

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

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Abstract

Termite mounds contribute to the spatial heterogeneity of ecological processes in many savannas, but the underlying patterns and determinants of mound distributions remain poorly understood. Using the Carnegie Airborne Observatory (CAO), we mapped the distribution of termite mounds across a rainfall gradient within a river catchment (~27 000 ha) of the Kruger National Park, South Africa. We assessed how different factors were associated with the distribution and height of termite mounds at three spatial scales: the entire catchment, among three broad vegetation types, and on individual hillslope crests. Abiotic factors such as the underlying geology and mean annual precipitation shaped mound densities at broad scales,

while local hillslope morphology strongly influenced mound distribution at finer scales, emphasising the importance of spatial scale when assessing mound densities. Fire return period had no apparent association with mound densities or height. Mound density averaged 0.46 mounds ha⁻¹, and exhibited a clustered pattern throughout the landscape, occurring at relatively high densities (up to 2 mounds ha⁻¹) on crests, which are nutrient-poor elements of the landscape. Mounds exhibited significant over-dispersion (even spacing) at scales below 60 m so that evenly spaced aggregations of termite mounds are embedded within a landscape of varying mound densities. The tallest mounds were found in dry savanna (500 mm.yr⁻¹) and were positively correlated with mound density, suggesting that dry granitic savannas are ideal habitat for mound-building termites. Mound activity status also varied significantly across the rainfall gradient, with a higher proportion of active (live) mounds in the drier sites. The differential spacing of mounds across landscapes provides essential nutrient hotspots in crest locations, potentially sustaining species that would otherwise not persist. The contribution to biodiversity and ecosystem functioning that mounds provide is not uniform throughout landscapes, but varies considerably with spatial scale and context.

Introduction

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

Among the many drivers of savanna heterogeneity, termites act as ecosystem engineers (Jones et al. 1994, Dangerfield et al. 1998), mostly through their transportation of soil nutrients both vertically and horizontally (Sileshi et al. 2010), as well as by altering soil

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

As well as being agents of ecological heterogeneity through mound construction, the distribution of termite mounds also varies with multiple environmental factors. Variation in the density of termite mounds has been observed at regional scales (two hundred 2 ha sampling belts spread across 981 000 ha), with *Macrotermes* preferring sandy, granitic soils to basaltic clay, and undulating topography over concave floodplains (Meyer et al. 1999). Similar patterns have been observed at finer hillslope scales (~1 km), with these termites avoiding areas with high clay content below seeplines in catena sequences (in order to escape inundation), while at the same time avoiding areas that are too sandy for mound construction (Levick et al. 2010a). Effects other drivers of landscape heterogeneity, such as fire and rainfall, have on termite mound distributions are poorly understood (but see Benzie (1986)), and competitive interactions between termite colonies also shape mound distributions, evidenced by the over-dispersion exhibited by termites at small spatial scales (< 100 m) (Korb and Linsenmair 2001, Pringle et al. 2010). Furthermore, despite the increasingly

recognized role played by termite mounds, few studies have examined how mound patterns vary at different ecological scales. Examination over a range of spatial scales is needed to facilitate a better understanding of how the role of termite mounds in structuring savannas varies across space, and providing information on the extent of their influence across different savanna landscapes. However, most studies have focused on small areas, which may poorly represent landscape complexity. In part, this is due to logistical constraints and difficulties with surveying large areas with accuracy.

The Carnegie Airborne Observatory (CAO) (Asner et al. 2007), an integrated LiDAR and hyperspectral system, provided an opportunity to survey large areas of savanna and map termite mound position and height (which relates directly to above-ground volume) across an entire river catchment. Using this remote-sensing technology, we were able to extend the limited coverage of previous studies and provide landscape level insights into termite mound patterns, in order to more fully understand drivers of spatial heterogeneity in African savannas. Our aims were to: i) investigate how patterns of termite mound distribution and shape vary across a savanna landscape (an entire river catchment); ii), explore how such patterns differ between broad vegetation types within this landscape; iii) determine the principal factors shaping mound densities across the catchment; and iv) quantify the species diversity of mound-building termites as well as how mound architecture (slope) varies across the catchment. We expected mound density to vary across the landscape in response to topographical features, being located primarily on crests away from drainage lines (following Levick et al. 2010a), as well as exhibit variation across vegetation types in response to factors such as rainfall and soil nutrients. Higher densities, with higher species diversity, were expected in wetter savanna areas due to higher levels of primary productivity conducive to increased termite diversity (Davies et al. 2012), while higher clay content in drier areas was expected to enable mounds to be taller and steeper here (Jouquet et al. 2004).

Methods

Study area

We conducted the study throughout the entire catchment of the N'waswitshaka River, a medium sized non-perennial tributary of the Sabie River in the southern Kruger National Park, South Africa. The catchment covers *ca.* 27 000 ha of gently undulating landscape and varies in altitude from *ca.* 630 m.a.s.l. in the south-west to *ca.* 280 m.a.s.l. in the north-east. The underlying geology consists of granite throughout the catchment except for a narrow gabbro intrusion in the southwest, leading to dark soils with much higher clay content than the granite derived soil. Mean annual precipitation (MAP), almost always in the form of rain, varies across the catchment, being highest (650 mm.yr⁻¹) in the west (Pretoriuskop) and lowest (500 mm.yr⁻¹) in the east (Skukuza). Mean annual rainfall at Napi (a transitional site between Pretoriuskop and Skukuza) and on the gabbro intrusion is between 550 and 600 mm.yr⁻¹. Most rainfall occurs during the hot summer months (October – March). The vegetation varies considerably across the catchment. In the wetter west (Pretoriuskop) it is dominated by nutrient-poor “sour bushveld” consisting of mostly *Terminalia sericea* and *Dichrostachys cinerea* while the drier east (Skukuza) is relatively nutrient-rich and dominated by an *Acacia nigrescens/Combretum apiculatum* association (Gertenbach 1983). A mosaic of these two vegetation types, with intermediate nutrient levels, occurs as a transition zone in the central region of the catchment (Napi), with *Combretum zeyheri* and *C. collinum* also becoming prominent. The gabbro intrusion is dominated by open savanna with dense grass cover, with some areas containing low-standing *Acacia nigrescens* and *Dichrostachys cinerea* shrubs (Gertenbach 1983). The area of each vegetation type surveyed differed in size, with Skukuza the largest at 17 653 ha, followed by Napi at 5 746 ha and Pretoriuskop at 1 694 ha. The gabbro intrusion covered the smallest area at 1 616 ha. Altogether, the four vegetation types covered the entire catchment. Due to the nature of

savanna ecosystems, spatial heterogeneity within the vegetation does exist within each vegetation type, but the dominant vegetation is extensive enough to ensure a broadly similar environment throughout each vegetation type. Within the catchment there are also distinct vegetation patterns resulting from catena processes with a distinct seepline (where water moving downslope through the soil accumulates against the clay-enriched zone of valley bottoms) being evident. Woody cover is generally higher on hill crests than the lowlands alongside river channels, where, apart from a riparian corridor, the grassy layer dominates (Levick et al. 2010a).

