ECOGRAPHY

Research

Spatial patterns and life histories of *Macrotermes michaelseni* termite mounds reflect intraspecific competition: insights of a temporal comparison spanning 12 years

Benjamin Wildermuth, Jens Oldeland, Carsten Arning, Felicitas Gunter, Ben Strohbach and Norbert Juergens

B. Wildermuth (https://orcid.org/0000-0002-6316-0170) ✉ (bmwildermuth6@gmail.com), J. Oldeland (https://orcid.org/0000-0002-7833-4903), C. Arning, F. Gunter (https://orcid.org/0000-0003-4570-3212) and N. Juergens (https://orcid.org/0000-0003-3211-0549), Biodiversity, Evolution and Ecology (BEE), Inst. of Plant Sciences and Microbiology, Univ. of Hamburg, Hamburg, Germany. BW also at: Forest Nature Conservation, Burckhardt Inst., Georg-August-Univ. Göttingen, Göttingen, Germany. – B. Strohbach (https://orcid.org/0000-0002-1542-1989), Biodiversity Research Center, Faculty of Natural Resources and Spatial Sciences, Namibia Univ. of Science and Technology, Windhoek, Namibia.

Termite mounds contribute to the heterogeneity and productivity of many semi-arid ecosystems worldwide. Regular spatial patterns of termite mounds are well documented but the underlying pattern-building mechanisms remain to be clarified.

This study analysed a comprehensive data set of *Macrotermes michaelseni* mound metrics, spatial patterns and dynamics, recorded 12 years apart within 1 km² of Namibian thornbush savanna. We used both unmarked and marked point pattern analyses to assess spatial distributions of termite mounds.

We recorded 485 termite mounds in 2007 and 2019. Out of the investigated 142 active termite mounds in 2007, 81 were active 12 years later. Only 2% (n = 3/129) of remnant mound sites in 2007 were newly colonised in 2019. All mounds were distributed at regular distances. Mounds higher than 2 m and long-term active mounds (active in 2007 and 2019) showed high regularity. Mounds up to 0.7 m height and new mounds occurred in clusters and showed a spatial repulsion to large and long-term active colonies. The spatial distribution of *Boscia albitrunca* trees generally clustered around termite mounds, but did not cluster around young colonies.

The results contradict the hypothesis of preferred colony settlement on previously inhabited mound sites. Remnant mounds are relatively unlikely to be recolonised when recently abandoned. The observed spatial patterns show that intraspecific competition between large colonies is the decisive factor for regular spatial patterns of termite colonies, whereas small and young colonies are limited to unoccupied patches. Surrounding trees are a pattern-building factor of only secondary importance.

The spatio-temporal scale in our study reveals general trends of termite mound life histories and spatial pattern-building mechanisms. Availability of not previously inhabited sites form the patterns of founding new colonies. Well-established mounds are highly regulated by intraspecific competition. This highlights that termites contribute to ecosystem heterogeneity through self-organised spatial regularity.

Introduction

Termites represent major decomposers in tropical ecosystems (Bignell and Eggleton 2000, Khan and Ahmad 2018) and are known to alter and influence soil properties like organic matter, nutrient and water availability (Wood 1988, Jouquet et al. 2006, 2016). The accumulation of nutrients and water in their nests provides highly fertile islands in sparse ecosystems (Konaté et al. 1999, Abe et al. 2009, Fox-Dobbs et al. 2010). Elevated mound structures above the nest, as built within the fungus-cultivating subfamily Macrotermitinae, create further habitat heterogeneity (Traoré et al. 2008a, Moe et al. 2009, Sileshi et al. 2010). Consequently, unique plant communities and the overall biodiversity are supported by termites (Arshad 1982, Kirchmair et al. 2012, Erpenbach et al. 2017, Leitner et al. 2020). In consideration of this enormous ecological importance, the term 'ecosystem engineers' was adapted for termites (Jones et al. 1994, Dangerfield et al. 1998, Okullo and Moe 2012). Bonachela et al. (2015) showed that termite mounds can stabilise dryland ecosystems with regard to climatic change. Pringle et al. (2010) underlined that ecosystem productivity and heterogeneity are especially promoted by regular mound distribution patterns.

