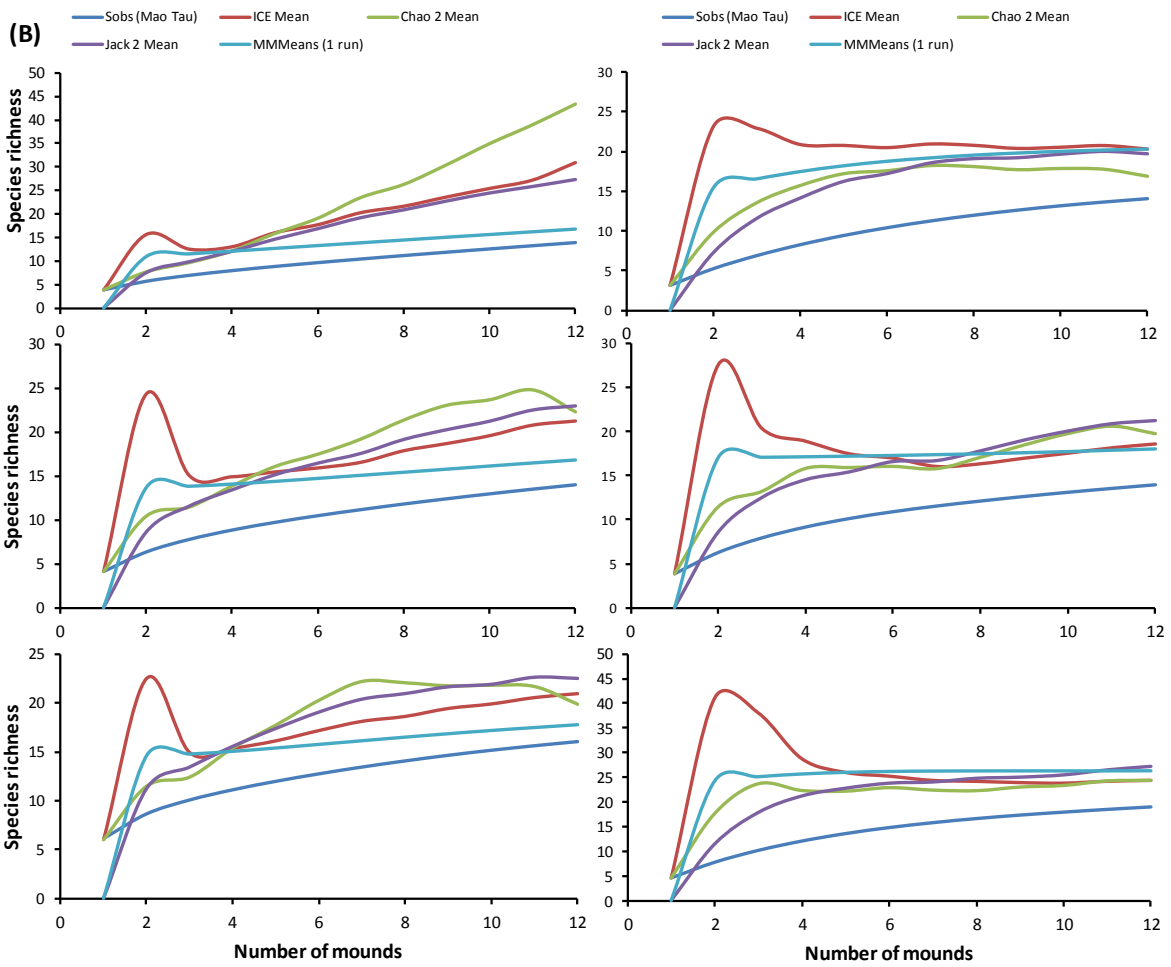
	sites			
Species	Granite mounds	Granite savanna	Basalt mounds	Basalt savanna
Indigofera demissa	ns	**65.1**	ns	ns
Indigofera astragalina	ns	**62.5**	-	-
Chamaecrista mimosoides	ns	**61.6**	-	-
Hemizygia petrensis	ns	52.0	-	-
Ceratotheca triloba	ns	51.2	-	-
Kyphocarpa angustifolia	ns	49.5	ns	ns
Hermannia tigreensis	ns	47.2	-	ns
Sesamum alatum	ns	42.0	-	-
Adiantum incisum	-	37.3	-	-
Seddera suffruticosa	ns	ns	50.2	ns
Tylosema esculentum	-	ns	45.2	ns
Corbichonia decumbens	-	-	43.5	ns
Phyllanthus parvulus	ns	ns	41.5	ns
Pupalia lappacea	-	-	37.3	-
Acalypha fimbriata	ns	-	36.2	ns
Acalypha indica	-	-	35.6	ns
Tragia okanyua	ns	-	33.8	ns
Indigofera sp.	-	-	ns	57.4
Indigofera daleoides	ns	ns	ns	53.2
Corchorus asplenifolius	-	-	ns	39.2
Phyllanthus angolensis	-	-	ns	38.5

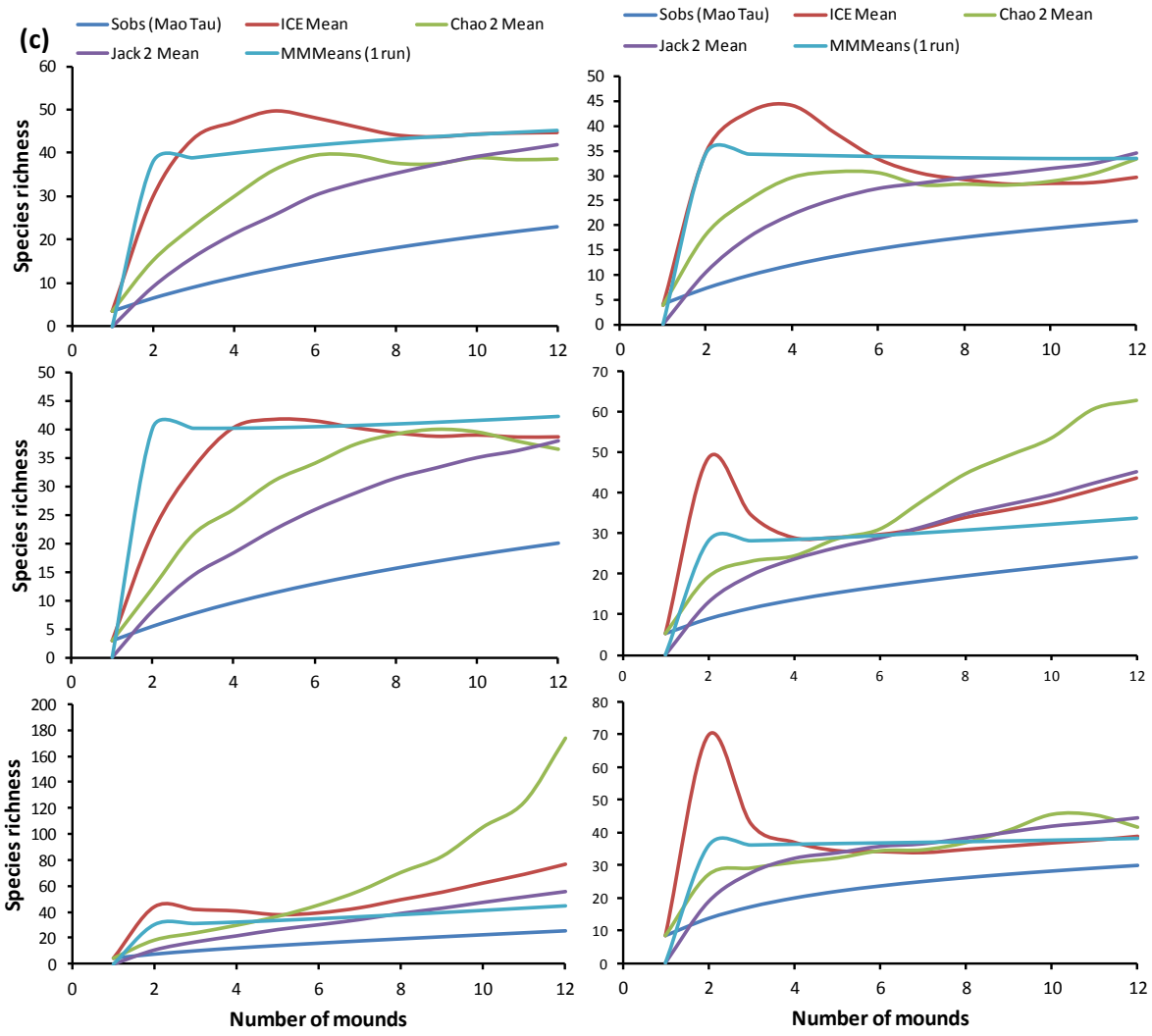
Boerhavia erecta	ns	-	ns	30.9



Figure 4S1: Diagrammatic representation of the sampling design for the herbaceous community composition around the mounds. Herbaceous plants were be sampled in each $1m^2$ quadrat at intervals of 1, 2, 4, 8 and 16m in the four cardinal points (adapted from Davies et al., 2014). The control is the savanna matrix plot.


(A)
Sobs (Mao Tau)
ICE Mean
Chao 2 Mean
Jack 2 Mean
MMMeans (1 run)
Species richness
Number of mounds


(B)
Sobs (Mao Tau)
ICE Mean
Chao 2 Mean
Jack 2 Mean
MMMeans (1 run)
Species richness
Number of mounds


(c)
Sobs (Mao Tau)
ICE Mean
Chao 2 Mean
Jack 2 Mean
MMMeans (1 run)
Species richness
Number of mounds

