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# Geology drives the spatial patterning and structure of termite mounds in an African savanna

JUSTICE MUVENGWI,[1,2,]† ANDREW B. DAVIES,[1,3] FRANCESCA PARRINI,[4] AND EDWARD T. F. WITKOWSKI[1]

[1]*Restoration and Conservation Biology Research Group, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa*
[2]*Department of Natural Resources, Bindura University of Science Education, Private Bag 1020, Bindura, Zimbabwe*
[3]*Department of Global Ecology, Carnegie Institution for Science, 260 Panama Street, Stanford, California, USA*
[4]*Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa*

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**Abstract.** Termite mounds perform important roles in savanna ecosystems, generating heterogeneity and influencing ecosystem processes across multiple trophic levels. However, the influence the environment and neighboring termite colonies have on mound spatial patterning and structure is poorly understood, despite the profound implications such dynamics can have on ecosystems. To better understand these drivers, we mapped the spatial distribution and size of active and inactive *Macrotermes* mounds in eight 1-km$^2$ plots on contrasting geologies, nutrient-rich granite and nutrient-poor basalt, in a semi-arid Zimbabwean savanna. Although mound density was not significantly different between basalt (5.5 mounds/ha) and granite (6.1 mounds/ha), termite mound structural attributes and spatial distribution patterns varied greatly between geologies. Mound size distributions differed between the geologies and mounds were 2.6 times taller and 3.9 times wider and had 15 times greater lateral surface area on granite. Subsequently, 6% of the total landscape was covered by mounds on granite compared with only 0.4% on basalt. On granite, large mounds exhibited significant over-dispersion at scales below 30 m, signifying density-dependent thinning. Furthermore, small mounds were clustered around large mounds, likely a result of the budding of new colonies comprising fully fledged castes less vulnerable to competition. In contrast, random patterning was evident on comparably homogenous basalt. Our results demonstrate the powerful influence geological substrate has 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, which maximizes mound production per unit area, and much larger mound sizes here.

**Key words:** Basalt; ecosystem heterogeneity; granite; *Macrotermes;* mark correlation; savanna landscapes.

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† **E-mail:** justicemuvengwi@yahoo.co.uk

## INTRODUCTION

Spatial heterogeneity across environments is a key facilitator of species richness, creating multiple niches that can be occupied by organisms with different specializations (Tilman 1988, 1994) 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 (Pringle et al. 2010, Bonachela et al. 2015). 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).

Termite mounds built by the genus *Macrotermes* (Blattodea: Termitoidae) are a conspicuous feature of African savanna ecosystems (Levick et al. 2010*a*) 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 (Moe et al. 2009, Davies et al. 2016*a*), 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. 2010*b*). 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).

When viewed in the dimension of self-organization, exploitation and/or interference competition between colonies plays a major role in shaping termite mound distribution in space (Korb and Linsenmair 2001, Pringle et al. 2010, Bourguignon et al. 2011), whereas over time, mound succession governed by extinction and re-colonization is more important (Darlington 2005). 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 over-dispersion among large mounds, and clustering among small mounds (Korb and Linsenmair 2001, Grohmann et al. 2010). 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). The mechanisms driving mound densities and distributions are therefore unclear, and further research is required.

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

Granitic landscapes are generally undulating, leading to catenal sequences with seeplines, midslopes, and crests (Levick et al. 2010*a*, Khomo et al. 2011). 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. 2010*a*, Davies et al. 2014). 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 with granite (Scholes 1990, Grant and Scholes 2006) as a result of their soil forming from rocks rich in basic cations, which when weathered produce fine-textured fertile alkaline soils that are generally black in color 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 coarse-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. 2010*a*), with too little limiting nest construction and too much causing water inundation, precluding nest construction (Jouquet et al. 2004, Levick et al. 2010*a*).

Despite the increasingly recognized 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-neighbor analysis, which mainly detects competition that leads to size reduction (Schuurman and Dangerfield 1997, Korb and Linsenmair 2001, Pomeroy 2005). Here, we complement the nearest-neighbor analysis with second-order spatial statistics capable of detecting mortality that is dependent on competition, such as Ripley's $K$-function and pair correlation function $g(r)$. We hypothesized that (1) 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 with basalt, (2) overall inter-mound distances are shorter on basalt compared with granite because of the undulating nature of the terrain on granite, with mounds expected to be absent from low-lying areas (Levick et al. 2010*a*, Davies et al. 2014), (3) colony death is a spatially random process at any given point in time on both geological substrates, and (4) 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°00′–22°15′ S, 30°15′–32°31′ E). Mean annual rainfall at the study site averages 466 mm, and mean monthly maximum temperatures range between 26°C in July and 30°C in January, whereas mean monthly minimum temperatures range between 9°C in June and 24°C 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. 2018). Herbaceous biomass production is higher on granite compared with basalt.