The genus *Macrotermes* Holmgren (1910) has been especially investigated in many studies on termite mound life histories and spatial patterns (Collins 1981, Korb and Linsenmair 2001, Muvengwi et al. 2018). Temporal studies on the colony life histories and spatial patterns of *Macrotermes* mounds essentially observed random distributions, high mortality rates of young mounds, and few recolonisations of abandoned mounds (Pomeroy 1976, 2005a, b, Collins 1981, Lepage 1984). However, those studies only covered small coherent areas up to 22 ha (Collins 1981) and a maximum observation period of 6.5 years (Pomeroy 2005b). Few recolonisations of abandoned mounds seem incongruent with the finding that newly established *M. bellicosus* Smeathman (1781) colonies show the highest survival rate when recolonising abandoned mound sites (Pomeroy 1976, 2005b). Referring to these results, Schuurman and Dangerfield (1997) proposed in a study on *M. michaelseni* Sjöstedt (1914) that recently abandoned mound sites may be beneficial for new colony establishment due to improved suitability by elevation above ground level (Schuurman and Dangerfield 1996), but this theory remained unproven. Since *Macrotermes* queens show lifespans of 10–20 years (Keller 1998, Wisselink et al. 2020) but *M. falciger* Gerstäcker (1891) mounds revealed ages up to 2200 years (Erens et al. 2015), mound sites must be colonised repeatedly. In sum, the mechanisms, patterns and frequencies of (re)colonisation remain unknown.

At a small spatial scale, various studies on the spatial patterns of *Macrotermes* mounds are available. Early studies on spatial patterns of termite mounds found either random (Lepage 1984, Schuurman and Dangerfield 1997) or aggregated patterns (Meyer et al. 1999). Later publications reported on regular spatial patterns of *Macrotermes* mounds (Davies et al. 2014, Mujinya et al. 2014). Further studies confirmed regular patterns when differentiating between mound size classes: large mounds (> 1.5 m (Korb and Linsenmair 2001); > 2 m (Grohmann et al. 2010)) showed regular patterns, and small mounds (≤ 1.5 m; ≤ 0.7 m) were clustered. Moreover, *Macrotermes* mound size and inter-mound distances are correlated (Pomeroy 2005a, Grohmann et al. 2010, Muvengwi et al. 2018). Mound size and colony size are generally assumed to be proportional (Darlington 1990, Meyer et al. 2000, Pomeroy 2005b), and thus mound height is commonly used for colony size estimations (Darlington and Dransfield 1987, Korb and Linsenmair 2000, Grohmann et al. 2010). However, this estimation remains ambiguous as the growth curve of *Macrotermes* mounds flattens after 6–12 years (Collins 1981, Darlington and Dransfield 1987) and repeated recolonisation over thousands of years seems possible (Erens et al. 2015). Still, mound sizes provide easily available surrogates for colony size in spatial analyses. Large and small mounds indicate competitively stronger and weaker colonies, respectively. Korb and Linsenmair (2001) and Grohmann et al. (2010) concluded that regular spatial patterns between large mounds are shaped by intraspecific competition (Jmhasly and Leuthold 1999). Intraspecific competition as a driving factor for spatial patterns is supported by the observation that regular patterns in *Macrotermes* mounds are more pronounced on nutrient-poor soils (Muvengwi 2018) and *Trinervitermes trinervoides* Sjöstedt (1911) mounds occur in higher densities when foraging resources increase (Hagan et al. 2017). Understandably, regular patterns can only occur within a homogeneous habitat without crucial influences by inundations. In the latter case, mound building termites avoid areas and drainage lines with high risk of inundation, which leads to aggregated mound patterns (Davies et al. 2014, Muvengwi et al. 2016). However, termite mound distribution patterns are considered as one of the major examples for competition-driven spatial self-organisation (Pringle and Tarnita 2017).

Another possible factor influencing termite mound distributions are mound-associated trees, which were shown to have facilitative effects on growth and activity of *M. michaelseni* mounds (Wildermuth et al. 2021). However, termite mounds are known to benefit associated trees themselves (Traoré et al. 2008b, Joseph et al. 2011, Støen et al. 2013) and typical termite mound-associated woody plants are mostly found on large termite mounds (Joseph et al. 2013, Wildermuth et al. 2021). Thus, it remains unclear whether this mutualism is initiated by the trees or the termite mounds.

As mentioned above, the available data lack sufficient temporal and spatial data of mound activity. Only one study on *M. subhyalinus* Rambur (1842) evaluated the activity of mounds over a decade (Mugendi 2020), hence the presumable lifespan of a *Macrotermes* queen (Keller 1998, Wisselink et al. 2020).