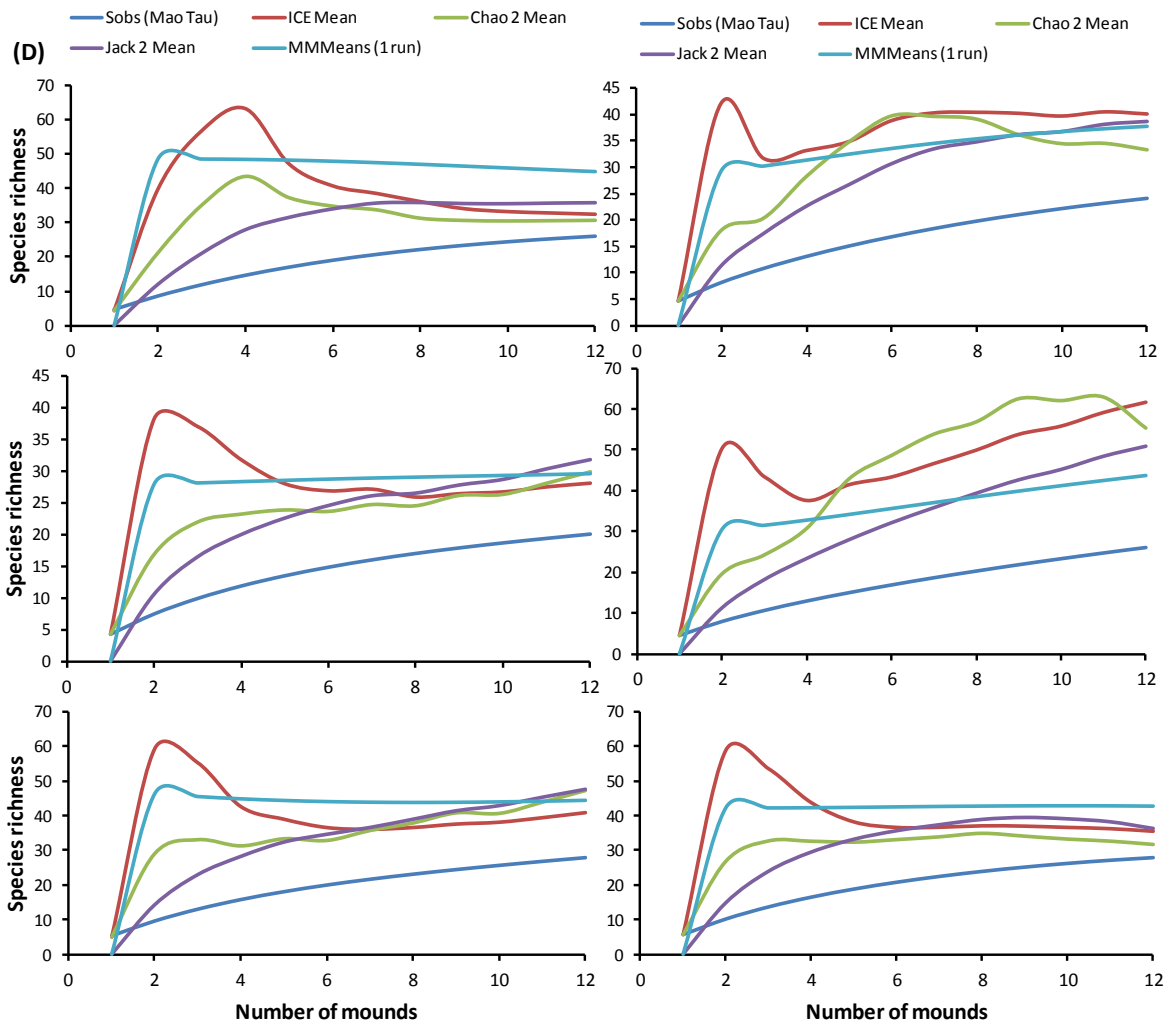


Figure 4S2: Sample-based species richness observed (Sobs) and richness estimators (ICE Mean, Chao 2 Mean, Jack 2 Mean and MM Means (1run)) for grass on granite (A), grass on basalt (B), forbs on granite (C) and forbs on basalt (D). Graphs are paired from small to large size category starting with mounds on the left and savanna matrix plots on the right.

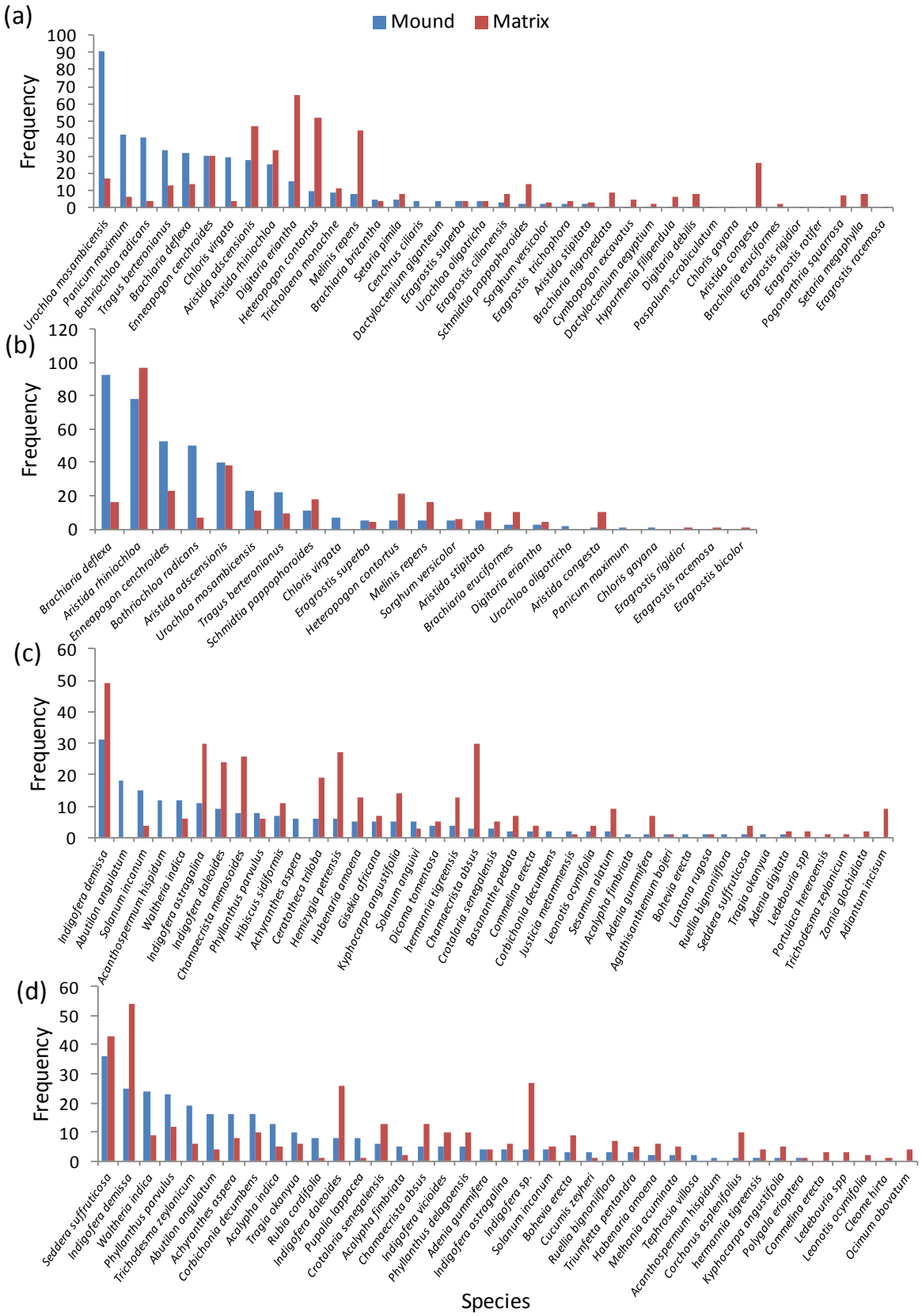

(a)
Mound
Matrix
Frequency
Urochloa mosambicensis
Panicum maximum
Bothriochloa radicans
Tragus berteronianus
Brachiaria deflexa
Enneapogon cenchroides
Chloris virgata
Aristida adscensionis
Aristida rhiniochloa
Digitaria eriantha
Heteropogon contortus
Tricholaena monachne
Melinis repens
Brachiaria brizantha
Setaria pimila
Cenchrus ciliaris
Dactyloctenium giganteum
Eragrostis superba
Urochloa oligotricha
Eragrostis ciliaensis
Schmidtia pappophoroides
Sorghum versicolor
Eragrostis trichophora
Aristida stipitata
Brachiaria nigropedata
Cymbopogon excavatus
Dactyloctenium aegyptium
Hyparrhenia filipendula
Digitaria debilis
Paspalum scrobiculatum
Chloris gayana
Aristida congesta
Brachiaria eruciformes
Eragrostis rigidior
Eragrostis rotifer
Pogonarthria squarrosa
Setaria megaphylla
Eragrostis racemosa
(b)
Frequency
Brachiaria deflexa
Aristida rhiniochloa
Enneapogon cenchroides
Bothriochloa radicans
Aristida adscensionis
Urochloa mosambicensis
Tragus berteronianus
Schmidtia pappophoroides
Chloris virgata
Eragrostis superba
Heteropogon contortus
Melinis repens
Sorghum versicolor
Aristida stipitata
Brachiaria eruciformes
Digitaria eriantha
Urochloa oligotricha
Aristida congesta
Panicum maximum
Chloris gayana
Eragrostis rigidior
Eragrostis racemosa
Eragrostis bicolor
(c)
Frequency
Indigofera demissa
Abutilon angulatum
Solanum incanum
Acanthospermum hispidum
Waltheria indica
Indigofera astragalina
Indigofera daleoides
Chamaecrista memosoides
Phyllanthus parvulus
Hibiscus sidiformis
Achyranthes aspera
Ceratotheca triloba
Hemizygia petrensis
Hobenaria amoena
Gisekia africana
Kyphocarpa angustifolia
Solanum anguivi
Dicoma tomentosa
hermannia tigrensis
Chamaecrista absus
Crotalaria senegalensis
Basananthe pedata
Commelina erecta
Corbichonia decumbens
Justicia metammensis
Leonotis ocymifolia
Sesamum alatum
Acalypha fimbriata
Adenia gummifera
Agathisanthemum bojeri
Bohevia erecta
Lantana rugosa
Ruellia bignoniiflora
Seddera suffruticosa
Tragia okanyua
Adenia digitata
Ledebouria spp
Portulaca hereroensis
Trichodesma zeylanicum
Zornia glochidiata
Adiantum incisum
(d)
Frequency
Seddera suffruticosa
Indigofera demissa
Waltheria indica
Phyllanthus parvulus
Trichodesma zeylanicum
Abutilon angulatum
Achyranthes aspera
Corbichonia decumbens
Acalypha indica
Tragia okanyua
Rubia cordifolia
Indigofera daleoides
Pupalia lappacea
Crotalaria senegalensis
Acalypha fimbriata
Chamaecrista absus
Indigofera vicioides
Phyllanthus delagoensis
Adenia gummifera
Indigofera astragalina
Indigofera sp.
Solanum incanum
Bohevia erecta
Cucumis zeyheri
Ruellia bignoniiflora
Triumfetta pentandra
Hobenaria amoena
Melhania acuminata
Tephrosia villosa
Acanthospermum hispidum
Corchorus asplenifolius
hermannia tigrensis
Kyphocarpa angustifolia
Polygala erioptera
Commelina erecta
Ledebouria spp
Leonotis ocymifolia
Cleome hirta
Ocimum obovatum
Species

Figure 4S3: Frequency of grasses and forbs on sampled mounds and savanna plots across all mound size categories in each geology (n=144) for (a) granite grass, (b) basalt grass, (c) granite forbs and (d) basalt forbs.

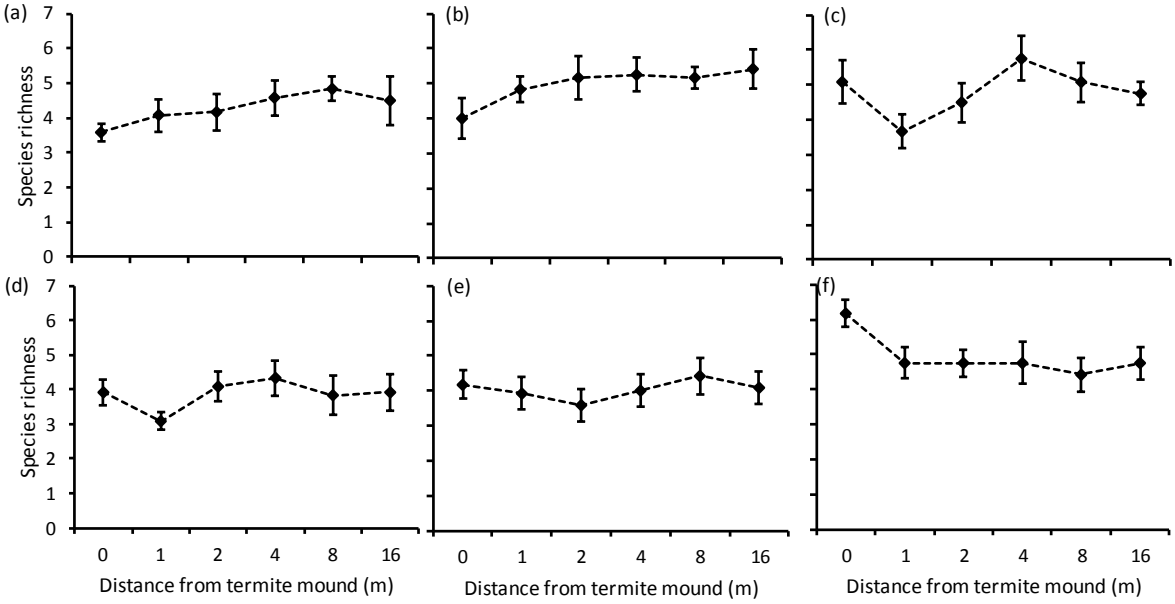


Figure 4S4: Variation in grass species richness with distance from the mound. a, b and c are small, medium and large mounds on granite, while d, e and f are small, medium and large mounds on basalt, respectively.

