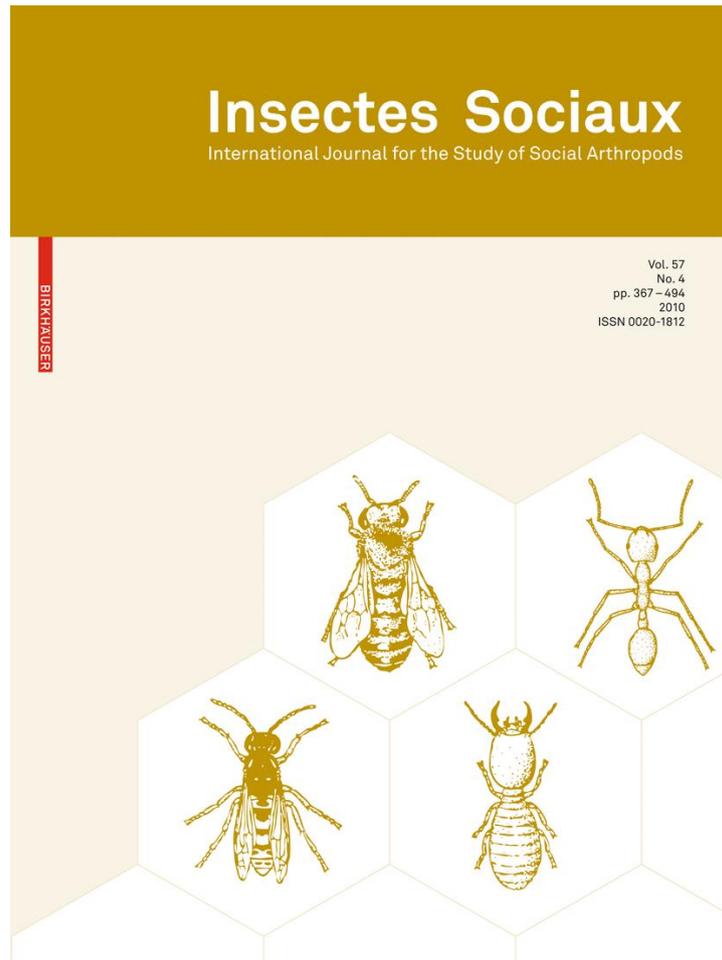


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Multi-scale pattern analysis of a mound-building termite species

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Abstract Termite mounds are a widespread feature in most African savannas. These structures exhibit high nutrient contents and often host a special vegetation composition. In this study, we analysed mound distribution patterns of a fungus-growing termite species, *Macrotermes michaelseni*, an important ecosystem engineer in the savannas of Namibia. Inhabited mounds taller than 0.7 m were regularly distributed. We view this pattern as a result of intraspecific competition. The heights of mounds taller than 0.7 m were correlated positively with their distance, such that mounds closer together, i.e. up to inter-mound distances of approximately 50 m, tended to be smaller than average. This indicates that intraspecific competition for foraging areas controls mound distribution pattern and colony size. Differences between mound heights increased on the spatial scale up to inter-mound distances of 80 m. We assume that the foundation of new colonies is only possible in unoccupied patches. In such patches, young colonies are able to

occur close together as they have a relatively low foraging demand and therefore a low spatial demand. In contrast, their critical distance to taller colonies with higher foraging demands is rather large, which leads to the observed increasing difference of mound heights with increasing distances between them.

Keywords Isoptera · Namibia · Point pattern · Savanna · Second-order statistics

Introduction

The phenomenon of scale is one of the most discussed topics in the ecological literature. This is due to the fact that most ecological patterns and their related processes as well as their perceptibility vary with the observational scale (Dungan et al., 2002; Haines-Young, 2005). Patterns are not only generated by certain ecosystem processes, but each pattern also has retroactive consequences onto the processes of its ecosystem (Levin, 1992).

The arrangement of objects that are irregularly or randomly distributed in the plane can be described by mathematical models, the so-called spatial point processes (e.g., Illian et al., 2008). These models help to deduce rules of causality from the observed distribution. Many ecological studies have dealt with dispersion patterns of plants (see Perry et al., 2006; Wiegand et al., 2007), but point patterns are also common for analysing the intra- and inter-specific behaviour of animals. Burrows or mounds are often used as spatial reference for the distribution of specimens or colonies of the target species. For example, Fisher et al. (2007) investigated the spatial clustering of burrows of a ground-living owl, Schooley and Wiens (2001) analysed

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kangaroo rat mounds in New Mexico and Crist and Wiens (1996) deduced, from the distribution of ant colonies, implications for ecosystem processes.

Globally, arid and semi-arid regions comprise more than 25% of the terrestrial surface and are inhabited by almost 30% of the human population (Millennium Ecosystem Assessment, 2005). In this biome, termites are most important for ecosystem functioning (Wood and Sands, 1978; Whitford, 1991). The fungus-growing Macrotermitinae play an especially prominent role across a range of spatial scales, e.g. from the modification of local water infiltration rates to the creation of regional landscape mosaics (Dangerfield et al., 1998). They enhance decomposition processes and alter nutrient content, texture and hydrological properties of soils through their foraging and building activities. Mounds built by *Macrotermes* species above their nests are common in most African savannas. These termitaria supply a critical resource of scarce micro-nutrients to wildlife (Mills et al., 2009) and host a special vegetation composition (Moe et al., 2009).