Airborne remote sensing and field data collection

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

For this study, the CAO LiDAR data were collected from 2000 m above ground level, providing terrain and woody vegetation elevation measurements at 1.12 m spatial resolution. All data collection flights were conducted within 2.5 h of solar noon. Digital terrain models (DTMs) derived from LiDAR were analysed in an object-based manner, using the multi-resolution segmentation algorithm in eCognition Developer 8 software (<http://www.ecognition.com/products/ecognition-developer>), to extract termite mound spatial

locations and size. Image segmentation was weighted towards changes in slope, and the classification hierarchy considered both the relative difference in elevation between neighbouring objects, and image object shape.

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

Analysis

We conducted data analysis at three spatial scales: throughout the entire catchment, among broad vegetation types within the catchment, and on individual hillslope crests. First,

catchment mound patterns were investigated using Ripley's K function, a second-order statistic that utilises information on all inter-point distances to provide information on spatial pattern, measuring deviations from spatial homogeneity. The expected distribution of landscape features under complete spatial randomness is plotted against spatial distance, as well as the observed distribution. When observed values fall below the expected distribution for spatial randomness, over-dispersion (even spacing) occurs, while values above the expected distribution indicate clustering. Statistical significance of spatial patterns can be evaluated by comparing the observed data with Monte Carlo envelopes from analysis of multiple simulations of a null model. For our data, 19 simulations were run, producing 95% confidence intervals for statistical testing (Wiegand and Moloney 2004). At this catchment scale we also investigated effects of hydrology (drainage lines) on mound locations. Using flow accumulation tools, drainage lines were mapped in ArcGIS software using DTMs derived from LiDAR, and from these networks, an index of drainage line size was calculated. These drainage lines reflect areas of flow accumulation and their size (order) is calculated in the same manner as traditional stream orders. Since we were interested in the effect of drainage lines (areas of flow accumulation) rather than streams, our index of drainage line size is higher than traditional stream orders. The nearest mound to each segment of a drainage line of a particular size was then calculated and differences between distances were compared with a Kruskal-Wallis test and post-hoc pairwise Wilcoxon rank sum tests (with a Holm correction for multiple comparisons).

Second, we compared mound distributions (patterning, density and height) using Ripley's K function (patterning) and Kruskal-Wallis with post-hoc pairwise Wilcoxon rank sum tests (densities and heights) across the four broad vegetation types present in the catchment: high rainfall, nutrient-poor savanna in the west (Pretoriuskop), low rainfall nutrient-rich savanna in the east (Skukuza), an intermediate rainfall and nutrient savanna

(Napi), and the narrow gabbro intrusion with intermediate to high rainfall in the west. The gradient of the mound slope was also assessed in three of the four broad vegetation types (excluding the gabbro intrusion where mound densities are extremely low) using one-way analysis of variance (ANOVA). Slope was compared for the entire mound as well as upper and lower measurements. The activity status and termite species occupying mounds was also investigated across these three sites. Factors that could influence the activity status of these mounds (vegetation type, mound height and mound slope) were compared using generalized linear models with a binomial error family and corrected for overdispersion. The most parsimonious model was selected using Akaike's information criterion (AIC).

Because Levick et al. (2010a) found that aggregations of termite mounds are located on crests in the same study region, we further investigated 54 crests across the catchment to determine the principal factors shaping mound distributions. Crests were chosen based on the DTM constructed from the LiDAR and stratified across the catchment, ranging in area from 14.6 ha to 172.6 ha (mean = 61.2 ha and median = 55.5 ha). For each crest, data on the following variables were attained either with the remote sensing or from existing datasets held by South African National Parks: crest area (determined from DTMs and defined as the area above the seepline, demarcated by the lowest extent of termite mound occurrence following Levick et al. 2010a), fire return period from 1941 to 2009 (half the crest must have burnt for a fire to be deemed to have occurred in a given year; the vast majority (82%) of fires considered burnt the entire crest when they did occur), mean annual precipitation recorded from 1910 to 2002 (Zambatis 2003), mean percentage woody cover measured with LiDAR at a spatial resolution 1.12 m and dominant geology, following Gertenbach (1983). Some spatial variation across the crests will inevitably be present for each covariate, however, crests were sufficiently small to limit any large variation and the values of each covariate were carefully inspected to minimise variation and ensure consistency across a

given crest. Linear models and linear mixed effects models were then fitted to examine relationships between these variables and mound densities and heights respectively. Candidate sets of models (454 and 452 candidate models were constructed for densities and heights, respectively), consisting of the above variables and all ecologically meaningful two-way interactions were ranked according to sample-size-corrected AIC_c (Burnham and Anderson 2002) and the best model for each response variable (mound density and height) selected. The top regression models for each response variable according to AIC_c are provided in Appendices 1 and 2, full sets are available from AB Davies on request. A difference (delta) in AIC_c of less than 2 was considered a threshold for determining whether one model performed better than another. All statistical procedures were conducted using R software version 2.15, using the packages spatstat (Ripley's *K*) and lme4 (linear mixed effects models) (R Development Core Team 2012).

Results

Field checks indicated that overall 75% of mounds were detected with the LiDAR survey. Detection rates varied across vegetation types, with an 83% detection rate at the dry site (Skukuza), 64% at the intermediate site (Napi) and 90% at the wet site (Pretoriuskop). Detection was likely lower at Napi because of a relatively high number of very small (< 0.5 m) mounds here compared to other sites (7 at Napi compared to 2 at Skukuza and 1 at Pretoriuskop). When mounds of this height class were removed from the ground validation, detection rates improved and were more similar across vegetation types (87% at Skukuza, 78% at Napi and 90% at Pretoriuskop). LiDAR therefore detected medium and large (> 0.5 m in height) mounds (which are likely more ecologically meaningful, see Joseph et al. 2013, Seymour et al. 2014) with similar, high accuracy at all three sites. Heights of detected mounds at the intermediate site were closely correlated with the LiDAR estimates ($r_s = 0.78$,

$p < 0.001$, $n = 25$). However, at the dry and wet sites, LiDAR underestimated mound height with a weaker, but statistically significant, correlation evident at the dry site ($r_s = 0.39$, $p < 0.05$, $n = 34$) and a weak and insignificant correlation at the wet site ($r_s = 0.50$, $p = 0.178$, $n = 9$).

Catchment-level patterns

The overall density of termite mounds across the N'waswitshaka catchment was 0.46 mounds ha^{-1} (a total of 12 505 mounds were detected, Fig. 1), with the mean overall termite mound height being 1.21 m (\pm standard deviation of 0.47 m). Ripley's K function showed that mounds exhibit significant over-dispersion (even spacing) at scales below 60 m (Fig. 2). At larger scales, however, mounds displayed a clustered pattern, indicating that evenly spaced aggregations of termite mounds are embedded within a landscape of varying mound densities, exhibiting a clustered pattern (Figs. 1 and 2). Levick et al. (2010a) recorded that such clusters occur on crests within this landscape in response to hillslope hydrological boundaries, resulting from patterns in sand and clay distribution.