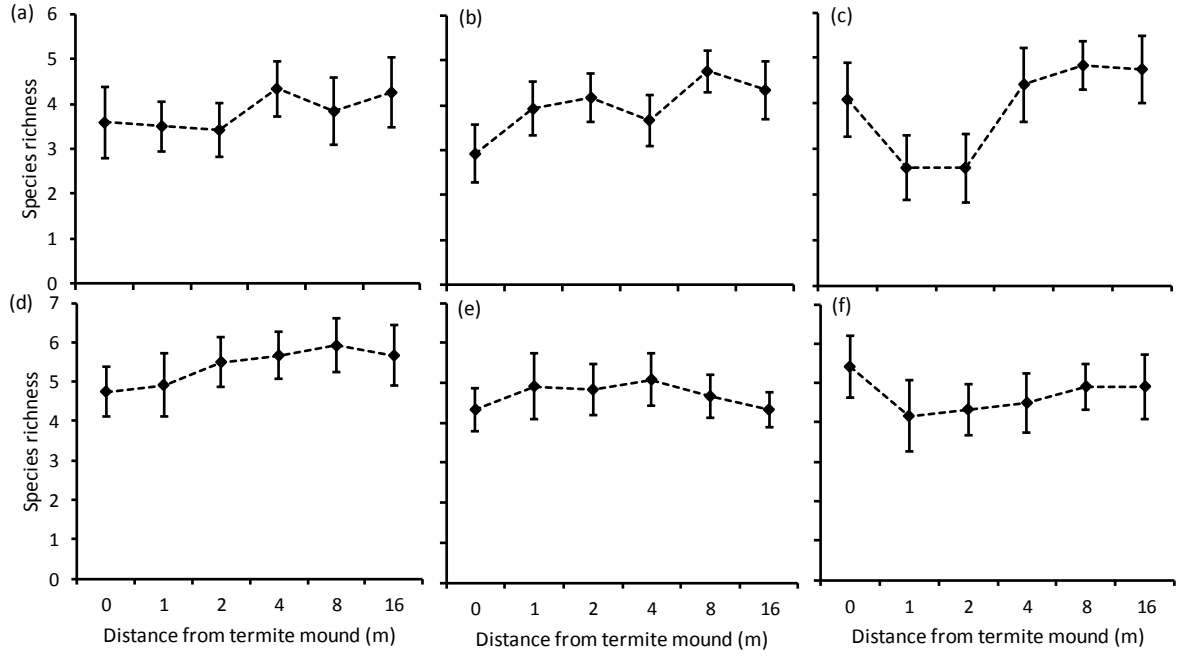


Figure 4S5: Variation in forb species richness with distance from the mound. a, b and c are small, medium and large mounds on granite, while d, e and f are small, medium and large mounds on basalt, respectively.

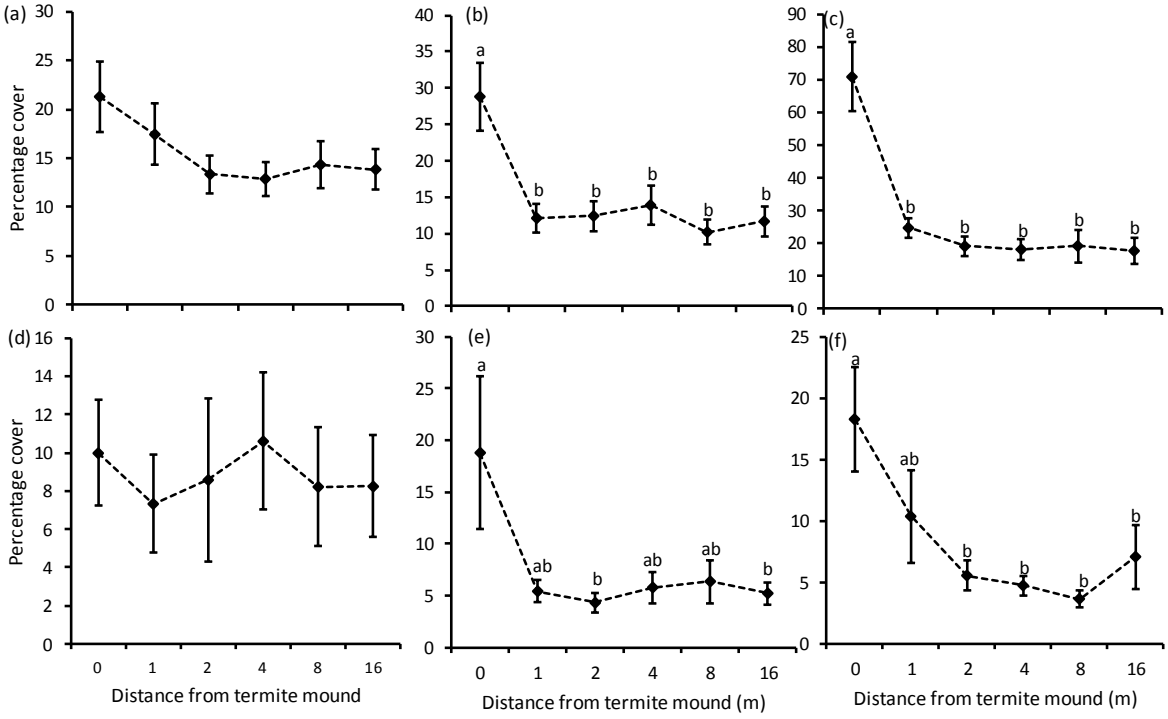


Figure 4S6: Variation in grass cover with distance from the mound. a, b and c are small, medium and large mounds on granite, while d, e and f are small, medium and large mounds on basalt respectively. Distance categories having different letters are significantly different (Tukey HSD, $P<0.05$).

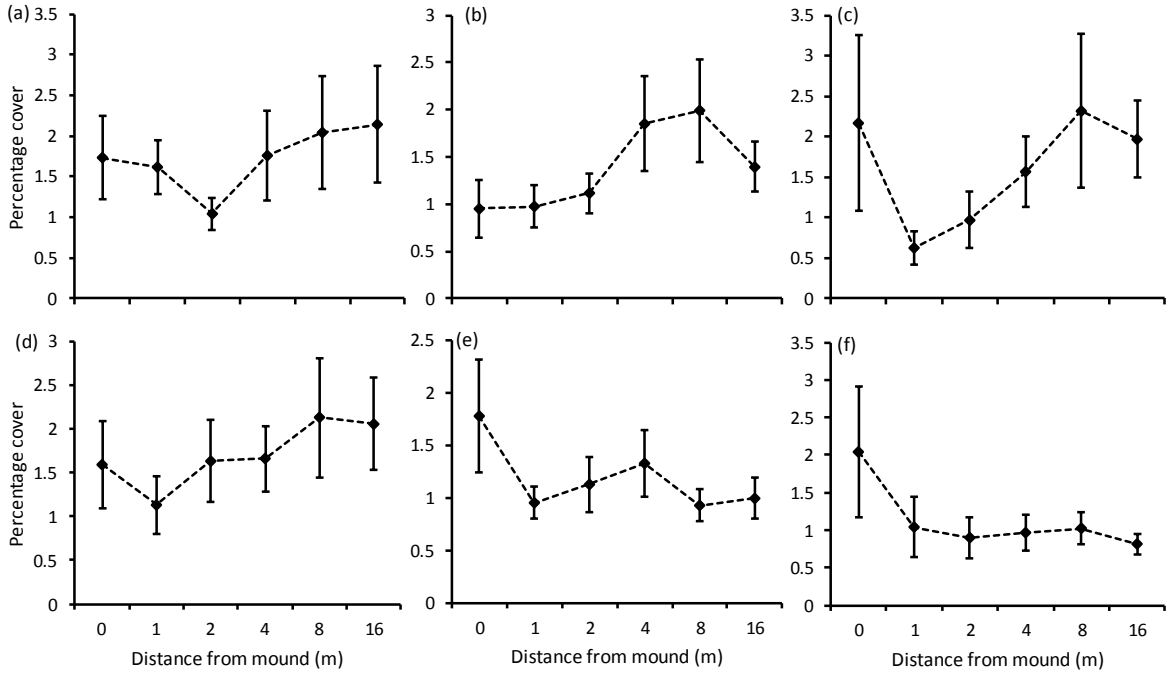


Figure 4S7: Variation in forb cover with distance from the mound. a, b and c are small, medium and large mounds on granite, while d, e and f are small, medium and large mounds on basalt, respectively. Distance categories having different letters are significantly different (Tukey HSD, P<0.05).

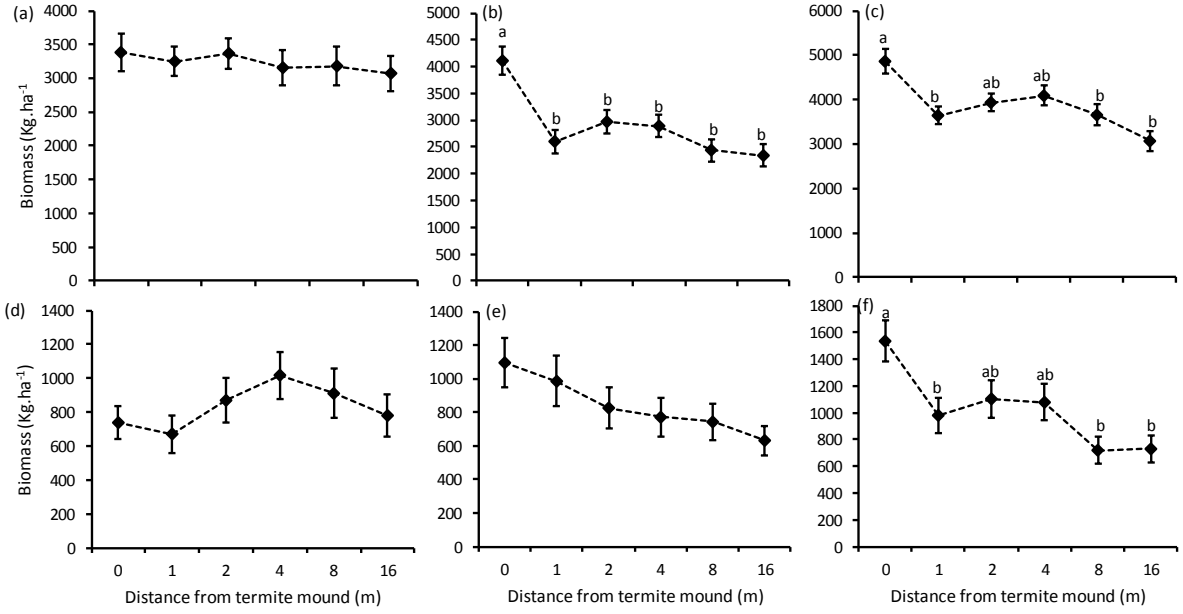


Figure 4S8: Change is herbaceous biomass with distance from mounds. a, b and c are small, medium and large mounds on granite, while d, e and f are small, medium and large mounds

on basalt, respectively. Distance categories having different letters are significantly different (Tukey HSD, $P<0.05$).