So far, studies on the spatial distribution patterns of *Macrotermes* mounds have yielded contradictory results. For example, an aggregation of mounds was found by Meyer et al. (1999), whereas a random pattern was determined by Collins (1981). Most studies have revealed a regularity of mound distribution and attributed this to intra- and inter-specific competition (Wood and Lee, 1971; Lepage, 1984; Levings and Adams, 1984; Pomeroy, 2005). Concerning mounds of *Macrotermes michaelseni* (Sjöstedt, 1914) in eastern Africa, regular distributions were described by Darlington (1982), Kaib et al. (1997) and Pomeroy (2005). However, in southern Africa, only two studies considered the spatial distribution of *M. michaelseni* and neither of them found significant deviations from a random pattern for active mounds (Schuurman and Dangerfield, 1997; Turner, 2000).

In most cases, only the distance to the nearest neighbour was analysed, not taking into account that further neighbours might also play a role in competition pressure. However, more complete information, namely on the effects of multiple neighbours, can be derived by methods that use second-order characteristics such as Ripley's *K*-function, the pair correlation function and related techniques (Illian et al., 2008). They offer the great advantage of providing information on various scales, and have been applied successfully in different fields of ecology. Concerning termite mounds, corresponding analyses were done by Spain et al. (1986) and Barot et al. (1999) for Australian and West African species, respectively, both finding regular distributions. Fisher (1993) revealed that termite mounds in Brazil, which were randomly distributed according to Clark-Evans nearest neighbour analyses, showed a clustered distribution with a minimum spacing between close

neighbours when applying second-order statistics. However, no comparable data are available for *M. michaelseni*.

In this study, we analysed the spatial distribution patterns of termite mounds built by *M. michaelseni* in a multi-scale approach based on second-order characteristics. Mound height was used as a surrogate for colony size, based upon findings that for this species, mound height is correlated positively with colony size (Darlington and Dransfield, 1987) as well as with the number of eggs (Kaib et al., 2001).

First, the distribution patterns of different mound categories defined by their height and status (inhabited vs. uninhabited) were investigated. Although only random patterns have been reported for *M. michaelseni* mounds in southern Africa to date, a regular distribution of inhabited mounds was expected as documented for many other *Macrotermes* species. Indeed, if intraspecific competition forces mound patterns, it should regulate the size and density of termite colonies. Hence, we secondly hypothesised that the height of a mound increases with its distance to further mounds. It is known from the literature that new mounds appear in certain years only. As we assume that such small, young mounds can occur close together (see second hypothesis), we thirdly test the hypothesis that the height differences of mounds increase with increasing distance between them.

Materials and methods

Mound mapping

Fieldwork was carried out in a central Namibian thorn-bush savanna (21.51°S, 16.73°E). The average annual rainfall of approximately 300–350 mm can vary considerably from year to year and occurs mainly in summer between November and May. Mean annual temperature is around 21°C, with an average maximum temperature of roughly 35°C in December, dropping to an average minimum temperature of 5°C during July (Mendelsohn et al., 2003).

Within a square site of 1 km², the position of each termite mound built by *Macrotermes michaelseni* was located at the beginning of the 2007 dry season, and its position was recorded using a GPS (Garmin III plus, accuracy ~3 m). Mounds were defined as being “inhabited” or “alive” when (1) *M. michaelseni* individuals were seen, (2) fresh mound structures built by this species were present, or (3) a hole drilled into the mound was repaired by *M. michaelseni* within 1 day. Otherwise, mounds were categorised as “uninhabited” or “dead”; this category also included almost entirely eroded mounds.

The total mound height and the basal diameter (both excluding the outwash pediment) were recorded. The bases

of the mounds were generally asymmetrical, and were therefore measured in the direction which seemed to best represent the average diameter. Mound height and mound diameter were correlated significantly (Kendall's rank correlation, $\tau = 0.53$, $p < 0.001$, $n = 444$). We used mound height for the analysis due to the asymmetry of the bases. Inhabited mounds were divided into three height classes: A1 (0–0.7 m), A2 (0.7–2.0 m) and A3 (>2.0 m). The reasons for this classification are explained in “Discussion”. Mounds larger than 0.7 m showed a similar pattern, and were merged to the category $A2 \cup A3$ for most analyses. There were no obvious trends in the density or height of mounds or the association between mounds within the study site, so that the requirement of site homogeneity for the chosen test statistics was met.

General distribution pattern

The general spatial distribution of mounds was analysed using the pair correlation function (pcf), which is known to be a valuable summary characteristic for homogeneous multi-scale point patterns (e.g., Perry et al., 2006). The function is related to the probability of finding a point at distance r from an arbitrary point of the pattern (see Illian et al., 2008 for further interpretation). Furthermore, there is a close relationship to the well-known K -function. With λ being the point density and $K(r)$ being Ripley's K -function, $\lambda K(r)$ reflects the mean number of points in a disc of radius r , centred at the typical point of the pattern. The pair correlation function $g(r)$ is given by the derivative of $K(r)$ (Wiegand and Moloney, 2004; Illian et al., 2008):

$$g(r) = \frac{K'(r)}{2\pi r} \quad \text{for } r \geq 0. \quad (1)$$

The shape of the pcf can be interpreted as follows: For a random point pattern, $g(r)$ is equal to 1. For a clustered pattern, $g(r)$ has values larger than 1 for small r and converges towards 1 with increasing values of r . The cluster diameter can be estimated from that value of r where $g(r)$ first approaches 1. Regular distributions result in $g(r) = 0$ for small r values, while for larger r , values greater than 1 and significant fluctuations around 1 are possible (see Fig. 1 and Illian et al., 2008).