Other studies of *Macrotermes* mounds did not mention longer time periods than 2–6.5 years (Pomeroy 1976, 2005a, b, Collins 1981, Lepage 1984). Given that the long-term study of Mugendi (2020) did not sample and analyse a coherent area, there is sparse information about patterns of *Macrotermes* mound life histories and percentages of recolonisation of abandoned mound sites. Furthermore, spatial relationships between contrasting mound sizes and activities over time are poorly understood. Indeed, the activity over time might be a crucial factor for distribution patterns which are supposedly shaped by intraspecific competition. Moreover, there is sparse knowledge on spatial relationships between trees and termite mounds of different sizes and activities. If mounds of different ages show different spatial interrelations with trees, we could draw conclusions on which of the mutualistic partners occurs first.

The aim of this study was to analyse *M. michaelseni* mound life histories and spatial patterns at an interval of 12 years (2007 and 2019). A detailed and comprehensive data set of *M. michaelseni* mounds within 1 km² of Namibian thornbush savanna was recorded by using ground truth methods. We aimed to quantify the recolonisation of remnant mounds over time. Further, we considered mound size and colony activity (2007 and 2019) to understand possible pattern-building parameters. All mound patterns were investigated for spatial interrelations with the distribution of the evergreen *Boscia albitrunca* (Burch.) Gilg and Gilg-Ben. (1915) in the study site. We hypothesised, as introduced by Schuurman and Dangerfield (1997), that termites prefer remnant mound sites for new settlement. Second, we expected that large and 'long-term' active mounds (2007 and 2019) show regular patterns, whilst small and newly founded active mounds occur clustered. Inherent to those patterns, we expected the clusters of small and newly founded colonies to be further apart from established colonies than expected by chance. In contrast, we expected that colonies that failed and disappeared within the years 2007–2019 did not show such repulsion to

competitively strong colonies. Finally, we hypothesised that established termite mounds are spatially closely linked to the evergreen tree species *B. albitrunca*, whilst newly founded colonies do not show such effect.

Material and methods

Study site

The study site was located in central Namibia, approximately 120 km north of Windhoek. In 2001, the BIOTA Africa project (Juergens et al. 2010, 2012) established the 1 km² biodiversity observatory 'Otjiamongombe' on the cattle farm 'Erichsfelde' (Fig. 1a). *Vachellia tortilis* (Forssk.) Galasso and Banfi (2008), *Senegalia mellifera* (Benth.) Seigler and Ebinger (2010) and *B. albitrunca* trees alongside Aristidoideae grasses dominate the vegetation (Strohbach 2019), representing a typical central Namibian thornbush savanna influenced by cattle farming. Climate conditions are semi-arid with mean annual temperatures of 20.6°C over the years 2010–2019 and an average annual rainfall of 317 mm falling during the summer season (Muche et al. 2018). A small riverbed dissects the western part of the observatory in a south–north direction. Whilst clayey luvisols dominate the north-eastern half, the south-western half mainly consists of calcisols (Fig. 1a). Termite mounds of *M. michaelseni* are distributed all over the observatory.

Mound and tree mapping

All termite mounds and eroded mound remnants (see example in Fig. 1b) in the observatory were mapped in 2007 and 2019 (Wildermuth et al. 2021) by two different observer teams, following the approach of Grohmann et al. (2010). We chose ground inspection as the most appropriate method since more than 30% of all termite mounds were concealed by the canopy of associated trees on aerial or satellite images. We
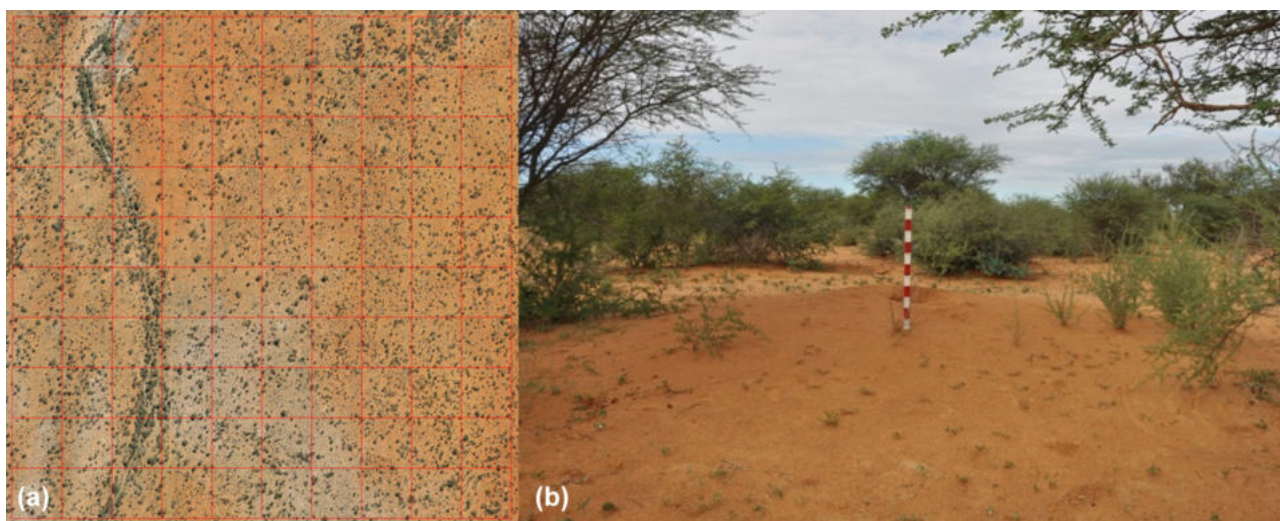