Chapter 5

Chapter 5: **Are termite mounds always grazing hotspots? Grazing variability with mound size, season and geology in an African savanna**

Abstract

The choice of foraging sites by large herbivores in the landscape is influenced by multiple factors, including forage quantity and quality. Termite mounds harbour highly nutritious plants compared to the savanna matrix, which makes them preferred foraging sites in many savannas. However, little is known regarding how termite mounds emanating from different geologies influence grazing. Furthermore, studies have only considered the effect of large mounds on grazing, making it difficult to draw general conclusions on the impact of mounds on grazing since effects of the many smaller mounds are unknown. We predicted grazing intensity to be higher on mounds relative to the savanna matrix on nutrient-poor geology (granite) but not on nutrient-rich geology (basalt), due to large differences in soil nutrients between mounds and the savanna on granite, but not on basalt. Moreover, the sphere of influence of mounds on grazing intensity was expected to be larger on the nutrient-poor landscape. In order to understand the effect of mounds on grazing between geologies, we measured grazing intensity on three different mound sizes (small, medium and large), across three seasons (hot wet: February, cool dry: July and hot dry: September), and at distances from mounds into the savanna. Grazing intensity on mounds was higher on granite compared to basalt. On both geologies, grazing was higher on large mounds compared to smaller mounds, and large mounds had a larger sphere of influence on grazing in the cool dry season, up to 8 m beyond mounds on granite and 2 m on basalt. When scaled up, mounds influenced 28% of the landscape on granite and 0.8% on basalt. Our study demonstrates that mounds are more important grazing sites for savanna herbivores on nutrient-poor landscapes, and that their importance varies across seasons.

Keywords – basalt, granite, grazing, mound size, termite mounds, nutrient hotspots, season, semi-arid savannas

Introduction

The distribution of mammalian herbivores is highly influenced by forage quality and quantity (Fryxell, 1991; McNaughton and Georgiadis, 1986; Wallace et al., 1995), although other factors such as predation risk, distance to water and inter and intra-specific competition also shape distributions (Cameron and du Toit, 2007; McNaughton, 1985; Redfern et al., 2003; Riginos and Grace, 2008; Smit, 2011; Stewart et al., 2002; Valeix et al., 2009). Although herbivore distributions are affected by landscape scale variation in soil and plant nutrients driven primarily by geology, rainfall and denitrification (including pyro-denitrification) (Asner et al., 2009; Crutzen and Andreae, 1990; Kruckeberg, 1986; Venter et al., 2003), ecosystem engineers such as ants, dung beetles and termites become important at fine spatial scales where their activities result in small scale nutrient-rich patches in the landscape (Jones et al., 1994). Foraging patches that are created by termite mounds on savanna landscapes form discrete spatial units differing from the surrounding areas in composition, quality and quantity and have the potential to cause changes in herbivore foraging behaviour (Davies et al., 2016b; Grant and Scholes, 2006; Chapter 4).

Termites (Blattodea: Termitoidae), through mound construction and foraging activities, redistribute soil particles both vertically and horizontally, altering soil physical properties (Bottinelli et al., 2015), nutrient availability (Holt and Coventry, 1990; Konaté et al., 1999; Lepage et al., 1993), hydrology (Mando et al., 1996; Turner, 2006) and topography (Joseph et al., 2013). These activities lead to well documented cascading effects on vegetation heterogeneity (Davies et al., 2014; Moe et al., 2009), with termite mounds often harbouring compositionally distinct and more nutritious forage compared to the surrounding savanna matrix (Davies et al., 2016b, 2014; Grant and Scholes, 2006; Chapter 4). This attracts herbivores and often results in increased foraging on mound vegetation (Fleming and Loveridge, 2003; Loveridge and Moe, 2004; Mobæk et al., 2005; Muvengwi et al., 2014).

However, two recent studies have disputed the observation that termite mounds are always focal feeding sites in savannas, finding herbivores to instead preferentially forage on savanna matrix vegetation (Muvengwi et al., 2013; Van der Plas et al., 2013). Both these studies attributed these unusual observations to minor differences in foliar nutrients between vegetation found on mounds and in the savanna matrix at their study sites. However, as useful as these two studies are in generating new insights into how the contribution of termite mounds to ecosystem function varies with landscape context, both were based on

observations at a single site, resulting in poor understanding of how termite mounds might vary in their importance for herbivores across broad savanna landscapes.

Geological variation (which is reflected by the soil composition) has an effect on the distribution of vegetation and herbivores across savanna landscapes (Naiman et al., 2003; Venter et al., 2003). Southern African savannas are characterized by two common, distinct geologies, basalt and granite, that differ substantially in soil nutrients and texture (Venter, 1990). Granites are weathered to produce nutrient-poor sandy soils, whereas basalts erode to produce soils rich in clay and basic cations (Grant and Scholes, 2006; Venter et al., 2003), contributing to bottom-up regulation of these ecosystems (Scholes et al., 2003). It is therefore highly likely that termite mounds located on these differing geologies will have disparate influences on herbivory. Termite mounds on nutrient-rich geologies (e.g. basalt) are expected to display fewer differences in vegetation composition and nutrition due to little difference between mound and matrix soils (Chapter 3), leading to mounds being less important for herbivores. In contrast, mounds on granite might be considerably more important for herbivores because of stark differences between mound and matrix soils and thus vegetation. Indeed, a recent study that investigated termite mound effects on herbivory across a landscape-level rainfall gradient found herbivory to vary with rainfall in response to changes in mound *versus* matrix nutrients and vegetation, although mounds were still always preferred by herbivores (Davies et al., 2016b). However, there are no studies elucidating the effect of termite mounds on herbivory across landscapes with varying geology, limiting our general understanding of mound effects on grazing across geological substrates and savanna landscapes more broadly.

Furthermore, foraging animals select food resources and foraging patches at different spatial and temporal scales (Bailey et al., 1996; Cromsigt et al., 2009). Savannas are known to harbour termite mounds of different sizes, which have varying effects on vegetation heterogeneity (Joseph et al., 2013; Seymour et al., 2014). Plant species composition on large mounds differs profoundly from that of the surrounding savanna, but such variation is less pronounced on smaller mounds (Joseph et al., 2013; Chapter 4). Moreover, larger patches of high quality forage are more attractive to grazers and/or browsers compared with smaller ones (Cromsigt and Olff, 2006; Pretorius et al., 2011). However, the effects of termite mound size on herbivory patterns, including across environmental gradients such as geology, have not been addressed. Moreover, erosion from termite mounds has an effect on the nutrition of

the surrounding herbaceous and woody plant community (Davies et al., 2016a, 2016b; Gosling et al., 2012), but how far into the matrix this effect extends in landscapes of varying forage quality, which in turn influences grazing intensity, remains poorly understood.

In order to understand how termite mounds located on different geological substrates influence herbivore grazing, we sampled mounds and the surrounding savanna matrix on granite and basalt geologies in a Zimbabwean savanna. The specific objectives were to: (i) determine how grazing intensity varies between termite mounds and the savanna matrix across seasons and geologies, and (ii) determine the spatial extent of mound effects on grazing intensity in relation to season and mound size, as well as whether there are thresholds of change in relation to distance and mound size on each geology. We hypothesized that mounds on landscapes emanating from nutrient-rich geologies (e.g. basalt) are of less importance to grazing herbivores than mounds on nutrient-poor geologies due to little difference in soil nutrients between mounds and the savanna matrix. Grazing was expected to decrease with distance from mounds on granite, whereas on basalt no difference between mound and matrix grazing was expected due to little variation in soil nutrients. Large mounds were expected to influence grazing more compared with smaller mounds following observations of patch size influencing the level of use by foraging herbivores (Cromsigt and Olff, 2006; Pretorius et al., 2011), and also because large mounds were expected to have higher levels of soil nutrients compared with smaller mounds.

Methods

Study area

The study was conducted in Gonarezhou National Park (21^0 00′ - 22^0 15′ S, 30^0 15′ - 32^0 31′ E), south eastern Zimbabwe. Two adjacent geological substrata (basalt and granite) with similar climatic and fire regimes were sampled. Granite lies to the east and basalt to the west of the park. Mean monthly maximum temperatures range between 26 ^{0}C in July and 33 ^{0}C in January, whereas mean monthly minimum temperature ranges between 11 ^{0}C in June and 24 ^{0}C in January (Fig. 5.1a). The average annual rainfall for the study site is 466 mm, and does not vary between the two substrata (Gandiwa et al., 2011). Above average rainfall was received between January and March of 2014, making it one of the wettest years in the history of the park. However, rainfall was generally below average between March-November 2014 (Fig. 5.1b). Fire return period across the entire study site was two years (E. Gandiwa, pers. comm.). The most common *Macrotermes* mound-building species on granite

were *M. subhyalinus* and *M. falciger*, and on basalt *M. ukuzii* was the most common (Chapter 1).