The pcf was estimated using the method recommended in Illian et al. (2008); for edge correction, the translation method was applied. The point patterns were tested for significant ($\alpha = 0.05$) deviations from complete spatial randomness using the L -test (Chiu, 2007; Illian et al., 2008). This test is considered as a powerful test, and can be easily applied if suitable software is available. It considers the maximum absolute deviation of the empirical L -function from the theoretical L -function of the Poisson process. If this deviation is larger than a critical value, which

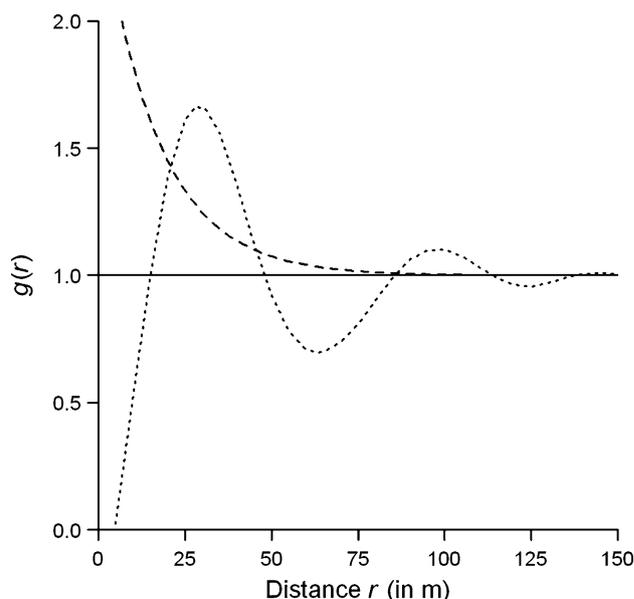


Fig. 1 Idealised theoretical pair correlation function for random (solid line), clustered (dashed line) and regular spatial pattern (dotted line)

depends on sampling area and sample size, the hypothesis of complete spatial randomness is rejected.

Spatial relationship between small and large inhabited mounds

Small mounds may show a different type of distribution compared to larger ones (in particular, clumped versus regular distributions, see Korb and Linsenmair, 2001a), and were included in this study. They are difficult to detect in the field, especially in dense vegetation. Therefore, small mounds were excluded in some studies on mound patterns (e.g. Pomeroy, 1983a). According to Pomeroy (1983b), the proportion of inhabited *Macrotermes* mounds, particularly those smaller than 0.5 m, can vary strongly between different years.

For analysing the relationship between small and large mounds, the mark connection function $p_{ij}(r)$ was applied, with the respective group numbers 1 (A1) and 2 (A2 \cup A3) as marks. This function was chosen because it is not cumulative as is $L_{ij}(r)$, and it does not depend on the number of mounds at a certain distance r' as does $g_{ij}(r)$. According to Stoyan and Stoyan (1994) and Illian et al. (2008), $p_{ij}(r)$ can be interpreted as the probability that two mounds at distance r have marks i and j ($i, j = 1, 2$). The behaviour of the mark connection function provides information on the association of marked points in point patterns (here: A1 vs. A2 \cup A3). High values of $p_{ij}(r)$, compared to values of the mark connection function in the case of independence, indicate that points in pairs of points

with distance r are frequently of different types. According to Illian et al. (2008), in the case of independence

$$p_{ij}(r) = 2p_i p_j \quad (2)$$

with

$$p_i = \frac{\lambda_i}{\lambda} \quad (3)$$

where λ_i denotes the density of points with marks i , and λ is the density of all points irrespective of their mark.

It was tested whether the compared groups are marked independently (random labelling) using the method of random reallocation. In this procedure, the points are kept fixed, while the marks (group numbers) of these points are randomly permuted. Pointwise envelopes for 99 simulations were obtained, which can be interpreted as being appropriate for an error probability of $\alpha = 0.01$ (Illian et al., 2008). The simulations yielded estimates of the multivariate L -function $L_{ij}(r)$, which is related to the number of points of type j in a disc of radius r centred at an arbitrary point of type i . If the empirical L_{12} -function leaves the envelopes ($L_{12,\min}$ and $L_{12,\max}$), the hypothesis of random marking is rejected.

In the following analyses, only inhabited mounds larger than 0.7 m ($A2 \cup A3$) were considered.

Correlation of mound height with distance to further mounds

We applied the mark correlation function $k_{mm}(r)$ with mound height as the continuous mark to mounds larger than 0.7 m ($A2 \cup A3$), in order to analyse whether the heights of termite mounds are correlated dependent on their distance to others, indicating intraspecific competition. Values of $k_{mm}(r) < 1$ occur if the product of the heights of two mounds r length units apart tends to be smaller than the square of the overall mark mean μ . If mound pairs with distance r are larger than average, in terms of the product of their heights, then $k_{mm}(r) > 1$. After Illian et al. (2008), $k_{mm}(r)$ is defined as:

$$k_{mm}(r) = \frac{c_{mm}(r)}{\mu^2} \quad \text{for } r > 0 \quad (4)$$

with $c_{mm}(r)$ being the mean of the product of the marks of a randomly selected pair of points with inter-point distance r , and μ being the overall mark mean.

To test for significance, pointwise envelopes for 99 simulations were obtained, where the points are fixed, but the marks are randomly permuted. The simulations were run for the mark-weighted L -function $L_{mm}(r)$, which is related to the mean of the sum of the products formed by the marks of a randomly chosen point and the marks of all points in the disc of radius r centred at that point (Illian

et al., 2008). If the empirical L_{mm} -function leaves the envelopes ($L_{mm,\min}$ and $L_{mm,\max}$), the hypothesis of independence of mound heights is rejected.