### 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 two hundred 100-ha ($1 \times 1$ 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 ±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 (Korb and Linsenmair 2001, Grohmann et al. 2010). If no repairs had occurred, the mound was classified as inactive. Mounds were further divided into large and small, with those having diameters >2.5 regarded as large on basalt and 10.8 m on granite (Appendix S1: Fig. S1).

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 (Appendix S1: Fig. S2). The longest diameter of the mound (d1) and the diameter perpendicular to d1 (d2) were measured using a tape measure (Appendix S1: Fig. S2). The edge of the mound was determined as the zone around the skirt of the termite mound where a change in soil color was visible or where changes in slope were noticeable and no eroded soil evident (Arshad 1982). Mounds were modeled 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. 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. 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-neighbor 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 (Meyer et al. 1999, Korb and Linsenmair 2001, 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). 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 neighborhood 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

$$g(r) = K'(r)/2\pi r, \quad \text{where} \quad K'(r) = dK(r)/dr \tag{1}$$

This function is defined as the expected density of points at a given distance $r$ from an arbitrary point divided by the intensity $\lambda$ of the pattern

(Stoyan and Stoyan 1994, Getzin et al. 2006). Consequently, the pair correlation function was interpreted as follows: $g(r) = 1$ random, $g(r) > 1$ aggregated, and $g(r) < 1$ regular distribution. For the univariate Ripley's K-function and the pair correlation function, analyses were performed for subplots sampled within the 1-km$^2$ plots which excluded areas that were not sampled (Fig. 1a–c, e, g).

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 pattern 1 (active mounds), divided by the intensity $\lambda_2$ of pattern 2 (Wiegand and Moloney 2004). The bivariate $g(r)$ statistic is defined as

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

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

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

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 (Ripley 1981, Diggle 2003), and was defined as

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

where $n_1$ 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 neighboring mound. $I_r(u_{ij})$ is an indicator function, being equal to 1 if $u_{ij} \leqslant r$, 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 centered 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

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

The distribution of inactive mounds in relation to active mounds was investigated using a random labeling model (Bourguignon et al. 2011). Under random labeling, $g$-functions are invariant, and therefore, $g_{12}(r) = g_{21}(r) = g_{11}(r) = g_{22}(r)$. Any departure from random labeling is evaluated by pairwise 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 (Getzin et al. 2006, Bourguignon et al. 2011).

*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 (Gatrell et al. 1996, Diggle et al. 2007), 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 (Appendix S1: Fig. S1). 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