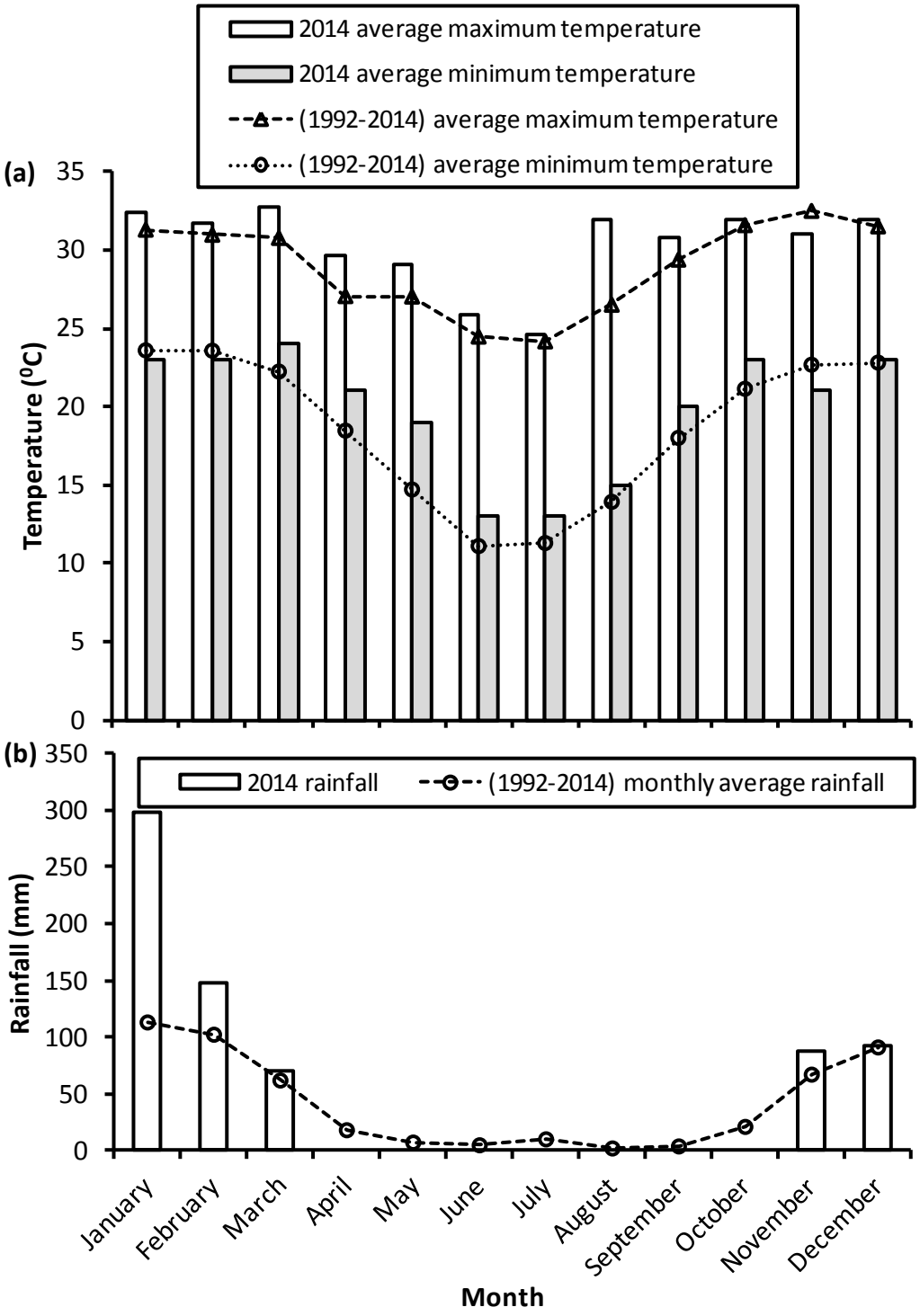


Figure 5.1: (a) Average monthly maximum and minimum temperatures recorded during the study period (2014) and between 1992-2014, and (b) total monthly rainfall recorded in 2014 together with monthly average rainfall between 1992-2014.

Common grasses on mounds on granite are *Urochloa mosambicensis*, *Panicum maximum*, *Tragus berteronianus*, *Chloris virgata* and *Brachiaria brizantha*, while the savanna matrix is dominated by *Digitaria eriantha*, *Melinis repens* and *Heteropogon contortus* (Chapter 4). However, a different suite of plants dominate mounds on basalt: *Brachiaria deflexa*, *Enneapogon cenchroides* and *Bothriochloa radicans*, whereas the savanna matrix is dominated by *Aristida rhiniochloa* and *A. stipitata* (Chapter 4). The common grazers and mixed feeders in the study area include buffalo *Syncerus caffer*, zebra *Equus quagga burchellii*, warthog *Phacochoerus africanus*, blue wildebeest *Connochaetes taurinus*, kudu *Tragelaphus strepsiceros*, eland *Taurotragus oryx*, waterbuck *Kobus elipsiprimnus*, sable antelope Hippotragus niger, elephant *Loxodonta africana* and impala *Aepyceros melampus*.

Sampling design

Seventy-two termite mounds from eight 1 km^2 plots were sampled to assess grazing of herbaceous vegetation by large mammalian herbivores across the two geologies (basalt and granite, four sampling plots on each). In each geological substratum, mounds were classified as either large, medium or small based on their lateral surface area (Muvengwi et al., 2013). In each 1 km^2 plot, three termite mounds were randomly sampled from each of the three size categories and their position marked using a hand held GPS. Because of distinct mound size differences (Chapter 3), size categories differed between the two geologies: mounds were classified as small when < 10 m^2 on granite *vs.* < 6 m^2 on basalt, medium when between 10-30 m^2 on granite *vs.* 6-10 m^2 on basalt and large when > 30 m^2 on granite *vs.* > 10 m^2 on basalt. A similar sized savanna matrix control plot for each termite mound was placed 16 m from the edge of each mound in a randomly chosen compass direction and on the same contour line. A different random compass direction was chosen only if another termite mound fell within 16 m in the first direction chosen. Transects were also marked, from the perimeter of each sampled mound in the four cardinal directions, and 1 m^2 quadrats were placed at distances of 1 m, 2 m, 4 m, 8 m and 16 m from each mound (Fig. 5S1). This was done in order to determine the sphere of influence of mounds on grazing with distance from the perimeter into the savanna matrix (Davies et al., 2016b). To calculate the percentage of the landscape influenced by mounds, the maximum distance to which mounds of the different size categories influenced grazing was added to the radius of each mound in that size category and the area subsequently calculated assuming a circular shape for sphere of influence (πr^2). The sum area of all mounds for each 1 km^2 plot was calculated and expressed

as a percentage. The average percentage for the four plots on each geology represented landscape scale influence of mounds on grazing.

Each sampled mound was divided into four quarters (Fig. 5S1), and grazing intensity visually estimated using the ocular estimate by plot method, where the proportion of aerial architecture of the herbaceous plants grazed in each quarter was expressed as a percentage (Heady, 1949). A similar procedure was repeated in the marked savanna matrix plot and in the quadrats along the transects. Data were collected over three seasons in 2014 (hot wet: February, cool dry winter: July and hot dry spring: September). For consistency, grazing intensity was estimated by one observer throughout the study. Grazing intensity across the three seasons was recorded in the same matrix control plots and transect quadrats, with their position marked using a white iron stake.

Data analysis

All analyses were performed using R statistical software version 3.2.3 (www.r-project.org). Relationships between grazing intensity (proportion of aerial architecture of grass plant grazed) and geology (granite or basalt), location (mound or savanna matrix), mound size (large, medium and small) and season (hot wet, cool dry and hot dry) were assessed using generalized linear models (GLMs) with binomial error distributions and logit link functions. In order to understand the spatial extent of mound effects on grazing, relationships between grazing intensity, distance from the mound, geology, mound size and season were assessed using generalized linear mixed-effects models (GLMMs) with binomial error distributions and logit link function using the R package *lme4* (Bates, 2007). Mound identity was modelled as a random effect for these analyses. For each dataset, we constructed 72 candidate models based on biological hypotheses and performed model selection using second order sample-size-corrected Akaike Information Criterion (AIC_c) in the R package *MuMIn* (Barton, 2016). The most parsimonious model for each dataset (Anderson et al., 2001; Tables S1and S2) was used for further analysis, using Type III likelihood-ratio χ^2-tests in the R package *car* (Fox et al., 2015). Results from these models were further subjected to post hoc testing using Tukey contrasts averaged across interaction terms when present using the R packages *multcomp* (Hothorn et al., 2016) and *mvtnorm* (Genz et al., 2016). The area of the landscape influenced by mounds was then compared between geologies with a Student's *t*-test.

Results

Grazing at mounds and savanna matrix plots

Geology, location, season and plot size had a significant effect on grazing intensity (Table 5.1), with the interactions between geology and location, geology and size, location and season, location and size and season and size being significant (Table 5.1). Tukey post-hoc tests revealed that grazing intensity was significantly higher ($p < 0.05$) on granite mounds compared to basalt (Fig. 5.2), and that for large mounds, grazing intensity differed between mounds and the savanna matrix across all seasons on both geologies (Fig. 5.2). The > 30m^2 plots were always selected, the 10-30 m^2 plots were selected all year on the basalt and only in the cool dry season on the granite, and plots < 10 m^2 were never selected for (Figure 5.2).

Furthermore, multiple comparisons revealed that grazing intensity was significantly higher ($p < 0.05$) on both large and small mounds compared to medium mounds on granite, while no significant difference ($p > 0.05$) was observed between large and small mounds. However, grazing intensity on basalt was significantly higher ($p < 0.05$) on large mounds compared to both medium and small mounds, while no difference was recorded between small and medium mounds (Fig. 5.2). Multiple comparisons further revealed that grazing intensity varied across all seasons on small and large mounds on granite, whereas on medium mounds there was no difference between the hot wet and hot dry seasons (Fig. 5.2a-c). Grazing intensity was significantly higher ($p < 0.05$) in the cool dry season compared to the hot wet and hot dry seasons on large mounds on basalt (Fig. 5.2d-f), but did not differ between small and medium mounds throughout the year (Fig. 5.2d-f).

Spatial influence of mounds on grazing

Geology, distance, season and mound size had a significant effect on grazing intensity patterns around mounds (Table 5.2). The interactions between geology and distance, distance and season, distance and size and season and size were also significant (Table 5.2). Post-hoc analyses revealed that grazing intensity at all distances along transects was significantly higher ($p < 0.05$) on granite compared to basalt across all seasons (February, July and September) and mound sizes (small, medium and large) (Fig. 5.3). The spatial extent of grazing was furthest ($p < 0.05$) in the cool dry season for large mounds on both granite and basalt, with grazing levelling off at 8 m from mound edge on granite and 2 m on basalt.

Table 5.1: Results of the best performing generalized linear model (GLM) from Type III likelihood-ratio χ^2-tests examining effects of geology, location (on or off mounds), season, patch size and their two-way interactions for the response variable grazing intensity.

Variable	**df**	χ^2	**p-value**
Geology	1	45996	< 0.0001
Location	1	75307	< 0.0001
Season	2	58262	< 0.0001
Size	2	35726	< 0.0001
Geology x location	1	2177	< 0.0001
Geology x size	2	79	< 0.0001
Location x season	2	800	< 0.0001
Location x size	2	18006	< 0.0001
Month x size	4	738	< 0.0001

In the hot dry season, grazing levelled off at 4 m from mounds on granite, whereas on basalt mound influence extended to only 1 m. However, there was also a sharp decline in grazing intensity from mounds up to 1 m during this same time period on granite. In the hot wet season, grazing intensity did not differ with distance from mounds for large mounds on basalt, whereas on granite grazing was higher up to 1 m from mounds (Figs. 5.3c, f). For medium mounds on granite, grazing intensity was significantly higher on mounds than at distances greater than 2 m from mounds, although there was no difference between the 1 m and 2 m distance classes. For small mounds, grazing intensity was highest at a distance of 1 m, whereas distances between 0 m and 2 m were not significantly different (Fig. 5.3a). There was no effect of distance on grazing intensity for small and medium mounds on basalt across all seasons (Fig. 5.3d-e).