Similarity of mound heights

Further information on the correlations of the mound heights can be obtained by means of the mark variogram $\gamma_m(r)$ which characterises the squared differences of heights of mounds dependent on their distance from each other (Illian et al., 2008: 344). The function has small values if the marks of mound pairs tend to be similar and large values if the mounds differ, for given distances r . If the marks are controlled by some co-variable, it is typical that $\gamma_m(r)$ has small values for small r and increases with increasing r .

Statistical remarks

An important characteristic of the introduced functions is the range of correlation r_{corr} (Illian et al., 2008), which was roughly estimated from the shape of the respective function. This is the distance up to which correlations in the marked pattern occur. Beyond this distance, the functions are theoretically constant, and their statistical estimates fluctuate around certain limits. For $g(r)$ and $k_{mm}(r)$, the limit value for large distances is 1, while for $p_{12}(r)$ it is $2p_1 p_2$ and for $\gamma_m(r)$ it is the variance of mound heights.

As is usual in spatial point process statistics (see Section 7.4 in Illian et al., 2008 and Chapter 6 in Diggle, 2003), for testing the independence hypotheses, we used refined versions of the L -function, namely $L_{12}(r)$ and $L_{mm}(r)$. This is analogous to the well-known Kolmogorov–Smirnov test in classical statistics. The main difference between the functions $L_{12}(r)$ and $L_{mm}(r)$ compared to $p_{12}(r)$ and $k_{mm}(r)$ is the cumulative nature of the L -functions.

Pairwise inter-mound distances were calculated to indicate the sample size at each distance for the functions $p_{12}(r)$, $k_{mm}(r)$ and $\gamma_m(r)$. To estimate $g(r)$, $p_{12}(r)$, $L_{12}(r)$, $k_{mm}(r)$ and $\gamma_m(r)$, to determine the significance envelopes and to compute pairwise distances, the software R (v. 2.8.1; R Development Core Team, 2008) was used with the package *spatstat* (v. 1.15-3; Baddeley and Turner, 2005). The resulting values of $p_{ij}(r)$ were multiplied by 2 to achieve comparability with Illian et al. (2008). For the calculation of $L_{mm}(r)$, *Pascal* applications written by D. Stoyan were used. The bandwidth of the functions $g(r)$, $k_{mm}(r)$ and $\gamma_m(r)$ were calculated using the default method given by *spatstat*. For the computation of $p_{ij}(r)$, the bandwidth (according to the term's usage in *spatstat*) was set to 4.4 in *spatstat* to achieve an informative plot.

Table 1 Statistical parameters and distribution types of termite mounds within the 1 km² study area

Mound category	Mound heights			No. of mounds	Deviation from random pattern
	Range (m)	Mean (m)	SD (m)		
All		1.3	0.9	444	Regular
Alive		1.7	0.9	256	Regular
A1	0–0.7	0.5	0.1	48	NS
A2	>0.7–2.0	1.4	0.4	115	Regular
A3	>2.0	2.6	0.5	93	Regular
A2 ∪ A3	>0.7	2.0	0.7	208	Regular
Dead		0.8	0.5	188	NS

Categories A1–A3 and A2 ∪ A3 refer to inhabited mounds. Where the pattern deviated significantly from complete spatial randomness (L -test, $p < 0.05$), the kind of deviation was specified according to the shape of the pair correlation function

NS not significant

Results

In the 1 km² area surveyed, a total of 444 mounds of *Macrotermes michaelseni* were identified. About 58% of them were inhabited (Table 1), reaching up to 4.4 m in height (mean 1.7 m).

General distribution pattern

The spatial patterns for all termite mounds, as well as for the inhabited ones, showed a regular distribution (Fig. 2). For both patterns, their deviation from complete spatial randomness was significant (L -test, $p < 0.05$). The only difference appeared for inhabited small mounds (A1, Fig. 3), where there was a tendency towards a clustered pattern. Large inhabited termite mounds (A2, A3 and A2 ∪ A3) were regularly distributed. Their deviation from complete spatial randomness was significant (L -test, $p < 0.05$). Mounds of category A2 ∪ A3 showed a range of correlation of about 70 m, which is in the same order as the mean distance to the third neighbour (73 m) in this group. The patterns of uninhabited mounds did not differ significantly from complete spatial randomness.

Spatial relationship between small and large inhabited mounds

For inhabited mounds of categories A1 (mark 1) and A2 ∪ A3 (mark 2), the empirical mark connection function $p_{12}(r)$ clearly exceeds 0.30 [$2p_1p_2$ with $p_1 = 48/256 = 0.19$ and $p_2 = (115 + 93)/256 = 0.81$; see “Materials and methods”] which is the limit value for independent marking (Fig. 4). This means that there is a higher probability than expected from the hypothesis of independent marking that, of two mounds that are less than 50 m apart, one mound belongs to the category A1 and the other one to A2 ∪ A3. According to the envelope test, the result is significant