Since mounds are clustered on crests, above the seepline of hillslopes, we investigated the effect of drainage line size on the distribution of termite mounds. Our results indicate that as drainage line size increases so does the distance to the nearest termite mound (Kruskal-Wallis $X^2 = 565.19$, $p < 0.001$). Pairwise Wilcoxon rank sum tests revealed that these differences were significant ($p < 0.05$) between all the different drainage line size classes except for comparisons between 3rd and 5th order drainage lines ($p = 0.83$) and between 4th and 6th order drainage lines ($p = 0.83$) (Fig. 3). Thus, there is a significant increase in the mean distance to the nearest mound when moving from a first order drainage line (barely discernible area of flow accumulation) to a second order drainage line and again to a third order drainage line (small ephemeral stream). However, drainage lines of third to sixth order

do not have a major impact on mound distance to drainage line, but an almost two fold jump in mean mound distance to drainage line is observed when moving to a seventh order drainage line, the highest available for our study site. It therefore appears that a threshold is reached at a seventh order drainage line (lower reaches of the N'waswitshaka River, a non-perennial river flowing most years during summer, and corresponding to a 5th order stream for this catchment) in terms of mound distance to water.

Mound patterns among vegetation types

Ripley's K function demonstrated that mounds were over-dispersed across all vegetation types at small spatial scales (Appendix 3, Fig. S1). The patterns at the drier sites in particular mirror those of the entire catchment with clustering occurring at spatial scales above 60 m (Fig. S1a and b). The wettest site (Pretoriuskop) displayed similar patterns (over-dispersion at small scales and clustering across the landscape), but with the overly-dispersed clusters of termite mounds being smaller in size (occurring below spatial scales of 45 m) (Fig. S1c). Ripley's K revealed irregular patterning on the gabbro intrusion, but with the same overall pattern of over-dispersed clusters of mounds (Fig. S1d). The irregular patterning could be due to much lower mound densities found here (i.e., small sample sizes) and the shape of the gabbro intrusion (being long and narrow).

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

intrusion ($0.18 \text{ mounds ha}^{-1}$), suggesting a strong effect of geology on termite mound densities (Fig. 4a).

Pairwise Wilcoxon rank sum tests showed that mound height varied significantly between all sites ($p < 0.001$) with taller mounds being located at drier sites (Skukuza and Napi). In contrast to mound densities, an effect of geology on mound height was not apparent (Fig. 4b). Mound diameter was significantly correlated with mound height ($r_s = 0.75$, $p < 0.001$, $n = 120$) and so excluded from analysis. Height was selected in preference to diameter because it is more readily obtained from LiDAR, and hence could be used in all analyses. Termite mounds were significantly steeper at drier sites (ANOVA, $F_{2, 117} = 12.25$, $p < 0.001$), with this pattern being consistent for both the upper and lower (pediment) sections of mounds, although differences in steepness were not significant for the pediment (ANOVA, $F_{2, 117} = 2.84$, $p = 0.06$) (Fig. 5). Tukey HSD tests also showed that overall, only mounds at the driest site (Skukuza) were significantly steeper than the other two sites ($p < 0.01$ compared to Napi, and $p < 0.001$ compared to Pretoriuskop), which did not differ significantly from each other ($p = 0.27$). This was also the case for the upper sections of mounds ($p < 0.001$ for comparisons between Skukuza and both Napi and Pretoriuskop and $p = 0.60$ for Napi compared to Pretoriuskop) (Fig. 5).

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

peaked at the intermediate site (Napi) with ten termite species sampled here. At the wettest site (Pretoriuskop), six species were sampled (Fig. 6b).

Mound patterns on crests across the catchment

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

causality (Appendix 4, Fig. S2). Furthermore, the second best model (with an AIC_c score only 0.05 greater than the top model) did not include fire and this interaction should thus be interpreted with caution (Appendix 1).

Discussion

Spatial patterns of termite mounds across the catchment

The integration of our results across three spatial scales provides novel insights into the spatial structuring of termite mounds, and hence ecological heterogeneity, in African savannas. At the full catchment scale, our recorded mound densities (0.46 ha^{-1}) are relatively low compared to other studies. Meyer et al. (1999) recorded *Macrotermes* mound densities of 0.73 ha^{-1} in northern Kruger National Park (KNP), while Levick et al. (2010a) recorded mound densities of $0.6 - 0.7 \text{ ha}^{-1}$ in an area of similar mean annual precipitation (MAP) and vegetation characteristics, also in southern KNP. Elsewhere in Africa, *Macrotermes* mound densities have been recorded as high as $1 - 4 \text{ ha}^{-1}$ in Uganda (Pomeroy 1977), $3 - 5 \text{ ha}^{-1}$ in Zambia (Trapnell et al. 1976), $4 - 22 \text{ ha}^{-1}$ (Lepage 1984) and $11 - 83 \text{ ha}^{-1}$ in Ivory Coast (Korb and Linsenmair 1998). The lower densities recorded for the N'waswitshaka catchment from our study are likely related to the scale at which the study was conducted. Most previous studies, including all those listed above, are field based and consider only one or a few patches in the landscape and infer from them the mound density for the area. In contrast, our measurements are across an entire catchment and hence averaged over different geology and hillslope types. However, there is the possibility that lower densities could be somewhat attributed to the resolution at which we operated the LiDAR, with small mounds escaping detection. Conservatively, patterns presented here are thus more reliably interpreted as those of larger termite mounds, which are likely to be more ecologically meaningful in terms of driving heterogeneity than small ones (see Joseph et al. 2013, Seymour et al. 2014 where

larger mounds were shown to be more influential than smaller ones). Nonetheless, our study as well as Meyer et al. (1999) and Levick et al. (2010a) record consistently lower mound densities for southern Africa than studies conducted in central and east Africa. Termites are restricted to sub-tropical and tropical regions with their diversity decreasing with increasing latitude (Eggleton 2000); lower mound densities are therefore expected for southern Africa where conditions are less optimal, being cooler and with stronger seasonality.

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

Clustered patterning in termite mound distribution has also been recorded in previous studies and seems to be driven mostly by hydrological controls, with termites avoiding areas with greater risk of inundation (Freyman et al. 2010, Levick et al. 2010a). This is also evident when drainage line effects are considered; termites avoiding even the smallest drainage lines (located approximately 130 m from them) and decreasing in proximity with increasing drainage line size, located up to *ca.* 280 m from high order drainage lines with large floodplains. Such patterning means that mounds will be most important for savanna heterogeneity at localised scales, on crests in landscapes with undulating topography.

Although limited to crests, this does not necessarily diminish the importance of mounds for creating landscape heterogeneity because crests are dominant features in these landscapes (accounting for about 35% of the landscape, S.R. Levick *unpublished data*) and the vegetation growing on them (apart from on termite mounds) is generally low in nutrients compared to lower lying regions (Grant and Scholes 2006). Our study was conducted in a landscape of undulating topography, how mound distributions are shaped in flatter regions warrants further investigation. In such flatter areas, termites will be unable to build mounds above seep lines to avoid inundation and instead may be influenced by cryptic ecological controls, such as ground water storage (JS Turner, *pers. comm.*). If true, termite mounds may be useful indicators of ground water dynamics, being absent or at lower densities where the water table is close to the surface.

On crests, mounds exhibit significant over-dispersion (even spacing), probably as a result of intra-specific competition (Darlington 1982, Korb and Linsenmair 2001, Pomeroy 2005), suggesting that at these smaller spatial scales, biotic factors (such as competition for resources) are responsible for distribution patterns. Pringle et al. (2010) demonstrated that such even spacing of termite mounds enhances their role in structuring spatial heterogeneity through minimising the mean distance between landscape features (termite mounds). Thus the even spacing of mounds on crests enhances the importance of the nutrient hotspots induced by them in these otherwise nutrient depauperate areas.