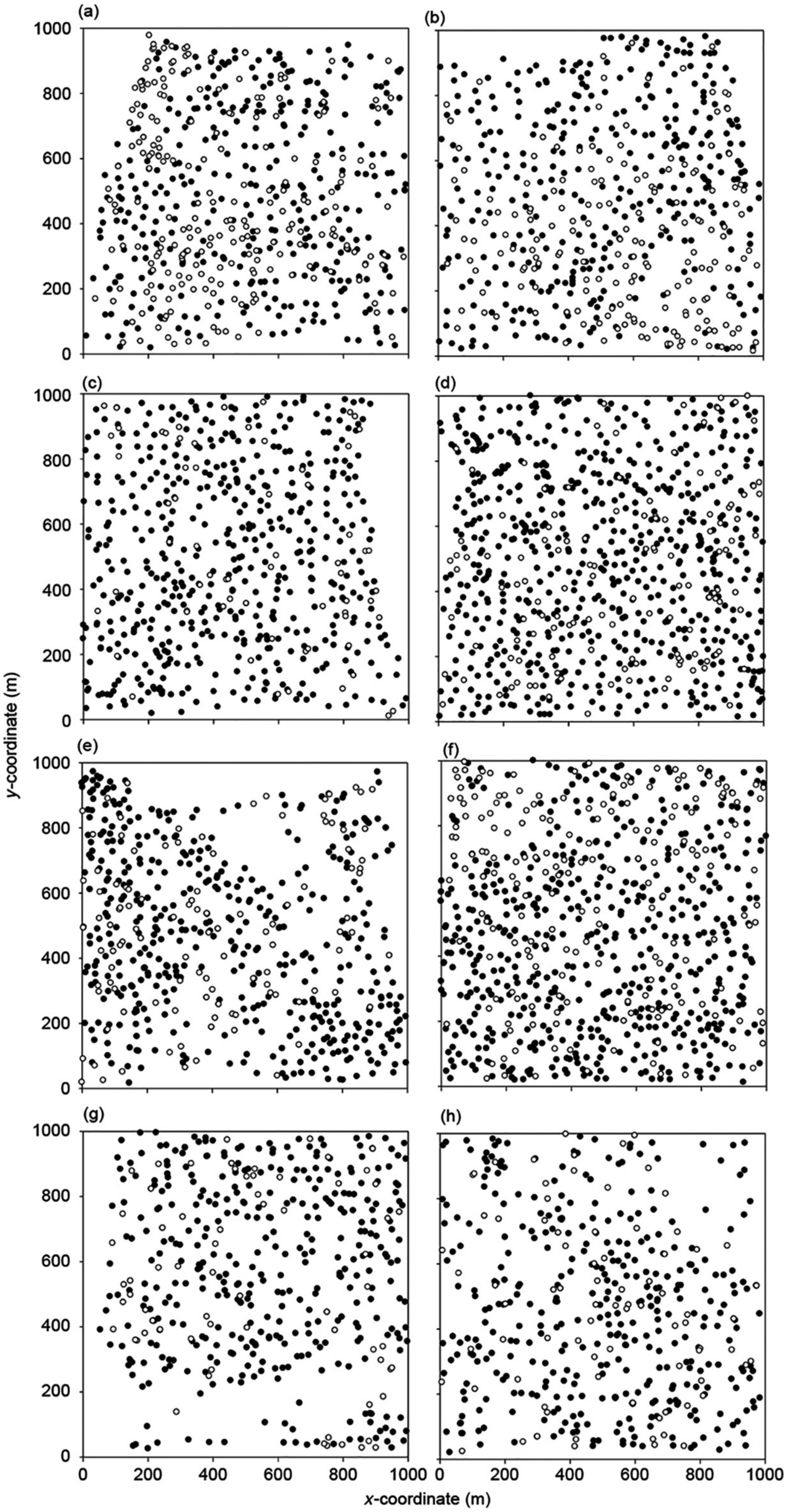

Fig. 1. Maps of termite mound locations on the different plots on granite (a–d) and basalt (e–h). Black circles represent active mounds and open circles inactive mounds.

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. 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 $g_{21}(r) - g_{22}(r) \ll 0$. Departure from the Poisson null model of CSR for all summary functions was evaluated using 5th lowest and 5th highest values of 999 Monte Carlo simulations to generate ~99% simulation envelopes.

*Mound spatial correlation.*—A mark correlation function (MCF) was applied to test for significant 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 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 $\mu$, 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 (Getzin et al. 2008, Grohmann et al. 2010). Departure from independent marking null model, which randomly shuffles the marks (diameters) between pairs of termite mounds, was evaluated using 5th lowest and 5th highest values of 999 Monte Carlo simulations to generate ~99% simulation envelopes.

*Nearest-neighbor analysis.*—Density-dependent competition between termite colonies (mounds) was assessed using the nearest-neighbor analysis (Shackleton 2002). We established the correlation between the combined diameters of the focal mound and its four nearest neighbors and the sum of the distances of the four nearest neighbors 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 ($6.07 \pm 0.50$ ha$^{-1}$) and basalt ($5.46 \pm 0.69$ ha$^{-1}$; $t = 0.710$, df = 5.50, $P = 0.507$) at the landscape scale (Fig. 1), but the mound height and diameter size–frequency distributions 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 mound height and diameter 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 four times larger in diameter (granite: 9.95 ± 0.11 m, basalt: 2.58 ± 0.03 m). When modeled 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). 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

Table 1. Summary of the univariate ($L(r)$ and $g(r)$) spatial distribution of active and inactive mounds on granite and basalt geological substrates.

| Geology/Plot | $L(r)$ | $g(r)$ |
|---|---|---|
| *Granite* | | |
| plot$_{G1}$ | Ra(0–40), Ag(40–400) | Ra(0–40), (220–400), Ag(40–220) |
| plot$_{G2}$ | Re(0–30), Ag(150–260), Ra(30–150), (260–450) | Re(0–30), Ra(30–450) |
| plot$_{G3}$ | Re(0–30), Ra(30–440) | Re(0–10), Ra(10–440) |
| 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(20–430), Ra(0–20), (430–450) | Ag(10–210), Ra(0–10), (210–450) |
| plot$_{B2}$ | Ag(30–500), Ra(0–30) | Ag(30–310), Ra(0–30), (310–500) |
| plot$_{B3}$ | Ag(40–330), Ra(0–40), (330–450) | Ag(10–140), Ra(0–10), (140–450) |
| plot$_{B4}$ | Ag(30–500), Ra(0–30) | Ag(20–250), Ra(0–20), (250–500) |

*Notes:* 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.