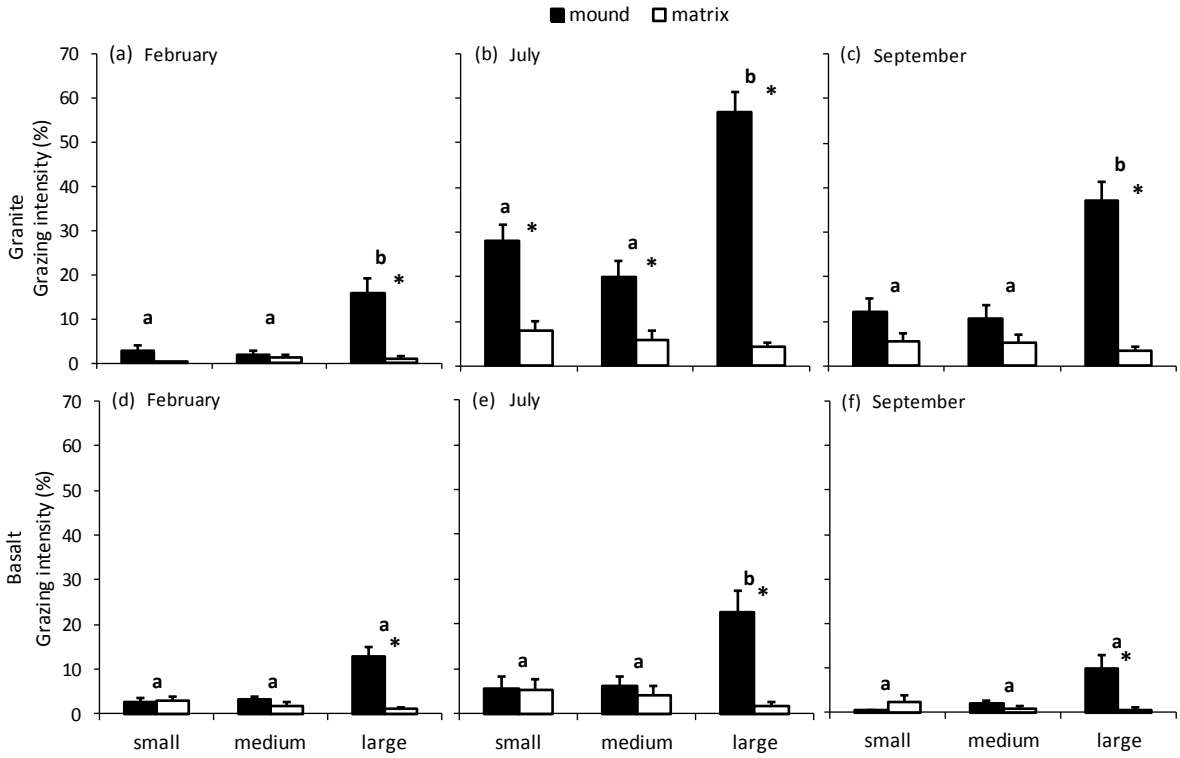


Figure 5.2: Mean ± S.E grazing intensity on termite mounds and in savanna matrix plots for small, medium and large mounds across three seasons (February (a, d), July (b, e) and September (c, f)) on granite (a-c) and basalt (d-f). Size categories with different letters are significantly different from each other (Tukey HSD, $P < 0.05$) and asterisks denote significant differences between mound and savanna matrix plots (paired *t* test, $P < 0.05$).

Although there was no significant difference in mound density between granite and basalt (Chapter 2), the proportion of the landscape affected by mounds in terms of grazing patterns was significantly different ($t = 8.398$, df = 3.05, p = 0.0033), with mounds influencing approximately 28% of the landscape on granite compared with only ~0.8% on basalt.

Discussion

Our results reveal that termite mounds alter the spatio-temporal patterns of grazing, substantiating previous studies where herbivory was more pronounced on mound vegetation compared with that in the savanna matrix (Davies et al., 2016b; Grant and Scholes, 2006). However, this study explicitly shows that mounds emanating from varied geologies have different effects on grazing, with mounds located on nutrient-poor geologies having a greater influence. Similar to other studies that investigated the influence of patch size on foraging herbivores (Cromsigt and Olff, 2006; Pretorius et al., 2011), the greatest effects were related

to large mounds compared with smaller ones on both geologies. Moreover, large mounds have been found elsewhere to have more substantial impacts on vegetation heterogeneity due to higher soil nutrient concentrations (Joseph et al., 2013; Chapter 4).

Table 5.2: Results of the best performing generalised linear mixed effects model (GLMM) from Type III likelihood-ratio χ^2-tests examining effects of geology, distance from mound, season, mound size and their two-way interactions for the response variable grazing intensity.

Variable	**df**	χ^2	**p-value**
Geology	1	19.96	< 0.0001
Distance	5	100362.90	< 0.0001
Season	2	153219.03	< 0.0001
Size	2	13.40	0.0012
Geology x distance	5	15914.86	< 0.0001
Distance x season	10	5152.97	< 0.0001
Distance x size	10	29369.89	< 0.0001
Month x size	4	5289.67	< 0.0001

Grazing intensity was higher overall on granite mounds compared with basalt, an observation that is attributed to marked differences in mound sizes, biomass production, plant species composition and *Macrotermes* species that constructed the mounds between the two geologies (Chapter 4), with mounds on granite being 15 times larger in lateral surface area than those on basalt (Chapter 3). Interestingly, comparing mounds of similar sizes, the large mounds on basalt and medium mounds on granite, there was no diffrence in grazing which shows that differences in grazing between the two geologies could be mainly coming from large mounds on granite. Variation in large herbivore densities across the landscape may also have an effect on the level of grazing observed (Davies et al., 2016b). Indeed, in the climatically comparable northern Kruger National Park (KNP), granite supports higher

herbivore biomass than basalt (Naiman et al., 2003). However, little is known about the temporal or spatial distributions of large herbivores in Gonarezhou National Park and further studies on herbivore distribution here are needed to determine if the same distribution pattern occurs. However, grazing in the matrix was similar between the two geologies, making it difficult to really attribute differences in grazing in tensity to herbivore density.

Also, grazing on basalt is likely to be more homogenous across the landscape because of better (nutrient-rich) forage distributed throughout, potentially diluting grazing patterns, whereas on granite grazing is more concentrated around mounds (Grant and Scholes, 2006). Although termite mounds have been observed to host forage of high quality compared with the savanna matrix, making them foraging hotspots (Davies et al., 2016b, 2014), this was largely true only on granite in our study (Chapter 4).

Higher grazing was consistently recorded on large mounds compared with the savanna matrix across all seasons on both geologies, a finding that we attribute to their increased size and more nutritious forage. In a study comparing soil nutrient composition between mounds and the savanna across mound size categories, large mounds had marked differences compared with the savanna matrix (Seymour et al., 2014; Chapter 4), which translates to higher quantity and quality forage occurring here. In addition, in some grazing and browsing experiments, foraging herbivore choices were highly influenced by patch size, with animals found to forage more on larger fertilized plots than small ones (Cromsigt and Olff, 2006; Pretorius et al., 2011). Moreover, positive feedback loops, through dung and urine deposition, enhance regrowth of palatable species with enough nutrients for production and maintenance of large herbivores (Davies et al., 2012; Grant and Scholes, 2006; Mobæk et al., 2005). Small and medium mounds on granite recorded higher grazing pressure compared with the savanna matrix during the cool dry season only, making mounds more important grazing foci in this season. However, in the nearby KNP, grazing around termite mounds was more pronounced in the hot dry season (Davies et al., 2016b). We suggest that differences between our study and KNP could result from much of the graze dwindling prior to the hot dry season in our study site, since GNP receives less rainfall compared with southern KNP, where the previous study was conducted. There was no difference in grazing between the savanna matrix and both small and medium mounds on basalt across all seasons, which is likely a result of fewer differences in soil nutrients between mound and matrix vegetation here, with concomittantly

little influence on forage quality and hence level of grazing. Indeed, our findings on basalt corroborate other studies where mounds have failed to emerge as foraging hotspots due to little difference in nutritional content of the forage between mounds and the savanna matrix (Muvengwi et al., 2013; Van der Plas et al., 2013)

Mound effects on grazing extended up to a maximum of 8 m beyond the edge of the mound on granite, but only up to 2 m on basalt, a difference likely resulting from striking differences in mound size between granite and basalt, as well as marked difference in soil nutrients between mounds and the savanna on granite compared with basalt. However, after controlling for size comparing large mounds on basalt and medium mounds on granite, both influenced grazing to the same distance from mound skirt. The sphere of influence, based on grazing intensity recorded with distance from the perimeter of mounds, expressed at the landscape scale indicates that mounds influence ~28% of the landscapes on granite, but only ~0.8% on basalt. In a similar study focusing on *Macrotermes* mounds, termite influence on grazing patterns was ~ 30% of a granitic landscape (Davies et al., 2016b), which is highly comparable with our calculations for granite. Erosion rates from large, taller mounds on granite are expected to be higher compared with the smaller mounds on basalt due to their steeper slopes that increase water run-off (Davies et al., 2016b). Moreover, the marked difference in soil nutrients between mounds and the savanna matrix on granite causes erosion from mounds here to be more influencial for forage quality at greater distances from mound perimeters than on basalt, explaining the increased grazing intensity around mounds on granite. Herbivores are more likely to graze around mounds harbouring higher quality forage that results in a larger 'ring' around the mound perimeter. The sphere of influence around mounds in terms of grazing was smallest during the wet season, indicating that mound effects on grazing operate on a spatio-temporal basis, with the largest effects observed during the dry season on nutrient-poor landscapes. In addition, productivity is highest during the wet season and plants have faster growth rates, recovering faster from herbivory and leading to grazing effects being less discernible (Maschinski and Whitham, 1989; McNaughton, 1983). Although the effect of small and medium mounds on basalt did not extend beyond the perimeter of the mounds, small and medium sized mounds on granite had some influence on grazing. Although all mound size categories had no influence on plant assemblages on basalt (Chapter 4), large mounds did influence grazing up to 2 m beyond mound perimeters.

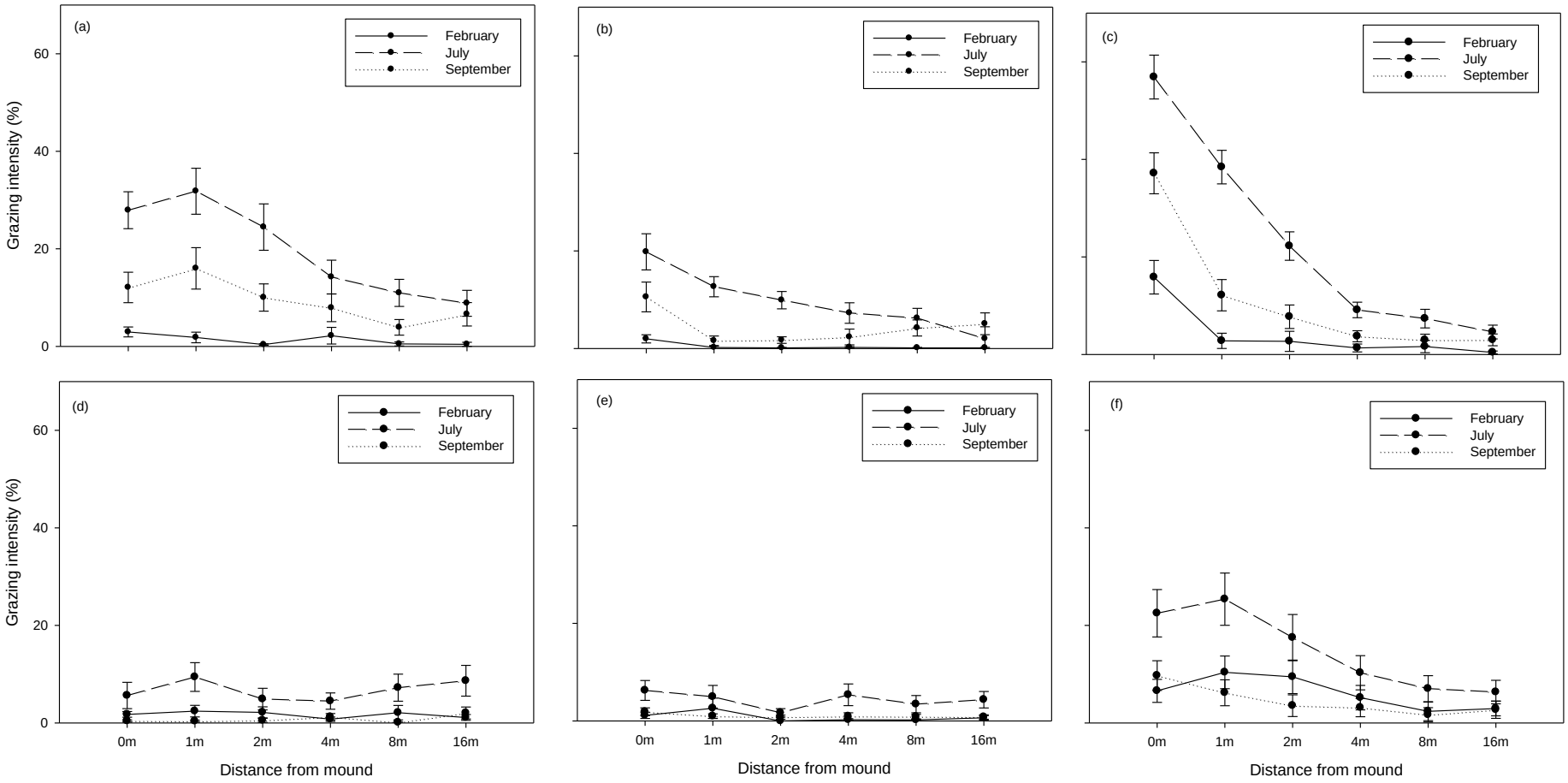


Figure 5.3: Mean ± S.E grazing intensity at different distances from termite mounds of varying sizes on granite and basalt geology; a-c and d-f represent small, medium and large mounds on granite and basalt, respectively.