Over broad vegetation types, mounds display variation in their density and height: densities increase with increasing MAP and mounds in wetter areas are significantly smaller (lower in height and diameter which corresponds to volume). Soils in these wet savannas are sandy with low levels of clay (Gertenbach 1983), and since *Macrotermes* require a sufficient amount of clay to construct mounds (Jouquet et al. 2004), it is likely that mound size here is constrained by a lack of clay. Smaller *Macrotermes* mounds support smaller termite colonies

(Meyer et al. 2000) which probably forage over smaller areas and is a possible explanation for increased mound densities in the wetter parts of the catchment. If mound spacing is driven by endogenous processes related to competition (Darlington 1982, Korb and Linsenmair 2001, Pomeroy 2005), smaller colonies will therefore be able to persist at higher densities, enabling higher mound densities in wetter savannas where mounds are smaller. Grohmann et al. (2010) demonstrated that larger *Macrotermes* mounds are further apart than smaller mounds, providing direct support for this notion. However, higher mound densities in the wet, upper reaches of the catchment are also likely due to smaller drainage lines present here which results in more crest relative to lowland area. Given the strong relationship between mound location and hydrological features, this may lead to overall higher densities of mounds in the wet, upper reaches of the catchment than in the drier, lower reaches where larger drainage lines result in lower crest: lowland ratios. This means that there is more available area for termite mound construction in the upper catchments (a higher crest: lowland ratio), and therefore higher mound densities when the landscape is considered overall, again emphasising the importance of spatial scale and comprehensive coverage when mapping termite mound distributions.

Mounds in the drier eastern areas of the catchment are steeper, but this is uncorrelated with activity. Hence, mound steepness is likely a function of soil characteristics that allow taller and subsequently steeper mounds, rather than emerging from higher termite activity. Jouquet et al. (2004) found that clay was the most important factor for mound stability and structure and the steeper, taller mounds in our study are all located on soils with higher clay content (on crests in drier savanna). Although crests have lower clay content than lower regions of the catena, the crests in the drier savanna have relatively more clay than crests in the wetter, Pretoriuskop, area. The steepness of mounds may affect their usefulness to savanna herbivores. If slopes are too steep, access by grazers and browsers to the nutrient-

rich vegetation growing on them may be precluded. Indeed, grazing on steep mounds was observed to be restricted to mound pediments (AB Davies, *pers. obs.*).

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

Mound densities on crests

When mound densities on crests (where the majority of mounds occur) were investigated, key correlates were the percentage of woody cover on the crest, the height of the mounds present, mean annual precipitation and the underlying geology. The relationship with mean annual precipitation shows a bimodal pattern instead of a linear response, with densities peaking at the wet and dry ends of the spectrum. As discussed above, the disparity between the overall landscape and crest patterns with relation to mound density is strongly related to scale, and

exists because our data were collected across a river catchment, with the low rainfall area being in the lower reaches of the catchment where drainage lines are generally larger, resulting in greater area being unsuitable for mound construction. By examining patterns among crests, such hydrological effects are accounted for and the potential drivers of mound density become apparent. The increase in density at the dry end of the rainfall gradient is likely driven by different factors to those at the wet end (where smaller mounds can be located closer together) since mounds here are much larger and the soils contain more clay (Gertenbach 1983), suggesting that crests in drier savannas can sustain much larger termite populations (high densities of large termite colonies). Furthermore, a far higher proportion of mounds are active in these drier savannas, which typically have higher nutritional value than wetter savannas. This may result in higher colony densities and numbers of individual termites. Since termites facilitate nutrient cycling (Lavelle et al. 2006), a positive-feedback loop may develop in these drier savannas, with more termites able to persist here which in turn increases nutrient cycling and maintains nutrient-rich savanna.

Moreover, at this hillslope scale, and in contrast to broad catchment patterns, mound height and density are positively correlated, suggesting that where colonies are large they also occur at high densities, with the tallest mounds located in the drier, nutrient-rich, sites where more termites can be sustained. The exception to this pattern is when mounds drop below ~1 m in height; here no pattern exists between height and density. This occurs because in some areas (wetter crests around Pretoriuskop), low mounds occur at high densities, but in most other areas (especially the gabbro intrusion) where mounds are low in height they occur at low densities (although difficulties in detecting small mounds with LiDAR should also be considered here). On such crests, termite colonies are both small and occur at low densities, indicating that such areas (gabbro) are sub-optimal habitat for termites. Although termite

mound age may also affect height, age determination is not readily achievable. Furthermore, there is little reason to expect differences in age classes in any one site compared to another.

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

Woody cover on a crest was a strong predictor of mound density, with increased cover coinciding with increased mound density. A large proportion of *Macrotermes* diet consists of dead wood (Donovan et al. 2001) and so where large amounts of dead wood are present, large numbers of termite colonies can survive, with smaller foraging areas needed per colony. Crests with high woody cover will inevitably produce more coarse woody debris and termites respond to this by occurring in higher numbers. Trees respond positively to termites, with higher densities of trees growing on and around mounds (Moe et al. 2009, Erpenbach et al. 2013). Although both mound density and woody cover are strongly linked to topographic position and soil conditions, an interesting positive-feedback loop may strengthen the relationship with higher levels of woody cover creating habitat conducive to *Macrotermes* and higher levels of *Macrotermes* activity creating areas conducive for tree growth, driving strong concomitant patterns in termites and woody cover. Trees growing on termite mounds are higher in nutritional content than those off mounds (Seymour et al. 2014)

and are preferred by browsing herbivores (Loveridge and Moe 2004, Levick et al. 2010b). Areas with high mound densities and high levels of woody cover are therefore likely to result in areas of high productivity for both tree and browsing herbivore diversity.

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

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

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Figure legends

Figure 1: Location of the N'waswitshaka catchment (study site) within Kruger National Park. The black dots represent termite mounds which exhibit a clustered distribution at the catchment scale and an over-dispersed one at the hillslope scale (see enlarged area). The catchment is displayed as a digital terrain model (DTM), with red areas representing high elevation and blue areas low elevation.

Figure 2: Results of Ripley's K -function analysis of termite mounds across the entire N'waswitshaka catchment. $L(r)$ values (a transformation of Ripley's K) are plotted against distance (r) in meters. The dashed line represents the distribution of mounds under complete spatial randomness, while the solid line represents observed mound distribution. Values below the dashed line indicate over-dispersion (even spacing) while values above the dashed line indicate clustering. 95% confidence intervals expected from a random landscape are plotted as grey lines, but are too close to the theoretical distribution (dashed line) to be noticeable.

Figure 3: Mean (± 1 SE) distance to drainage channel of termite mounds as a function of stream order. Mean distances are calculated as the distance of the nearest termite mound to each segment of the particular stream. Letters indicate significantly different distance classes. Stream orders do not follow traditional classifications and rather incorporate areas of high flow accumulation; thereby first order streams are not streams in the conventional sense, but rather drainage lines where water may accumulate during wet periods.

Figure 4: Mean (± 1 SE) **a)** termite mound density and **b)** height in each of four vegetation landscapes in the Kruger National Park. The solid line on each graph represents the overall density and height for the entire catchment. Letters indicate significantly different distance classes.