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 (0–30 m) on granite, signifying intense intra-specific competition between colonies at these spatial scales (Table 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 1). On basalt, both the $L(r)$ and $g(r)$ functions detected only two patterns, random and aggregation, with termite colonies exhibiting a random distribution at spatial scales of <30 m and >210 m in all plots other than plot$_{B3}$ (Table 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 2, Fig. 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 2).

Table 2. Summary of the bivariate ($L_{12}(r)$ and $g_{12}(r)$) spatial pattern of active and inactive mounds on granite and basalt geological substrates.

| 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) |

*Notes:* 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.

### Random labeling—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]; Figs. 1a–d, 2a–d). On basalt, inactive mounds were generally spatially randomly distributed in three plots (Fig. 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. 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 and 40 m on granite (Figs. 3a–d, inserts and 1a–d). This indicates that small termite colonies were tolerated around large ones. 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. 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 labeling across all scales (Fig. 3b, main figure). On basalt, small mounds departed slightly from the null model of random labeling 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. 3e–g, inserts). However, when all mounds (both active and inactive) were considered on granite, spatially homogeneous mingling among mound sizes was observed, indicating that both cases, small mounds and controls (large mounds), followed the same overall pattern (Appendix S1: Fig. S3a–d). Unlike when only active mounds were considered, there was minor clustering of

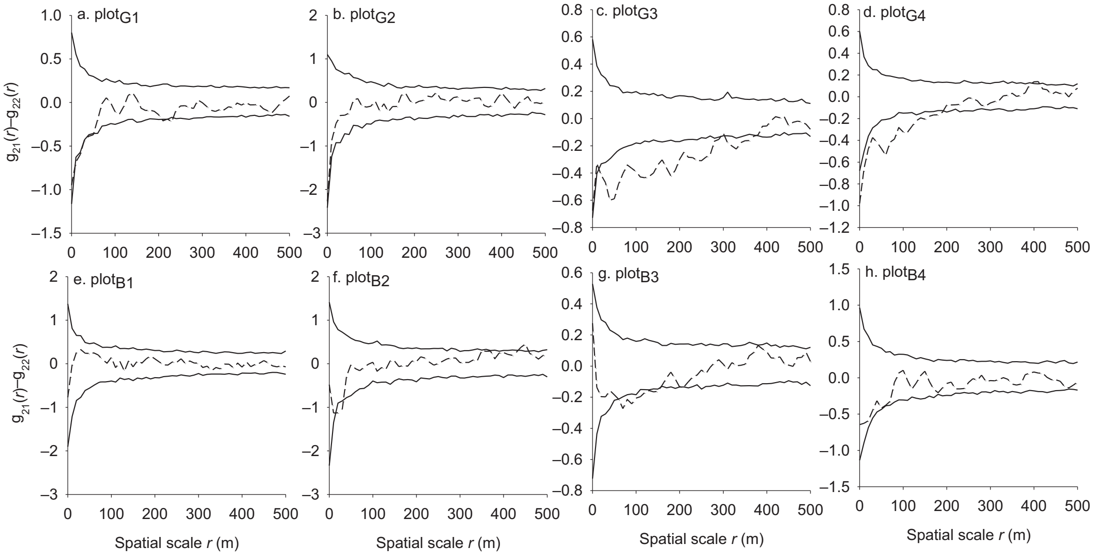

Fig. 2. Bivariate random labeling ($g_{21} - g_{22}(r)$) used to investigate whether colony death was a random process among mounds in plots located on granite (a–d) and basalt (e–h) geologic substrates. Under the null model random labeling, the observed pattern (dark broken line), $g_{21}(r) - g_{22}(r) = 0$ ($x$-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. Departure from the Poisson null model was evaluated using 5th lowest and 5th highest values of 999 Monte Carlo simulations to generate ~99% simulation envelopes, solid lines.