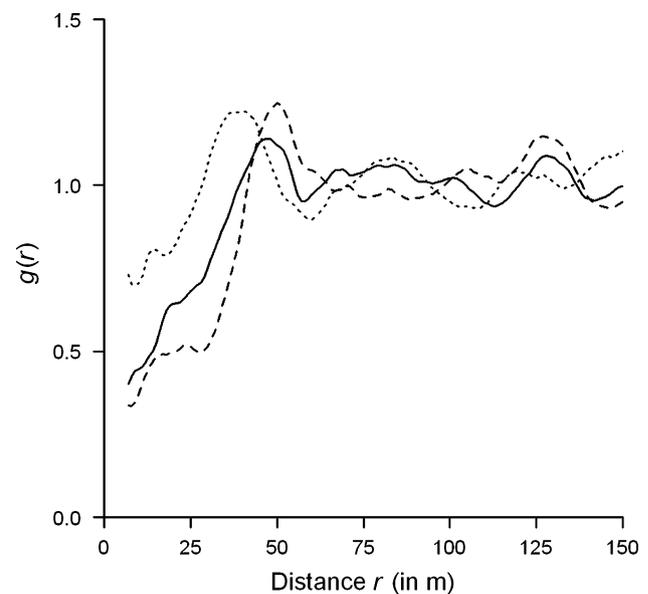


Fig. 2 Pair correlation functions for termite mounds within the study plot of 1 km² (all mounds: solid line; inhabited: dashed line; uninhabited: dotted line). All three functions indicate regularity, but that of uninhabited mounds is not significant (Fig. 1; Table 1)

(Fig. 5) as the empirical L_{12} -function is partly outside the envelopes.

Small mounds (A1) show a different pattern than larger ones. First, they are not distributed regularly, and second, they occur closer to larger mounds than expected by chance. Therefore, mounds smaller than 0.7 m were excluded from the following analyses; see “Discussion” for a more detailed argumentation.

Correlation of mound height with distance to further mounds

Concerning inhabited mounds larger than 0.7 m (A2 ∪ A3), the mark correlation function $k_{mm}(r)$ with mound height as

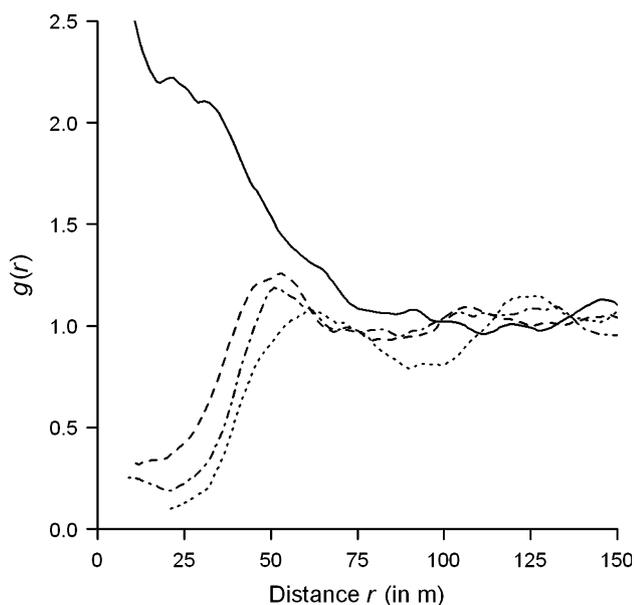


Fig. 3 Pair correlation function for inhabited mounds: A1: solid line; A2: dashed line; A3: dotted line; A2 \cup A3: dot and dash line. The function for A1 shows a tendency towards a clustered distribution (see Fig. 1). All other functions indicate regularity; the deviation from a random pattern is significant (see Table 1)

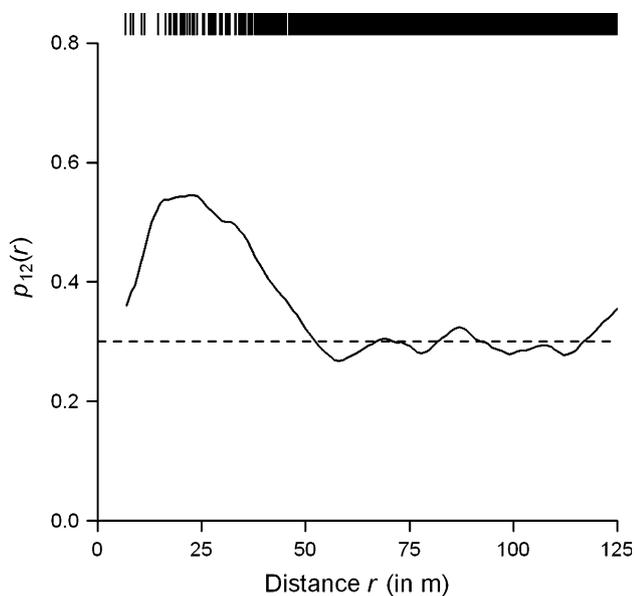


Fig. 4 Mark connection function $p_{12}(r)$ (solid line) describing interactions between termite mounds of category A1 (mark 1) and A2 \cup A3 (mark 2). The large probabilities $p_{12}(r)$ in comparison to $2p_1p_2 = 0.30$ (dashed line, $p_1 = 0.19$, $p_2 = 0.81$; see “Materials and methods”) corresponding to independent marking indicate a tendency of points less than 50 m apart to belong to different categories. Each vertical stripe above the plot indicates when there is at least one mound pair exhibiting the inter-mound distance plotted beneath

continuous mark was smaller than 1 up to a range of correlation of approximately 50 m (Fig. 6). Thus, the product of the heights of two mounds with distance less than 50 m to