Figure 5: Mean (± 1 SE) angle (steepness) of termite mounds in three broad vegetation types, stratified according to the entire mound and the lower and upper sections. Letters and symbols indicate significantly different distance classes.

Figure 6: a) Proportion of termite mounds (out of a total of 40 per site) that are active in each vegetation landscape and **b)** the relative proportions of termite species sampled from mounds in each vegetation landscape.

Figure 7: Relationships between a) mean annual precipitation, b) mound height, c) percentage woody cover and d) underlying geology on termite mound densities. A LOESS smoother has been added to the scatterplots (a – c) to aid visual interpretation.

Figure 1:

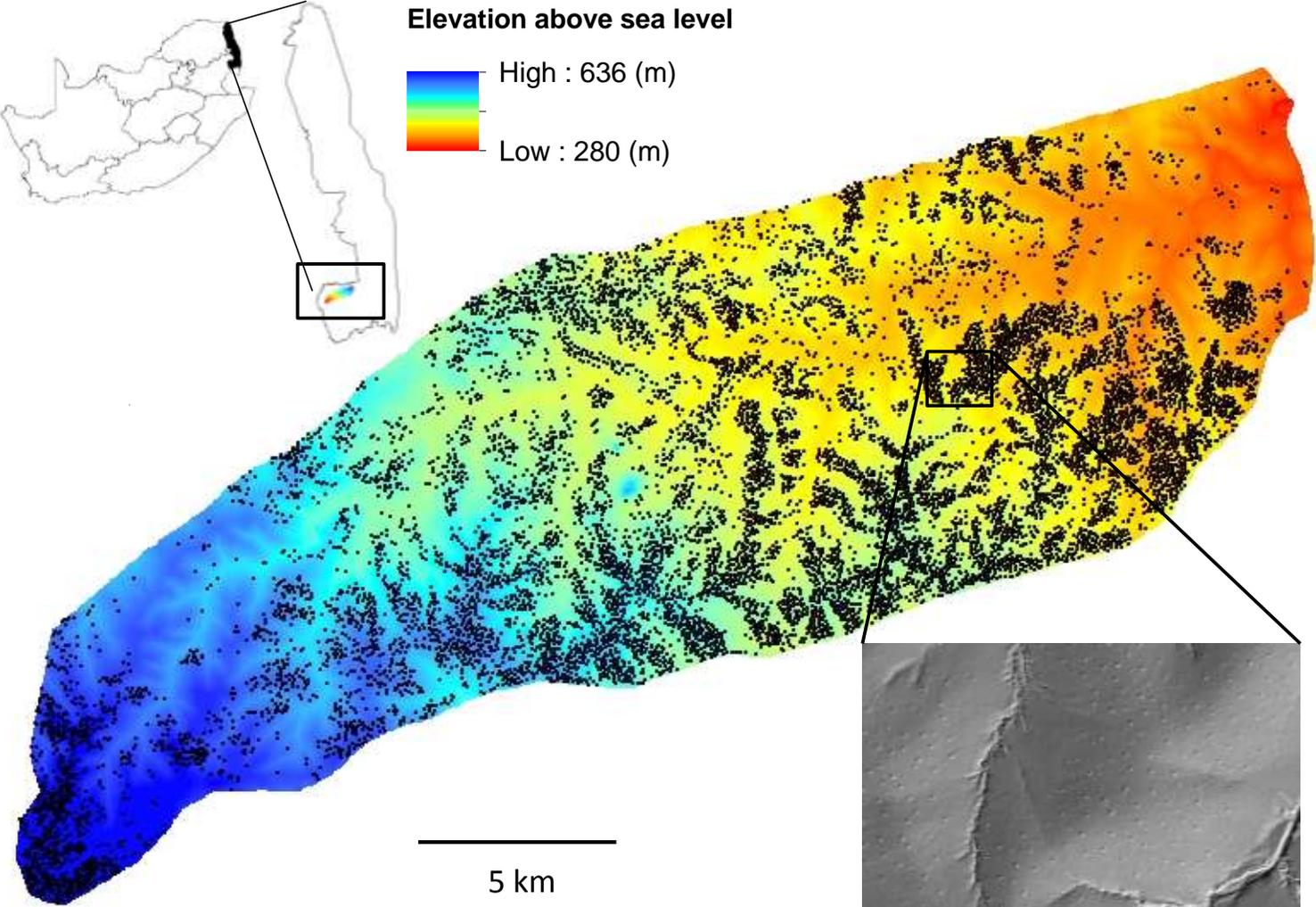


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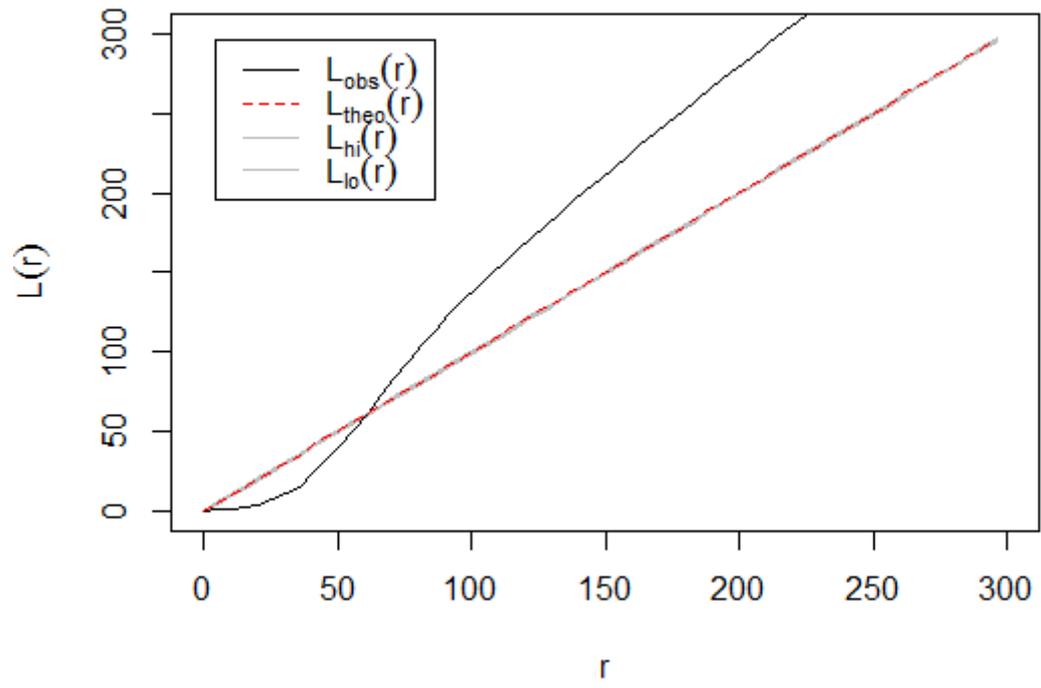


Figure 3:

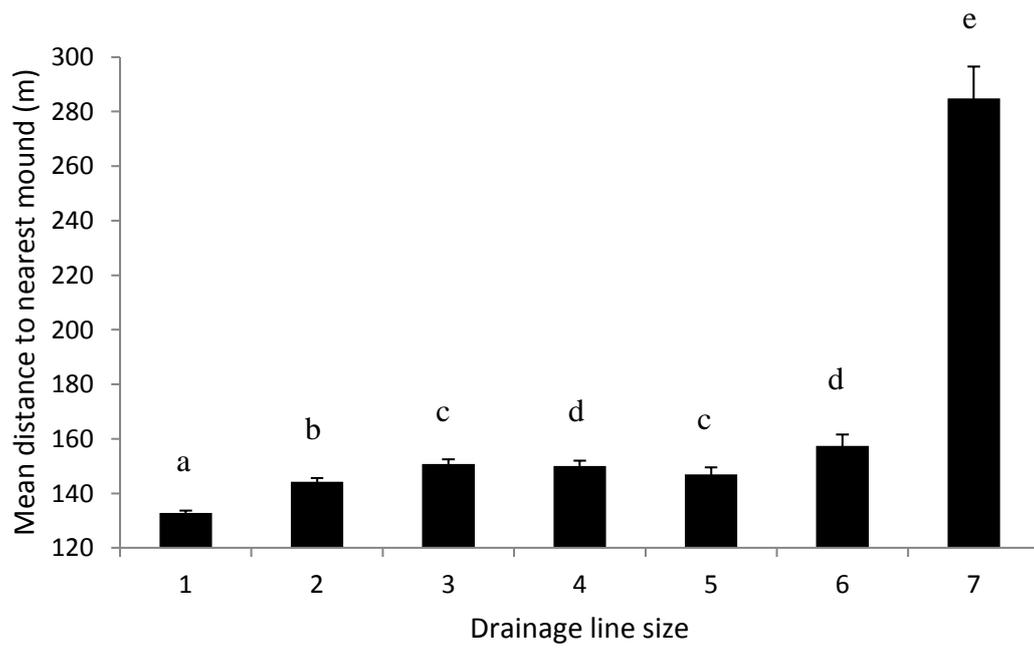
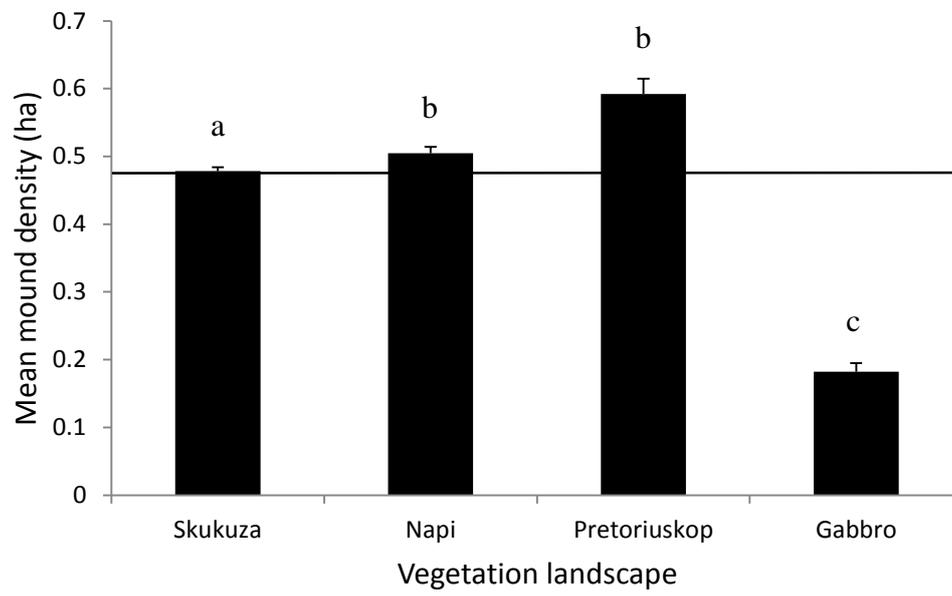


Figure 4:

a)



b)