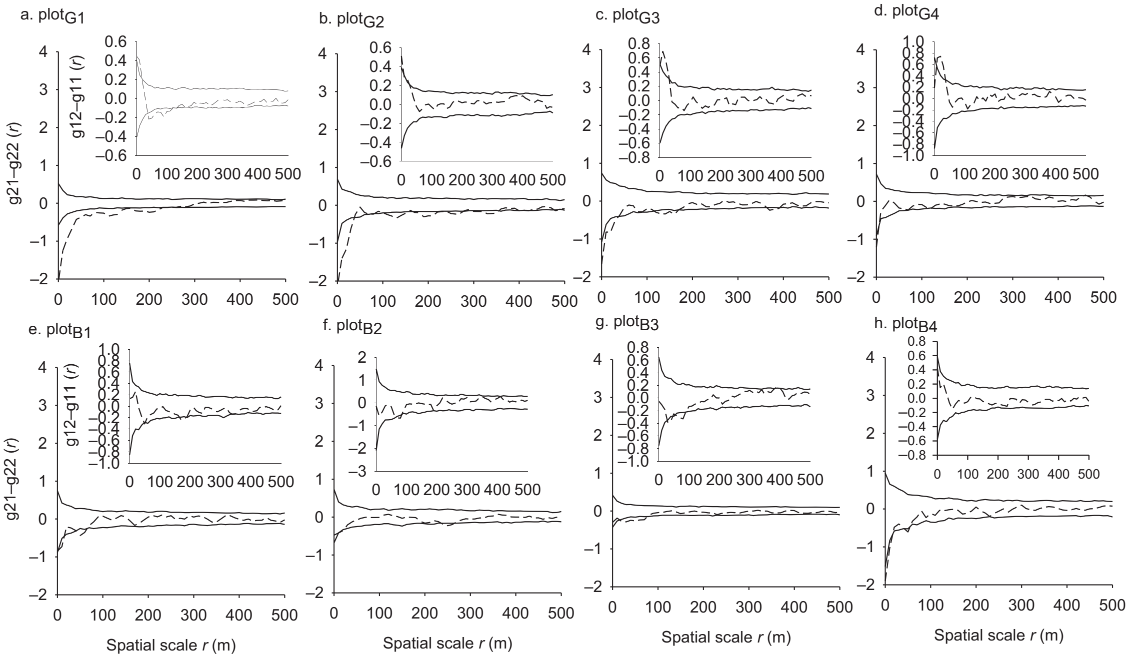

Fig. 3. Spatial distributions of large and small mounds analyzed with a case–control technique. The large mounds represent the control pattern (pattern 1), and the small mounds represent the cases (pattern 2). The small insert figures ($g_{12}(r) - g_{11}(r)$; figure above the main figures a–h) evaluate 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 broken line represents the observed pattern and the solid lines 99% confidence limits.

small mounds that was independent of large mounds. When all mounds were considered (i.e., both active and inactive) on basalt, there was no extra clustering of small mounds independent of large mounds, indicating that there was mingling between the two size classes (Appendix S1: Fig. S3e–h).

### *Mound spatial correlation*

The mark correlation function $k_{mm}(r)$ indicated that the sizes of the diameters of large mounds on granite were negatively correlated at spatial scales between 0 and 20 m across three out of four plots (Fig. 4b–d). In plot$_{G4}$, a weak negative correlation was further shown at a scale between 250 and 480 m (Fig. 4d). However, there was a significant positive correlation of large mounds between 40 and 80 m in plot$_{G3}$ on granite (Fig. 4c). In plot$_{B1}$ and plot$_{B3}$, significant positive correlations were demonstrated at spatial scales of 50–100 and 20–60 m, respectively, signifying a lack of competition at these spatial scales (Fig. 4e, g). However, a weak marginal negative correlation was experienced across almost all scales in plot$_{B4}$ (Fig. 4h).

### *Nearest neighbor*

There was a significant positive correlation between the combined sum of mound diameters of the focal mound and its four nearest neighbors and the sum of the four distances from the focal mound for all the plots on granite and basalt (Fig. 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-neighbor 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. 5). However, mean nearest-