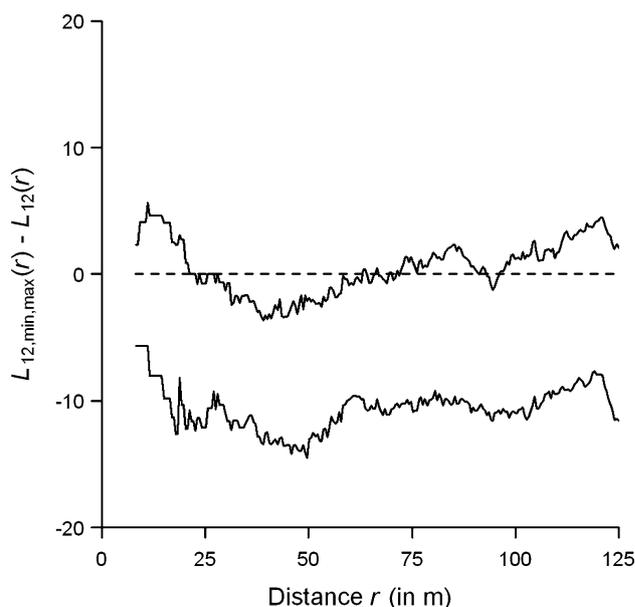


Fig. 5 Envelopes $L_{12,\min}(r) - L_{12}(r)$ and $L_{12,\max}(r) - L_{12}(r)$ (solid line) for the association of termite mound categories A1 (mark 1) versus A2 \cup A3 (mark 2), resulting from 99 simulations obtained by random labelling. The hypothesis of independent labelling is rejected since $L_{12}(r)$ (here set to 0, dashed line) is partly outside the envelopes. This shows that the deviation of $p_{12}(r)$ from 0.30 shown in Fig. 4 is significant

each other is smaller than on average. The L_{mm} -function is partly outside the envelopes obtained by 99 simulations of random distribution of mound heights, indicating that the result is significant (Fig. 7).

Similarity of mound heights

The mark variogram $\gamma_m(r)$ for mounds of category A2 \cup A3 is decreasing in r for small r (Fig. 8). In contrast, the mark variogram is increasing for r larger than 25 m until it reaches the level of the variance of the marks (0.54 m^2). The latter part of the mark variogram for r larger than 25 m resembles part of a typical geostatistical variogram, indicating that mounds less far apart are more similar in their heights compared to those further apart. However, a typical geostatistical variogram would start in the origin [$\gamma_m(0) = 0$], or at least start monotonically, but in Fig. 8 the mark variogram is not monotonic.

In searching for a cause of the unusual variogram form for small r , we analysed all mound pairs with distances less than 25 m. Only eight mound pairs showed such small inter-mound distances. At such a small sample size, even one mound pair with an extreme value for $\gamma_m(r)$ can have a strong impact on the shape of the function. For most pairs, the differences between their heights were much less than expected by chance. However, the mound pair with the minimum distance between them (8.0 m) was characterised

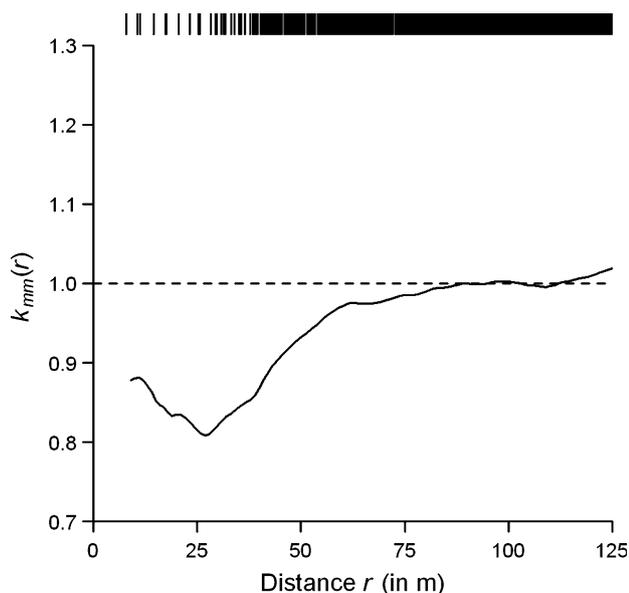


Fig. 6 Mark correlation function for heights of mounds of category $A2 \cup A3$ (solid line). There is some tendency that mounds close together are smaller than average. The test of independent marking shown in Fig. 7 demonstrates that the deviation of $k_{mm}(r)$ from 1 (dashed line) is significant. Each vertical stripe above the plot indicates when there is at least one mound pair exhibiting the inter-mound distance plotted beneath

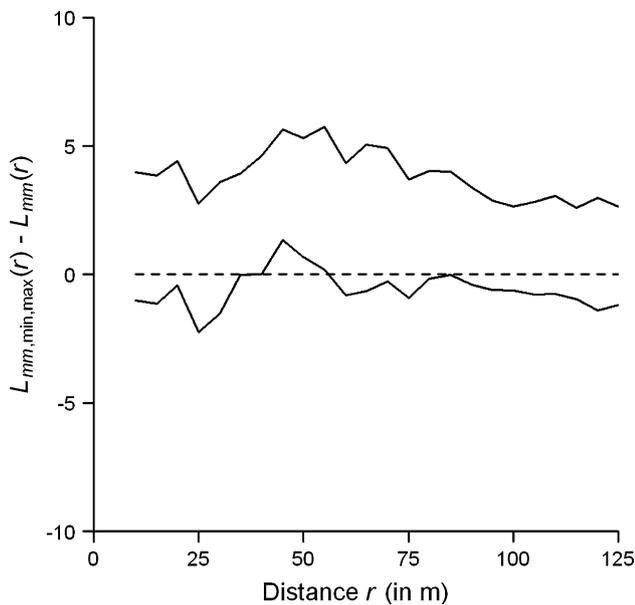


Fig. 7 Envelopes $L_{mm,\min}(r) - L_{mm}(r)$ and $L_{mm,\max}(r) - L_{mm}(r)$ (solid lines) resulting from 99 simulations for the height of larger inhabited termite mounds of category $A2 \cup A3$. The hypothesis of independence of mound height from distance to further mounds of category $A2 \cup A3$ is rejected since $L_{mm}(r)$ (here set to 0, dashed line) is partly outside the envelopes. This shows that the deviation of $k_{mm}(r)$ from 1 in Fig. 6 is significant

by an extraordinary large difference in their heights (0.8 vs. 3.1 m). To exclude the influence of this pair, we ran a second calculation of the mark variogram without the small