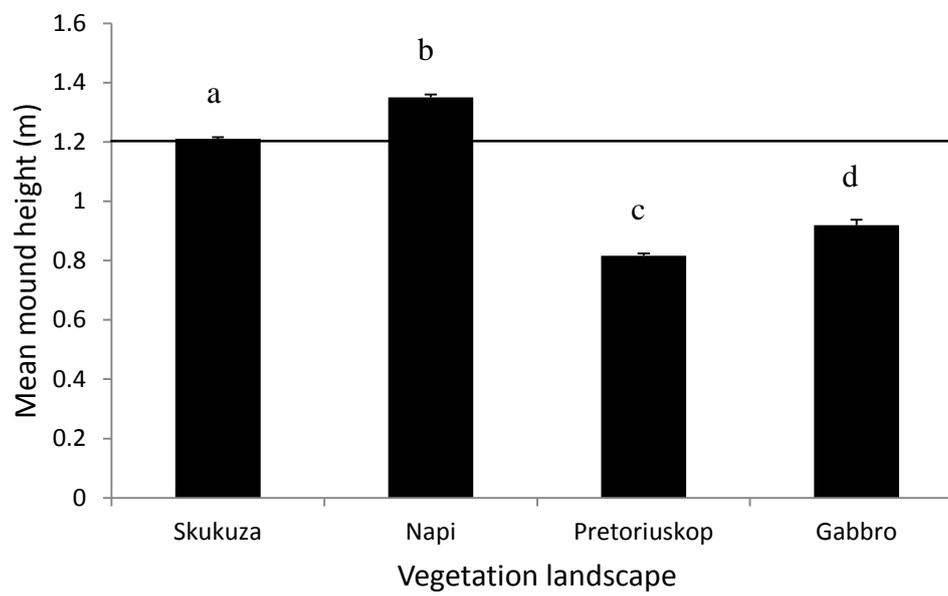


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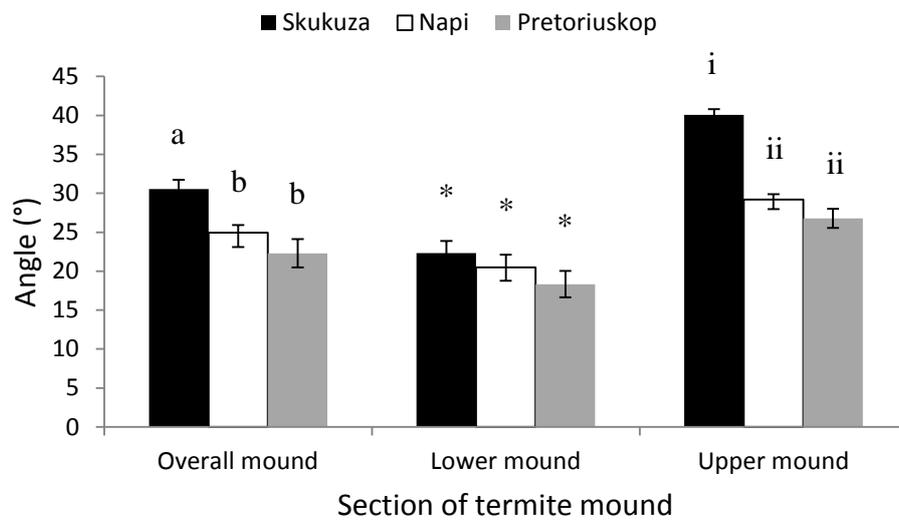
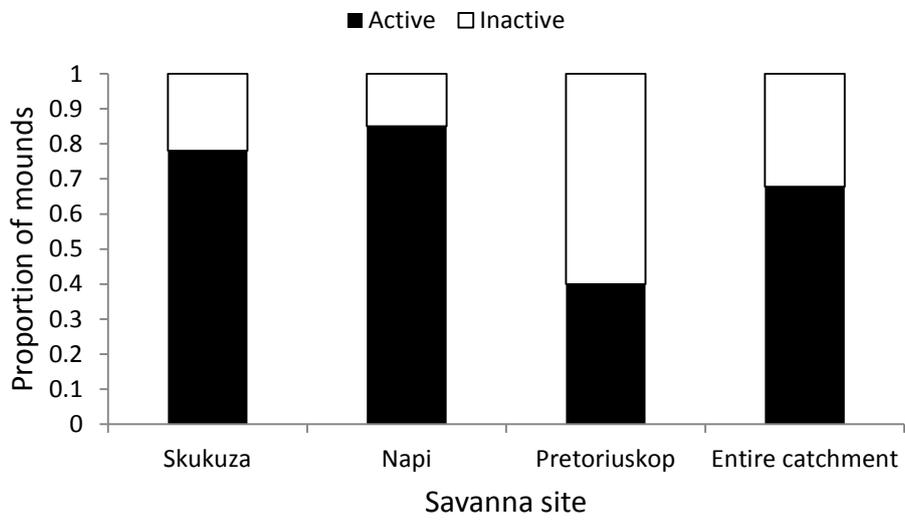
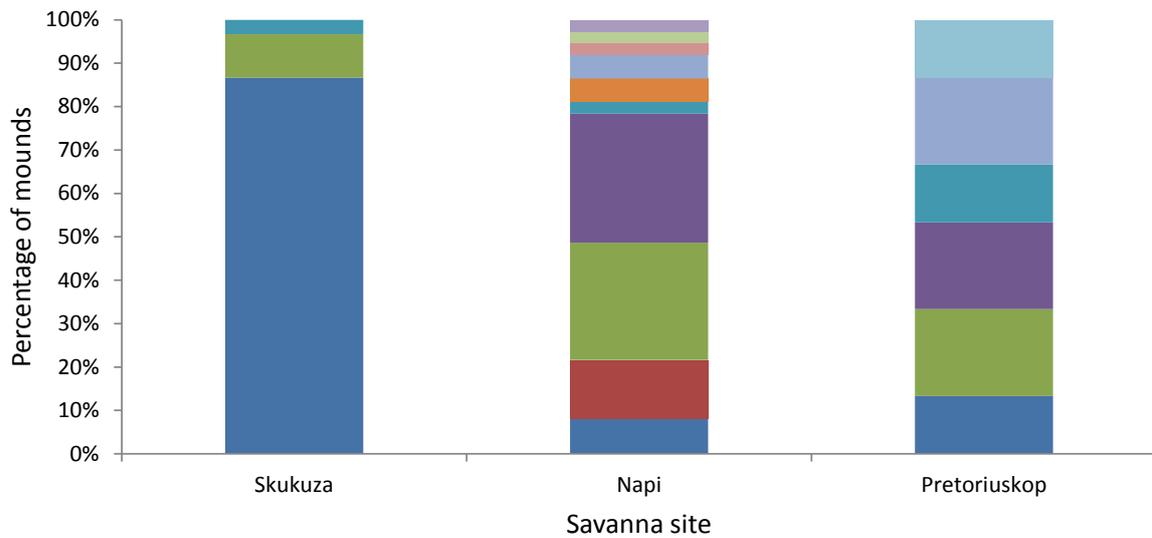


Figure 6:

a)

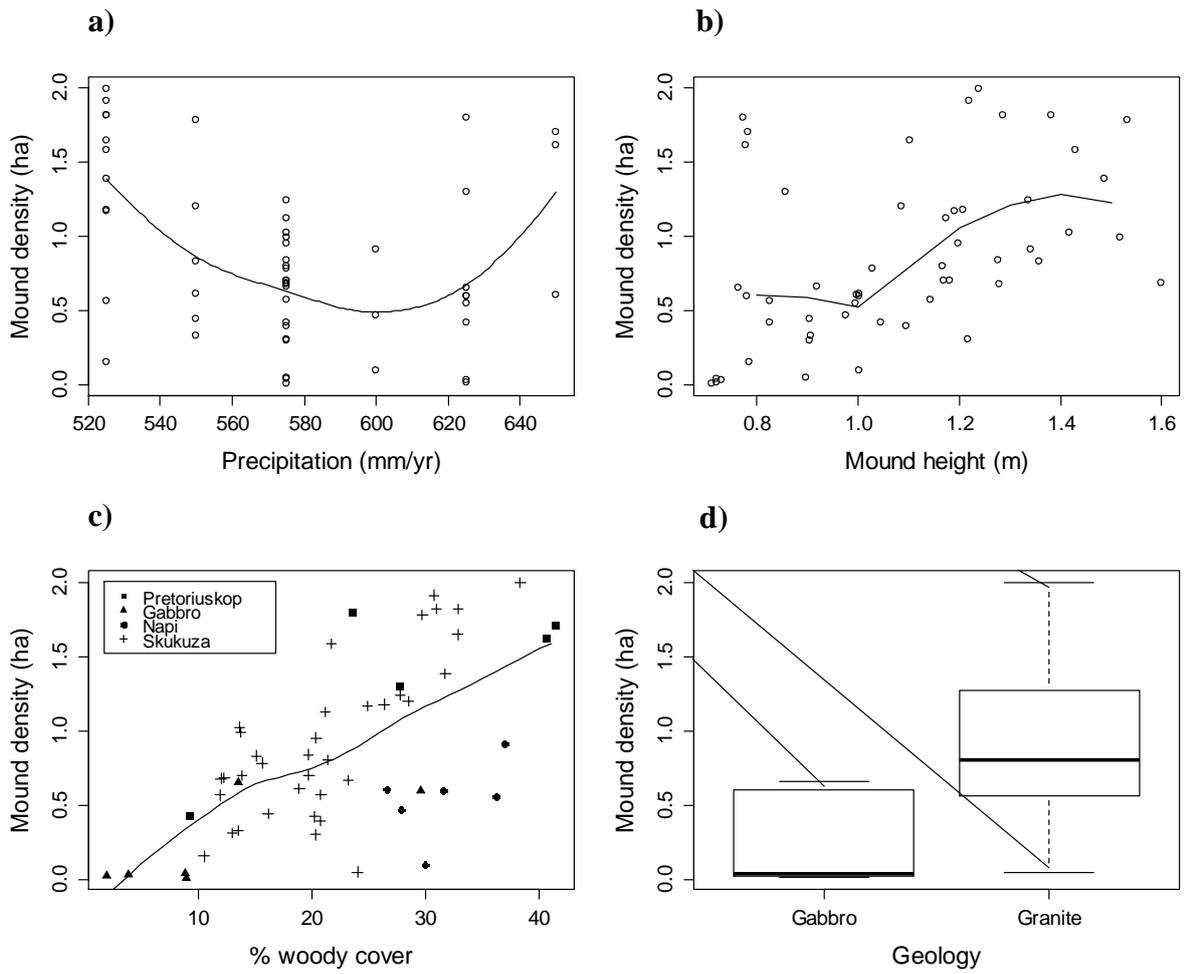


b)



- Macrotermes falciger
- Macrotermes natalensis
- Trinervitermes spp.
- Amitermes spp.
- Ancistrotermes spp.
- Odontotermes sp 1
- Odontotermes sp 2
- Allodotermes rhodesiensis
- Angulitermes spp.
- Microcerotemes spp.
- Microtermes spp.