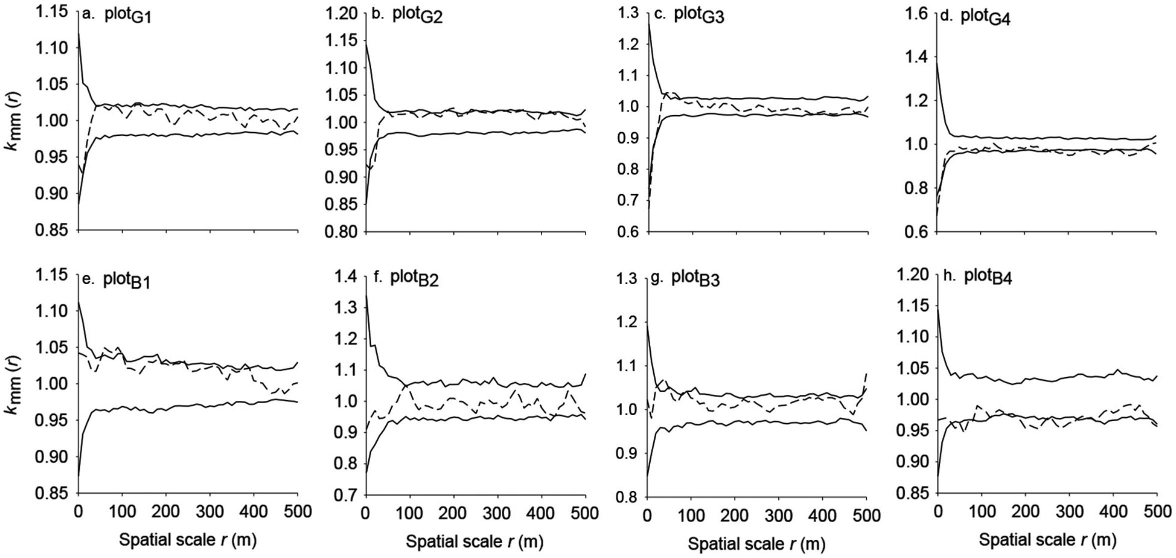

Fig. 4. The mark correlation function $k_{mm}(r)$ for large mounds on granite (a–d) and basalt (e–h), with diameters >9 and 2.5 m, respectively. Marks are treated independently, positively or negatively correlated at distance $r$ if $k_{mm}(r) = 1$, $k_{mm}(r) > 1$, or $k_{mm}(r) < 1$, respectively. A negative correlation is considered significant if $k_{mm}(r)$ (dark broken line) falls below the 99% confidence limits (solid lines).

neighbor 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 geologic substrate can have a powerful influence on the spatial distribution and structure of termite mounds, making an important contribution 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 with the smaller, randomly distributed mounds on basalt. Furthermore, within the mound aggregations on granite, termite mounds were over-dispersed compared with 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.

### Termite mound densities

The lack of a strong geologic 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; Meyer et al. 1999, Davies et al. 2014, Mujinya et al. 2014). However, functionally similar *Odontotermes obesus* had similar nest densities in ferralsol and vertisol soils (Jouquet et al. 2015), suggesting that geologic effects on mound densities can be variable. 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 (KNP), 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. 2010*a*, Davies et al. 2014, 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 (Levick et al. 2010*a*, Davies et al. 2014).