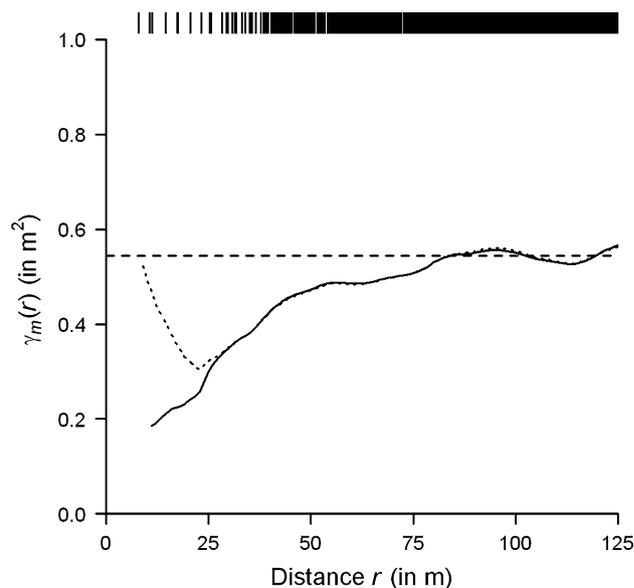


Fig. 8 Mark variograms for all heights of mounds of category $A2 \cup A3$ (dotted line) and for the heights without the mound that is highlighted in Fig. 9 (solid line). The variance of the marks (0.54 m^2 for both calculations) is indicated by the dashed line. The latter mark variogram (solid line) shows that there is a tendency that mounds close together are smaller than on average. Each vertical stripe above the plot indicates when there is at least one mound pair exhibiting the inter-mound distance plotted beneath

mound of this mound pair (Fig. 8, the mound which was excluded is marked by the filled circle in Fig. 9). This time, the mark variogram is monotonically increasing in r , up to an inter-mound distance of 80 m. From there on, only random fluctuations around the variance of the marks (again, 0.54 m^2) can be observed, and the mark variogram can now be easily interpreted: there is some spatial correlation of the mound heights in that members of mound pairs less than 80 m apart tend to be more similar in their heights than members of randomly selected mound pairs.

Discussion

General distribution pattern

The statistical analysis of the pattern of all mounds showed a significant regular spatial distribution of *Macrotermes michaelseni* mounds. This pattern is pronounced in inhabited mounds, particularly so for larger ones of the categories A2 and A3. Such regularity has been described already for several mound-building termite species, and is generally interpreted to be a result of intraspecific or interspecific competition (Wood and Lee, 1971; Lepage, 1984; Pomeroy, 2005). In contrast, earlier investigations of *M. michaelseni* did not detect any deviations from a random dispersion in Botswana and Namibia (Schuurman and

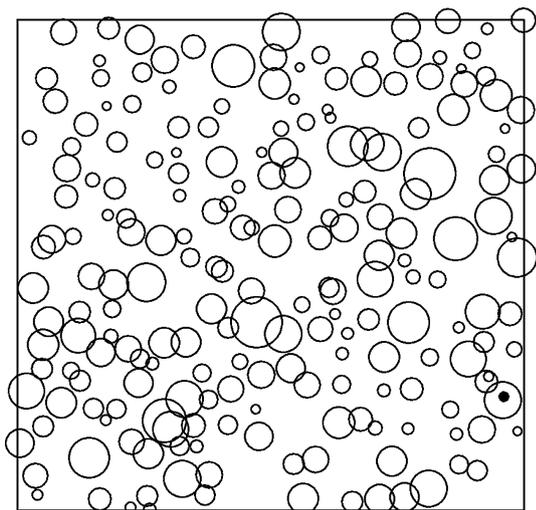


Fig. 9 Spatial distribution of mounds of category $A2 \cup A3$ within the study site of 1 km^2 . Circle diameters indicate the relative heights of mounds (0.8–4.4 m). The filled circle represents one mound which was excluded for the calculation of the mark variogram in Fig. 8. This mound, together with the nearby mound of greater height, is responsible for the strange shape of the mark variogram calculated from all mounds $>0.7 \text{ m}$

Dangerfield, 1997; Turner, 2000), but did so in East Africa (Kaib et al., 1997).

Small inhabited mounds, i.e. less than or equal to 0.7 m, showed no significant deviation from a random distribution, but a tendency towards a clustered pattern. Only few data on the distribution pattern of small mounds can be found in the literature. Most authors either counted larger mounds only, because small ones were difficult to find, or differences in mound heights were not taken into account. Korb and Linsenmair (2001a) found, in two out of eight plots, a significantly aggregated distribution of *M. bellicosus* mounds less than or equal to 1.5 m in height.

In addition to intraspecific competition, the distribution of mounds might be influenced by interspecific competition. Mounds of other termite species were sparse; only a few small mounds built by *Trinervitermes* species were observed within the study site. The genus *Odontotermes* does not build mounds in this region, but is very abundant in the study area. Literature on competition between *Macrotermes* and *Odontotermes* is rare, but indicates that *Macrotermes* outcompetes *Odontotermes* in competition for food resources (Korb and Linsenmair, 2001b; Schuurman, 2006). However, these reports refer to competition for food resources, and no direct conclusions as to the competition pressure for establishing, enlarging or defending nests can be drawn.