Figure 7:



Appendix 1: The top eight regression models for mound densities that received considerable empirical support ($\Delta_i < 2$) according to the second order Akaike Information Criterion (AIC_c). The top selected model we used in the final analysis is in bold. Δ_i is the difference between a model's AIC_c value and that of the model with the lowest AIC_c; the Akaike weight w_i is the likelihood of a given model's being the best model in the set. MAP is mean annual precipitation.

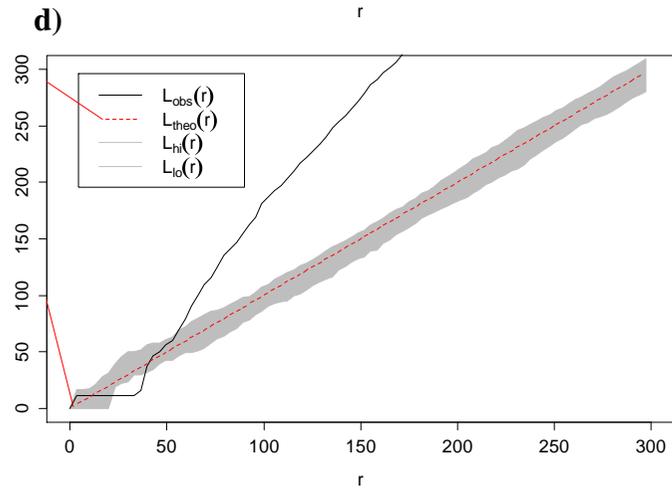
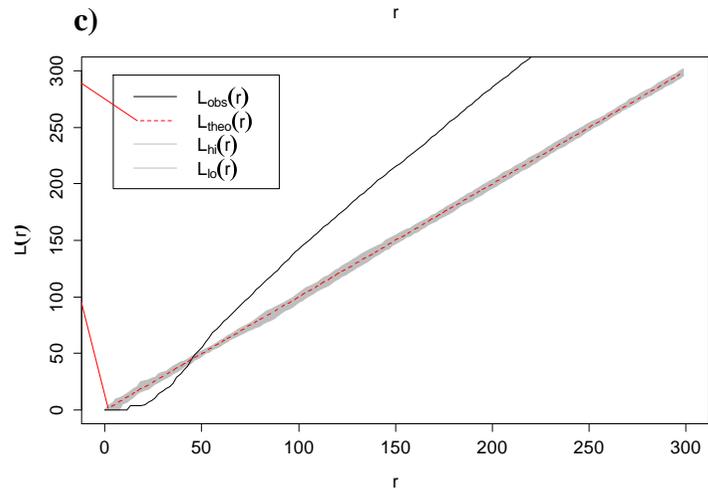
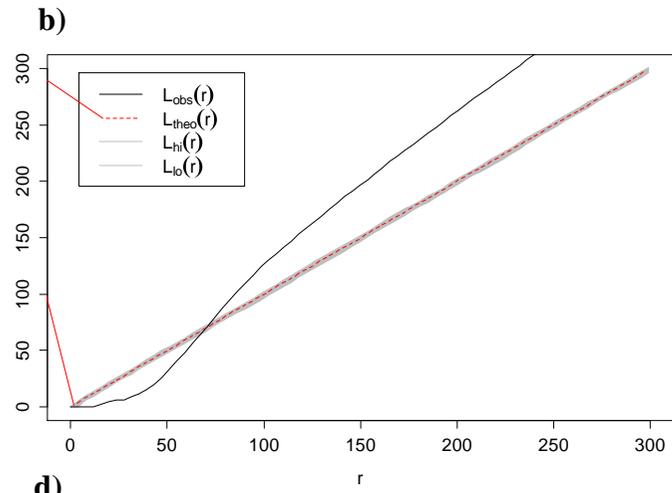
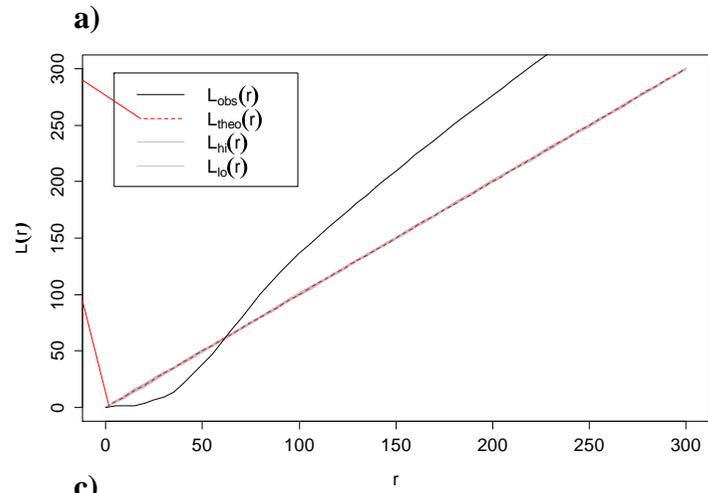
Rank	Form of regression model	AIC _c	No. parameters	Δ_i	w_i
1	% woody cover + Mound height + MAP + Geology + Fire regime + Mound height*MAP + Fire regime*MAP	36.8	8	0.00	0.044
2	% woody cover + Mound height + MAP + Geology + Mound height*MAP	36.9	6	0.05	0.043
3	% woody cover + Mound height + MAP + Mound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

	Mound height*MAP	38.6	7	1.78	0.018
8	% woody cover + Mound height + MAP + Fire regime +				
	Mound height*MAP + Fire regime*MAP	38.7	7	1.86	0.017

Appendix 2: The top regression models for mound height that received considerable empirical support ($\Delta_i < 2$) according to the second order Akaike Information Criterion (AIC_c), as well as the next best performing models ($\Delta_i < 5$), provided for comparative purposes. The top selected model we used in the final analysis is in bold. Δ_i is the difference between a model's AIC_c value and that of the model with the lowest AIC_c ; the Akaike weight w_i is the likelihood of a given model's being the best model in the set. MAP is mean annual precipitation.

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

Appendix 3, Figure S1: Results of Ripley's K -function analysis of termite mounds across each of the broad vegetation types, a) Skukuza, b) Napi, c) Pretoriuskop and d) the gabbro intrusion. $L(r)$ values (a transformation of Ripley's K) are plotted against distance (r) in meters. The dashed line represents the distribution of mounds under complete spatial randomness, while the solid line represents observed mound distribution. Values below the dashed line indicate over-dispersion (even spacing) while values above the dashed line indicate clustering. 95% confidence intervals expected from a random landscape are plotted as the area shaded grey.



Appendix 4, Figure S2: Conditional plot showing how mean annual precipitation (MAP) and fire return period interact to affect termite mound densities. Plots are be read from left to right, bottom to top, starting in the bottom left hand corner and ascending with MAP. On each panel, a linear model is added to aid visual interpretation.