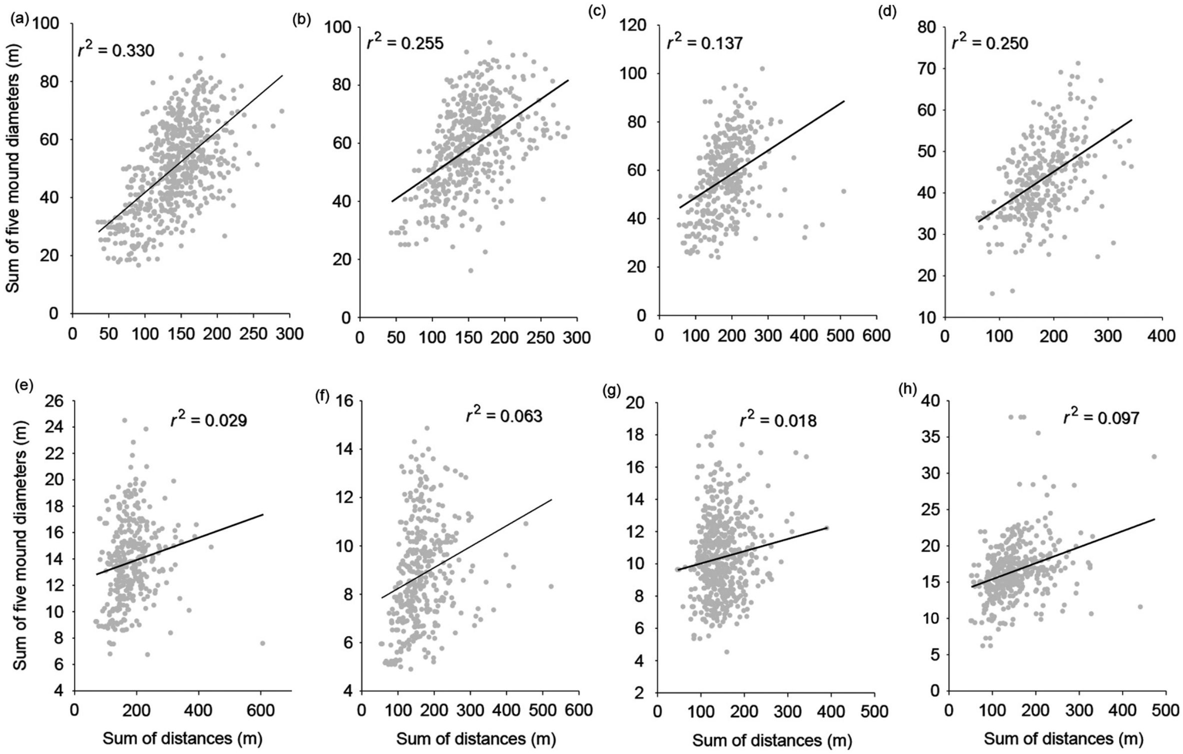

Fig. 5. Nearest-neighbor analysis showing the correlation between the sum of the distances to the four nearest mounds from the focal mound and the sum of the mound diameters of the focal mound and its four nearest neighbors on granite (a–d) and basalt (e–h). The dark line represents the slope of the regression line when the two variables have been converted to *z*-scores.

Given the comprehensive field surveys employed in our study, the probability of detecting small mounds was likely higher compared with remote sensing studies. However, when excluding mounds below 0.5 m in height from our results, mound densities were still considerably higher on granite (5 $ha^{-1}$) and basalt (2 $ha^{-1}$) than recorded previously in studies that focused on *Macrotermes* species on similar geologies. Nevertheless, although small mounds are of less ecological significance relative to larger ones (Joseph et al. 2013), mounds generally increase in size with age (Bourguignon et al. 2011) and the future ecological impacts of small mounds should not be underestimated, making it important to understand their spatial patterns. Remote sensing does, however, enable the surveying of much larger areas, yielding important insights into broadscale patterns of larger mounds, and should also not be discounted (Davies et al. 2014, Mujinya et al. 2014).

Although at very large spatial scales (when remote sensing is applied) there is high inclusion of sparsely populated lower catenal sections, potentially resulting in overall lower mound densities (Davies et al. 2014), we recorded mounds in all sections of the catena. Rainfall in our study site was markedly lower than southern KNP where mounds were absent from low-lying regions that become water inundated (Levick et al. 2010*a*, Davies et al. 2014). Inundation might therefore be less of a challenge for mound construction in lowlands in our study site, as was also recorded in low rainfall regions of northern KNP (Levick et al. 2010*a*), enabling termite colonies to establish closer to drainage lines and resulting in higher mound densities compared with areas of higher rainfall. Furthermore, our recorded mound densities are comparable to studies from further north in Africa that used similar field-based methods (Trapnell et al. 1976, Pomeroy 1977, Lepage 1984). Termite diversity decreases with latitude (Eggleton 2000), and Gonarezhou is warmer than KNP, potentially providing better conditions for termite colony growth and establishment, and therefore higher mound densities.

### *Mound structural differences*

Mound height (2.6 times), diameter (3.9 times), and lateral surface area (15 times) were significantly larger on granite than basalt, demonstrating a strong influence of geology on mound structure. The swelling and shrinking characteristics of clays on basalt make them unstable, likely limiting nest size due to increased mound degradation (Jouquet et al. 2015). Size differences in mounds between basalt and granite could also be attributed to too much clay on basalt that lowers maximum colony size because of slow soil permeability and more frequent periods of inundation and hence termite colonies being unable to grow as large as they do on granite, leading to mounds being smaller in both height and diameter (Levick et al. 2010*a*).

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 were also larger (in height and diameter) than inactive mounds on granite. Inactive mounds are not maintained and will erode without repair, thereby decreasing in size (Korb and Linsenmair 2001), which is exacerbated on the steeper catenal slopes on granite (Khomo et al. 2011). However, although active mounds on basalt were taller, they were smaller in diameter than inactive mounds. In similar ways to granite, differences in height could 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 (hillocks) around the mound skirt given the strikingly flat terrain on basalt (Jouquet et al. 2015).