Not only the distribution of termite mounds but also the proportions of different mound categories might be influenced by predators. For example, in some regions, doryline ants are important predators of termites (e.g., Bodot, 1961,

1967; Collins, 1981; Darlington, 1985). However, while doryline ants are present in central Namibia, no evidence of them attacking termite colonies could be detected in the region. Instead, armadillos (*Oryzomys azer*) attacks are more likely, but they affect only a small percentage of mounds. At the study site, five out of the 188 dead mounds showed signs of armadillo attacks, with destroyed fungus gardens clearly visible.

The attribution of mounds to different height classes was based on long-term field experience. Abandoned mounds less than or equal to 0.7 m in height seem to erode at a much slower rate than taller ones. If inhabited mounds survive up until a height of approximately 0.7 m, they thereupon often grow very fast. At a height greater than 2.0 m, mounds seem to be able to enlarge their chimney rapidly (within some days), but the chimney also becomes more vulnerable, with a higher risk of breaking. The above-mentioned positive correlation between the size of a colony or its egg production with mound height (Darlington and Dransfield, 1987; Kaib et al., 2001) holds not only for *M. michaelseni*, but also for further *Macrotermes* species (Darlington, 1990; Darlington et al., 1992; Meyer et al., 2000) and also for several different termite groups (see reviews by Lepage and Darlington, 2000; Josens and Soki, 2010).

Spatial relationship between small and large inhabited mounds

According to the mark connection function, small mounds (A1) occur closer to larger ones ($A2 \cup A3$) than expected by chance. Several reasons might cause such a pattern. If two colonies were founded in the same year but one of them had better conditions for growth, the faster-growing colony may suppress the growth of the colony nearby. Another explanation could be that the small colonies are related to the large ones nearby, and thus, are not eliminated because the strength of competition between genetically related colonies should be less strong than among non-related colonies, as found by Kaib et al. (2004). However, Brandl et al. (2005) suggest that budding is absent in *Macrotermes michaelseni* in East Africa. Darlington (1982) proposed that the removal of nascent colonies prevents the durable establishment of younger colonies in the territories of mature ones, but according to Abe and Darlington (1985), subterranean colonies are able to survive close to mature ones in small areas into which the mature colonies do not extend their subterranean galleries. Possibly, not only subterranean but also small mound-building colonies are able to survive in the direct vicinity of large ones, for example if the large colony is stressed by interspecific competition.

Genetic analyses of colony relationships combined with long-term observations on mound growth would be useful in revealing the causes of the observed spatial distribution

patterns of small mounds. Since we are not certain as to how large mounds might influence the patterns of small mounds and since small mounds are not likely to have a strong impact on large mounds and ecosystem functioning, small mounds were excluded from the following analyses.

Correlation of mound height with distance to further mounds

The mark correlation function revealed that for those colonies of category $A2 \cup A3$ which are up to approximately 50 m apart, there is a tendency to be smaller than the average. We assume that the distance between colonies is determined by their foraging demand and the competition pressure. Small colonies theoretically have smaller foraging demands and hence smaller foraging zones around their mounds. In conclusion, they are characterised by lessened competition with other nearby colonies when compared to larger colonies.

Information on foraging zones is sparse in the literature. According to Darlington (1982), findings from an excavated *Macrotermes michaelseni* nest in Kenya showed that the main foraging zone has a radius of 10–35 m around the mound. In Kenya, the distance between mounds fell within double the range of the main foraging zone described, indicating that intercolonial competition for food rules mound distribution (Kaib et al., 1997).

Our data also point to this conclusion, but experimental approaches to the size of foraging zones with regard to competition pressure, foraging demand and food availability should be undertaken to underline that competition for food resources rules mound distribution.

Similarity of mound heights

The mark variogram for mounds larger than 0.7 m in height revealed a strange pattern for small r , which was caused by the extraordinary difference in the heights of the single mound pair with shortest inter-mound distance. This unusual occurrence of two mounds with short distances between them, but considerable differences in their heights, might have several causes. According to our data, this is, however, a rare configuration. Possibly the large colony was somehow weakened, e.g. by infestation of its fungus garden, intraspecific competition caused by the second nearest neighbour (a 1.9 m tall mound, 48 m to the northwest) or interspecific competition.

When excluding the smaller mound of this unusual pair, the mark variogram showed that the differences in mound heights are increasing with increasing distance of the mounds (Fig. 9). Such a mark variogram shape is often observed in geostatistics when regionalised variables such as soil properties, vegetation or precipitation are investigated. They also appear for marked point patterns

when the marks are correlated with environmental factors. However, this is not given in the present study since the study site is relatively homogeneous, especially at a scale up to 80 m, so that variations in the habitat characteristics are unlikely to cause the differences in the mound heights.

More likely, the foundation or growth of colonies in certain years might cause the pattern. According to Pomeroy (1983b), new mounds occur almost exclusively in years with high rainfall following drought years. Most likely, they establish themselves in unoccupied patches, for example where old colonies have died. As young colonies have a low foraging demand, they can occur closer together than large ones, the latter being able to outcompete smaller colonies within their territory. These mechanisms lead to a pattern where small mounds of the same age cohort with similar, relatively low heights stand more closely together, and their distances to taller mounds increase synchronously with the height of the taller mound.

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