Similarly, although small mounds on granite had no influence on plant assemblages, they, together with medium mounds, influenced grazing up to 2 m beyond the mound perimeters. It therefore appears that the way in which mounds influence plant assemblage composition differs from the way they influence herbivory patterns. We suggest that although the grass species assemblages did not differ between mound and matrix on basalt, grass nutrition probably did (at an individual plant level). Therefore, it is not only a mound-driven species response (different plant species growing on mounds) that leads to increased grazing at mounds, but also nutritional differences at the individual tuft level. Furthermore, large mounds on granite influenced plant assemblages up to 4 m (Chapter 4), whereas their sphere of influence on grazing herbivores was up to 8 m from the mound edge. Similarly, a previous study found mounds to influence the nutritional composition of plants, and hence grazing, at further distances from their perimeter compared with their effect on plant assemblage composition (Davies et al., 2016b). Therefore, the spatial extent of mound influence on herbaceous plant nutritional composition is likely much larger than effects on herbaceous plant species composition.

Our findings demonstrate that termite mounds are important foraging hotspots in nutrient-poor savannas. When the effect of mounds on grazing is scaled up to landscape scale, indeed, mounds have far reaching effects on grazing, influencing up to ~28% of the landscape. Because mounds have the potential to produce high quality and quantity forage, they increase the potential of savannas to support a diverse pool of grazers throughout the year, thereby increasing ecosystem functioning. Therefore, we call for serious consideration of the management and conservation of termite mounds, especially in nutrient-poor landscapes where they are likely to be key structures for large herbivore production and maintainance.

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Table 5S1: The five most parsimonious regression models for grazing intensity between mounds and the savanna matrix plots determined using second order Akaike Information Criterion corrected for sample size (AIC_c). The most parsimonious model in bold was used for further analysis. *k* is the number of fitted parameters, including the intercept, used to build the model; ΔAIC_c is the difference between a model's AIC_c value and that of the model with lowest AIC_c and the Akaike weight (w_i) is the likelihood of a given model's being the best model in the set.

Rank	Regression model	AIC_c	*k*	ΔAIC_c	w_i
1	**geology + location + season + size + geology x location + geology x size + location x season + location x size + season x size**	**343189.0**	**10**	**0.00**	**1**
2	geology + location + season + size + geology x location + location x season + location x size + season x size	343264.0	9	79.94	0
3	geology + location + season + size + geology x location + geology x size + location x season + location x size	343918.7	9	729.7	0
4	geology + location + season + size + geology x location + location x season + location x size	343973.5	8	784.49	0
5	geology + location + season + size + geology x location + geology x size + location x size + season x size	343984.7	9	795.65	0

Table 5S2: The five most parsimonious regression models for grazing intensity with distance from mounds into the savanna matrix determined using second order Akaike Information Criterion corrected for sample size (AIC_c). The most parsimonious model in bold was used for further analysis. *k* is the number of fitted parameters, including the intercept, used to build the model; ΔAIC_c is the difference between a model's AIC_c value and that of the model with lowest AIC_c and the Akaike weight (w_i) is the likelihood of a given model's being the best model in the set. For all models, mound identity was the random effect.

Rank	Regression model	AIC_c	*k*	ΔAIC_c	w_i
1	**geology + distance + season + size + distance x geology + distance x season + distance x size + month x size**	**826197.4**	**9**	**0.00**	**0.856**
2	geology + distance + season + size + distance x geology + distance x season + distance x size + geology x size + season x size	826201.0	10	3.57	0.144
3	geology + distance + season + size + distance x geology + distance x size + season x size	831306.8	8	5109.38	0
4	geology + distance + season + size + distance x geology + distance x size + geology x size + season x size	831310.4	9	5112.93	0
5	geology + distance + season + size + distance x geology + distance x season + distance x size	831799.8	8	5602.38	0

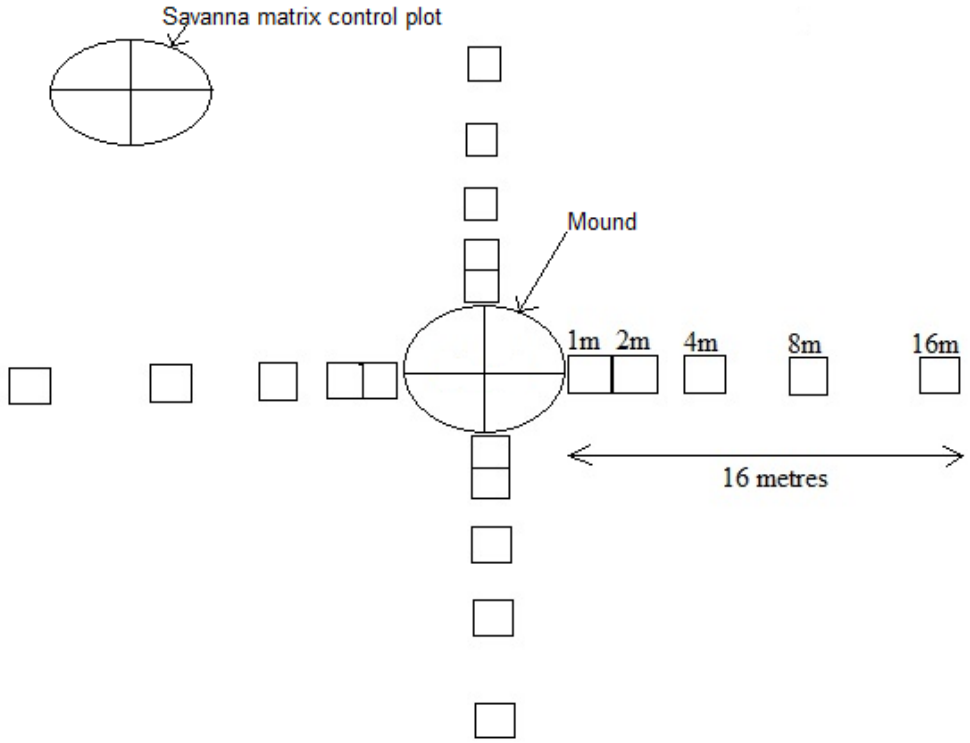


Figure 5S1: Diagrammatic representation of the sampling design for measuring grazing intensity on and around termite mounds. Grazing intensity was estimated in each mound quarter, savanna matrix control plot quarter and $1m^2$ quadrats at intervals of 1, 2, 4, 8 and 16m in the four cardinal directions (adapted from Davies et al., 2014b).

Chapter 6

Chapter 6: Synthesis

Conclusions and recommendations

My study presents some novel insights on termites that encompass aspects of their diversity, density and the spatial distribution of their mounds, the cascading effects that these termite mounds have on vegetation spatial heterogeneity, and how the herbaceous plants growing on these mounds influence spatial and temporal patterns of grazing across landscapes of varying geological substrates in the savannas of Gonarezhou National Park (GNP), Zimbabwe (Fig. 6.1). The main aim of this study was to determine whether termite mounds influence spatial patterns in plant species diversity and grazing between geological substrates in Gonarezhou National Park. Although effects of termites on ecosystem function have been previously documented (e.g. Holdo and McDowell, 2004; Joseph et al., 2014; Muvengwi et al., 2013), rarely have effects been considered at the landscape scale or between varying geological substrates. Unique to this study is the effect that geology has on the diversity of termites and the engineering role termites can have on nutrient-rich and nutrient-poor geologies. The engineering role of termites is not only reflected in the epigeous mounds that they build; tunnelling and foraging activities in the intermound matrix are also important for the improvement of soil structure and nutrients, consequently improving ecosystem structure and function. In order to demonstrate the underlying mechanisms responsible for differences in spatial and temporal patterns of termite species diversity, I predicted higher species diversity on nutrient-rich geology based on the productivity diversity hypothesis (Tilman et al., 2001; Chapter 2).

In testing the effect of geology on termite species diversity, it emerged that functional and taxonomic diversity of termites were higher on granite despite lower soil nutrient concentrations here compared with basalt, a finding divergent from the formulated hypothesis that nutrient-rich sites would harbour more species because of increased productivity. It appears that in nutrient-rich sites, few termite species can dominate, possibly as a result of competitive exclusion (Grime, 1973). Furthermore, dominance by only a few termite species on nutrient-rich basalt was reflected in the similarity in termite abundance on the two geologies, while species richness and diversity were highly different. Because of the aridity