### *Spatial distribution of mounds*

Over-dispersion was generally recorded at small spatial scales on granite, whereas no such patterning was detected on basalt at any spatial scale. Nearest-neighbor analysis confirmed some size reduction competition on granite even though mean NN distance was not significantly different between the geologies, which may indicate that the observed over-dispersion could emanate from competition. 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 could lead to colonies being able to occupy any space. In contrast, environmental heterogeneity on granite, due to catenal sequencing, leads to the concentration of mounds on crests (Davies et al. 2014), 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 similar food resources, with workers and soldiers demonstrating both inter- and intra-specific competition, although intra-specific competition is more evident (Jmhasly and Leuthold 1999). Competition between termite colonies could therefore be an important driver of mound distributions. However, caution is required when interpreting these potential mechanisms because multiple mechanisms could act in concert to determine patterns. Moreover, competition can lead to several different distribution patterns (Pielou 1960, Levings and Adams 1984, Ryti and Case 1992). In addition, higher vegetation cover on basalt could lead to the random distribution of mounds, unlike on granite where vegetation is more sparse (Muvengwi et al. 2017) and is sometimes clustered, which could lead to clustering of mounds at small scales, although it is also possible that the clustering of mounds results in the observed clustering of vegetation (Bonachela et al. 2015).

Inactive mounds (resulting from colony death or abandonment) displayed different distribution patterns relative to active mounds on the two geologies: They were randomly spaced on basalt and clustered on granite. Clustering on granite suggests the influence of local factors on colony death, such as disease, water inundation (Levick et al. 2010*a*, Bourguignon et al.

2011), or aardvark (*Orycteropus afer*) attack (that was more apparent on granite, J. Muvengwi, *personnel observations*). Although aardvark did attack mounds on basalt, there were clear signs of failure, possibly due to these mound soils (built primarily by *M. ukuzii*) being harder. 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 on basalt likely resulted from internal causes, such as aging and/or hostile inter-colony competition, resulting in a random distribution of inactive mounds.

### *Density-dependent competition*

There were clear signs of density-dependent thinning on granite where fewer large mounds were present around other large mounds, compared with small mounds around large mounds. This indicates that as mounds grow larger, they become over-dispersed, and also the mark correlation function partly indicates negative size correlation of the diameters up to small scales of 20 m. The over-dispersion of large mounds at small spatial scales can be attributed 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. There is also a possibility that small mound-building colonies are able to survive in the vicinity of large ones, for example, if the large colony is stressed by interspecific competition (Grohmann et al. 2010). Furthermore, competition from other termite species that are not part of the *Macrotermes* guild could influence the ultimate spatial patterning of *Macrotermes* mounds.

Another plausible explanation is that neighboring 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. Colony migration is also a possibility, 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 previously occupied by inactive mounds, within which young colonies can establish at a particular post-mortality age. However, when all mounds were considered (i.e., both active and inactive), small and large mounds were spatially homogeneous in distribution. Large mounds persist for a long time in the landscape (Bourguignon et al. 2011) and could have exerted density effects in the past that still influence current distributions. On basalt, large and small colonies generally exploited the environment in a similar manner, as reflected by their random distribution that was similarly reflected in the distribution of inactive mounds on basalt, with large and small mounds exploiting the environment in similar ways.

### *Implications for savanna ecosystems*

From our results, we infer that geology influences termite mound structure and spatial patterning, showing that the driving mechanisms are closely related to geology across savanna landscapes. Therefore, the functional roles of termite mounds are unlikely to be equal across landscapes, with mounds on granite predicted to have more significant effects on ecosystem functioning than on basalt for several reasons. First, they are over-dispersed at small spatial scales (0–30 m) on granite, but not basalt, which has important ecosystem consequences because over-dispersion leads to mounds having a greater positive effect on consumers across trophic levels by reducing the average distance from any point in the landscape to a mound (Pringle et al. 2010). Second, mounds on granite are larger than on basalt and cover 15 times more surface area, leading to stronger effects on plant heterogeneity and growth (Joseph et al. 2013). Finally, granites are nutrient-poor relative to basalts, which means that mounds will likely be more important as generators of spatial heterogeneity on granite because of stronger differences between mound and matrix soil nutrients here (Grant and Scholes 2006, Muvengwi et al. 2017). Our study contributes to the increasing number of studies demonstrating variable effects of termite mounds on ecosystem properties (Muvengwi et al. 2013, O'Connor 2013, Davies et al. 2016*b*, Erpenbach et al. 2017), complementing these recent findings by demonstrating that not only do the ecological effects of mounds vary with landscape context, but so do the drivers determining their distribution and structure, which will greatly influence the potential of mounds to affect ecosystems.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2148/full