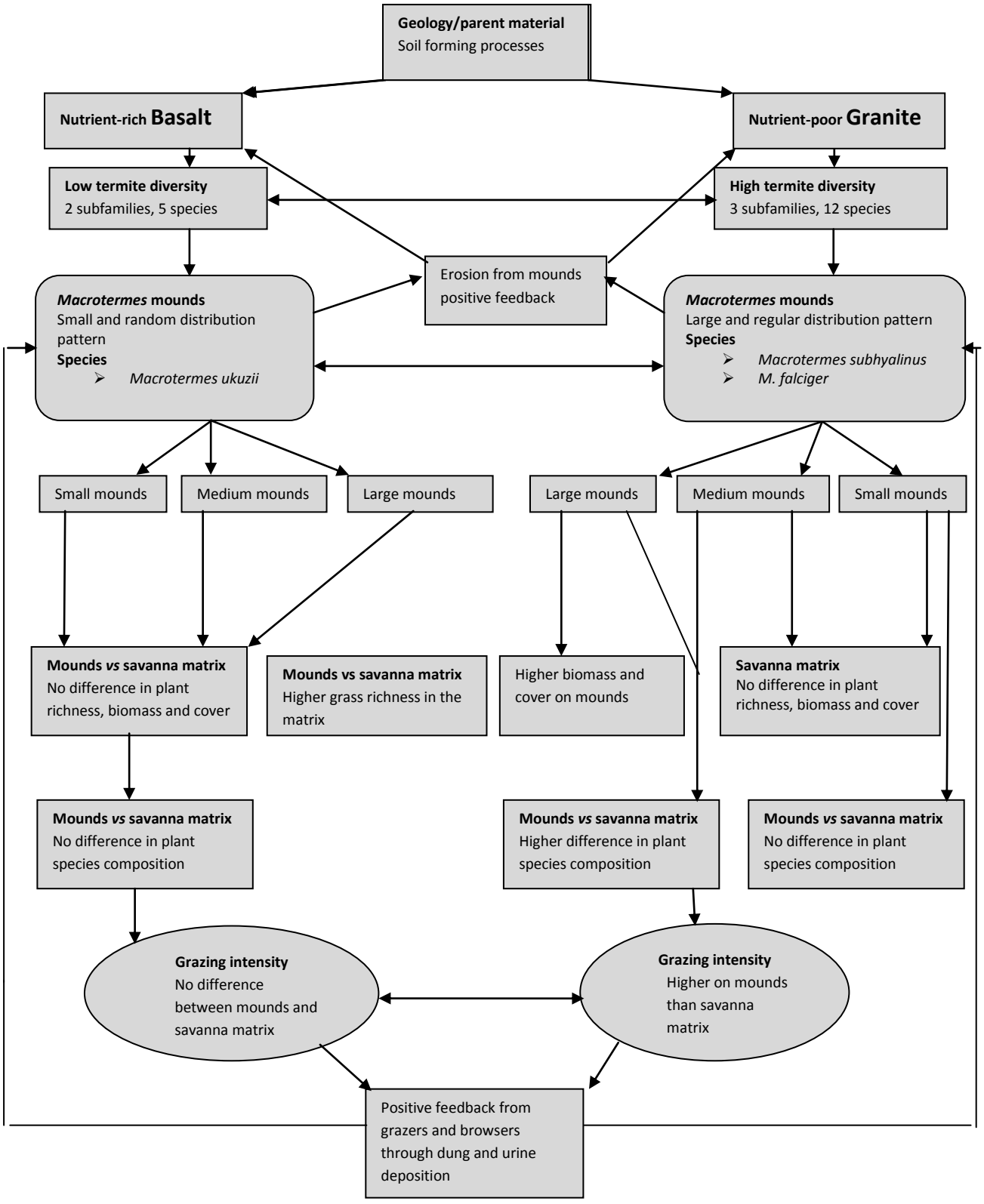


Figure 6.1. A synoptic presentation of geology and how it influences termite species diversity, mound size and spatial distribution, and the cascading effects on vegetation heterogeneity and grazing. Long double arrows represent differences between geologies, whereas the one sided arrows connect variables and factors within geologies.

of my study system (annual average rainfall of 466 mm), the engineering role of other ecosystem engineers such as dung beetles is short lived, likely making termites even more important for nutrient cycling, especially on granite where their functional diversity was higher than on basalt.

Twelve termite species belonging to three subfamilies and two feeding groups were recorded on granite compared with five species belonging to two subfamilies and one feeding group on basalt. Geology has a strong effect on termite diversity; therefore I suggest that more studies be carried out in other systems with varied geologies, incorporating other environmental gradients such as rainfall, temperature and altitude in order to deepen our understanding of how these factors might interact with geology to shape termite species diversity. Because termites are soil dwelling organisms, soil temperature is also likely to influence termite activity and diversity. Although this was suggested as a driver of the low diversity on basalt (Chapter 2), there is a need for empirical studies investigating whether soil temperature impacts termite diversity. The distribution and activity of elephants across landscapes that span different geologies is likely to have an effect on termite diversity, because of the apparently 'wasteful' feeding habits of elephants that drop woody debris as well as their behaviour of felling trees, making more food available for termites *(see* also Holdo and McDowell, 2004). Therefore, when investigating food availability, this aspect should also be linked to elephant spatial distributions in order to determine how their dung and the biomass that they leave on the ecosystem floor (Owen-Smith and Chafota, 2012), might affect termite diversity. A higher diversity of *Macrotermes* species was recorded on granite, hence I predicted a higher density of epigeous mounds on granite (Chapter 3).

Although the density and size of mounds built by *Macrotermes* has been estimated using Light Detection and Ranging (LiDAR) at a landscape scale (Davies et al., 2014), no study has focused primarily on comparing these mound dynamics at a landscape scale across varying geologies. Furthermore, mounds on basalt are generally too small (< 0.5 m in height) to be detected with sophisticated technology such as LiDAR, at least in terms of its current detection limits (Davies et al., 2014). Understanding the size, density and spatial distribution of mounds provides information on the level of influence mounds are likely to have on geologies where they occur. Mounds were larger and over-dispersed on granite, a spatial pattern associated with competitive interactions and high abundance, biomass and reproductive output of consumers across trophic levels compared with the random pattern

exhibited on basalt (Pringle et al., 2010). Because of the general uniformity of the basalt landscape, the probability of mounds occupying at any point in space is high. Although topography is an important factor influencing the distribution of mounds (Davies et al., 2014a), in this extreme semi-arid savanna system, topography may not have an effect on the distribution of termites because even low lying areas are occupied by mounds due to low risk of water inundation (Levick et al., 2010). Furthermore, mounds occupied a much larger proportion of the landscape on granite (6%) relative to basalt (0.4%) showing that at the landscape scale, mounds on nutrient-poor geologies could have a significant effect on vegetation heterogeneity (Chapter 4). Due to the snapshot nature of this study, causes of patterns observed were mostly inferential; future studies should establish experiments where mechanisms can be determined. Ecological patterns are not static, but rather dynamic over time, hence I suggest the establishment of permanent plots where periodic assessments of recruitment of new mounds can be undertaken to better understand termite mound dynamics and inform direction for the conservation of termites and the important ecosystem roles they perform. Also, genetic tests of large and budded colonies can be carried out. Although the ecology of *Macrotermes* species is similar, further studies on the spatial distribution of mounds should seek to identify all the mounds to the level of the termite species, in order to establish mechanisms leading to the observed patterns. It is not only the termite species that need to be considered in ecosystem management and conservation, but also the mounds that they build because these can last for centuries, with several recolonisations, and thereby improve ecosystem heterogeneity and function.

The accumulation of nutrients in termite mounds provides unique habitats for plants, increasing heterogeneity in an otherwise homogeneous landscape (Figure 6.1). Mounds located in systems where there is little difference in soil nutrients between the savanna matrix and the mounds are less likely to have an effect on vegetation heterogeneity. Landscape variability prompted two questions: 1) do termite mounds act as sources of vegetation heterogeneity in landscapes spanning nutrient-rich and nutrient-poor geologies? And 2) are mounds of all sizes important for herbaceous vegetation heterogeneity? Large mounds on granite had significant differences in soil nutrients compared with the savanna matrix, whereas on basalt there was no difference. The spatial extent of mound effects on plant assemblages extended far beyond the mound perimeters into the savanna matrix on granite, whereas mounds had no influence on assemblage composition beyond their perimeters on

basalt. Similarly, mounds had higher soil nutrients compared with the savanna matrix on granite, but not on basalt, likely leading to the stronger mound effects on granite where they subsequently act as nutrient hot-spots. I suggest that the frequent visits to mounds by grazing and/or browsing large herbivores causes hoof erosion on the steep slopes of large mounds. Furthermore, digging into mounds by animals such as elephants in search of nutrients (geophagy) and aardvark which feed on termites, increases the rate of erosion, thereby likely increasing the sphere of influence of mounds on plant species diversity beyond the mound edge. Mounds harboured plant species that were not common in the surrounding savanna, four grass species on granite and four different grass species on basalt. Because mounds host high quality forage and large trees (Joseph et al., 2011), they attract organisms from different taxa, some of which are highly mobile (e.g. birds) that drop off unique propagules (mostly seeds from fleshy fruits) from far away distances, ultimately increasing ecosystem diversity. Mound effects on herbaceous plant diversity are not uniform across landscapes, but are more pronounced on dystrophic geologies. Furthermore, mound size is of paramount importance in terms of the size of the effect termite mounds have on plant diversity, with mound size effects being more consequential on nutrient-poor geologies. Since termite mounds are larger on granites, they become even more important as generators of savanna heterogeneity on this nutrient-poor geology. Further studies considering other geologies are encouraged in order to make broad conclusions based on a wider spectrum of studies.

My findings reveal that termite mounds contribute to spatio-temporal patterns of grazing in savannas (Figure 6.1), corroborating previous studies where herbivory was more pronounced on mounds compared to the savanna matrix (e.g. Davies et al., 2016b; Grant and Scholes, 2006; Mobæk et al., 2005). Furthermore, this study explicitly shows that mounds emanating from varied geologies have different effects on grazing, with mounds located on nutrient-poor geologies having a greater influence. Marked differences in soil nutrients between mounds and the savanna matrix on granite has the potential to not only influence biomass production (Chapter 4), but also forage palatability and therefore increase grazing levels at such sites. The cascading effects of mounds on nutrient-poor geologies can then lead to higher herbivore biomass on these geologies than would otherwise be expected. In terms of considering mounds of different sizes as foraging patches, it was the large mounds that were utilized more, which is similar to other studies that investigated the influence of patch size on foraging (Cromsigt and Olff, 2006; Pretorius et al., 2011). Moreover, large mounds have also

been confirmed to have a substantial impact on tree heterogeneity (Davies et al., 2016a; Joseph et al., 2013). Higher biomass production on granite mounds compared with basalt mounds could lead to such landscapes supporting grazing herbivores longer into the dry season. Because grasses growing on mounds are highly palatable across all seasons, mounds on the nutrient-poor granite in particular can be viewed as small patches of *sweetveld* embedded in the expansive *sourveld*.

Overall, my investigation on the effect of geology on termite species diversity, mound size and spatial distribution, and the effect of mounds emanating from different geologies on plant diversity and grazing patterns has yielded insights on the interplay between geology and termites. It is clear that mound-building termites on nutrient-poor geologies such as granite are ecosystem engineers, with mound basal area covering ~6% of the landscape, and mounds influencing ~19% of the landscape in terms of herbaceous plant species composition and ~28% of the landscape in terms of large herbivore grazing. On the other hand, termites may not emerge as ecosystem engineers in nutrient-rich environments (basalt). Here, mound basal area covered only ~0.4% of the landscape and influenced ~0.4% of the landscape in terms of herbaceous plant species composition and ~0.8% of the landscape in terms large herbivore grazing.

Conservation implications

Biodiversity conservation and improvement is the main goal for most organizations that are involved in conservation programmes. Unfortunately, their focus is mostly on the large bodied emblematic species such as lions and elephants, ignoring the small taxa, including invertebrates. However, in order to conserve diversity, there is a need to establish what is present in an ecosystem in terms of species composition so that sound conservation and management policies can be crafted. Termites are one such invertebrate group that are widely distributed in tropical and subtropical savannas. Their engineering roles are important for ecosystem functioning across multiple spatial scales. Considering that GNP is a semi-arid environment, where the action of other invertebrates important in nutrient cycling, for example dung beetles, is short lived, termites are likely to be the most important soil taxa, and therefore activities such highly frequent fires that disrupt the establishment of termites should be avoided. No doubt, invertebrates like termites can reliably be used as indicator species, although it is not a common practice in the literature. Considering that the

significance of mounds to vegetation heterogeneity and grazing is not uniform across landscapes or across termite mound sizes, management policies should also vary when different geologies are considered.

In an era where there is high human population growth coupled with government policies that increasingly emphasises agricultural production to achieve food security, it is clear that most wildlife reserves will suffer the consequence of size reductions due to increases in demand for land, and GNP has not been spared (Mombeshora and le Bel, 2009). The erection of fences around conservation areas with the aim to reduce human wildlife conflict usually follows, hindering wildlife migration between reserves (Boone and Hobbs, 2004). In such instances, the high density of large mounds is even more important for conservation because they are able to sustain wildlife populations by providing sufficient nutritious forage across seasons, particularly during the dry season when forage is most limited. Considering that mounds not only improve plant diversity, but also animal diversity, the importance of mounds in biodiversity conservation should not be underestimated.

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