Figure 1. (a) Map of the 1 km² study area 'Otjiamongombe'; each grid cell covers 1 ha. (b) Outwash pediment of a remnant termite mound. Red and white sections of the scale indicate 10 cm.

recorded mound sites with ± 3 m accuracy with a handheld GPS (Garmin, Schaffhausen, Switzerland). The measured mound parameters were mound height, diameter of the conical mound base and the outwash pediment (cm). In 2007, mound heights were exclusively recorded as height above the pediment. We tested mounds with closed or almost closed ventilation for activity by breaking a hole through the walls. If the hole was repaired the next day, we assumed the mound to be active. Mounds with open ventilation systems or no signs of activity were recorded as inactive and outwash pediment remains without any elevated mound structure were recorded as remnant (Grohmann et al. 2010, Wildermuth et al. 2021).

In 2019, we additionally recorded the location of every *B. albitrunca* above 1.50 m height in the observatory. Furthermore, we identified and recorded every tree above 1.50 m total height that was located within the outwash pediment of a termite mound. These trees were classified as 'partner trees' (Wildermuth et al. 2021).

Data analysis

We prepared and analysed all data in R ver. 4.1.0 (<www.r-project.org>). Mound heights above the pediment of 2007 and 2019 were compared with a paired t-test. We considered disappeared mounds in 2019 to be 0 m in height, whereas new mounds were calculated as 0 m height in 2007. We calculated relative proportions of active, inactive and remnant mounds and the respective change in activity after 12 years (2007–2019).

Table 1. Results of the pair correlation functions (PCFs) for all mounds and subsets. R = regular, P = Poisson (random), C = clustered. Significant deviation from the theoretical Poisson distribution was assessed by visual inspection of ~99% envelopes, obtained from the 5th-lowest and 5th-highest value of 999 Monte Carlo simulations. The distribution values in parentheses indicate the spatial scale at which the spatial patterns deviated significantly from the Poisson distribution. Mound heights in 2007 were recorded as height above the outwash pediment (n mounds and distribution patterns in italics).

	n		Distribution	
Mound category	2007	2019	2007	2019
Total	388	344	R (5–15 m) C (40–50 m)	R (5–15 m)
Small (≤ 0.7 m)	*233*	137	*C (40–50 m)*	C (15–55 m)
Medium (> 0.7–2 m)	*103*	107	*R (10–35 m)*	P
Large (> 2 m)	*52*	100	*R (25–30 m)*	R (7–45 m)
Medium and large (> 0.7 m)	*155*	207	*R (2–40 m)*	R (0–30 m)
Active	142	163	R (8–35 m)	P
Inactive	117	117	P	P
Remnant	129	64	C (60–75 m)	P
Long-term active (07 and 19)		81		R (15–40 m)
New (19)		97		C (15–90 m)
New and active (19)		64		C (7–90 m)
Disappeared (07–19)		141		C (40–50 m)
				C (70–80 m)

We used pair correlation functions (PCFs) to analyse the spatial patterns of all termite mounds and individual subsets, as well as all *B. albitrunca* trees in the observatory. PCF is a commonly used multi-scale method to classify spatial patterns into random, regular or clustered processes (Illian et al. 2008). We tested for intensity gradients across the observatory with the 'spatstat' function 'cdf.test' (Baddeley et al. 2015). Significant gradients were found for all analysed mound categories except large mounds (> 2 m height), remnant and inactive mounds (2007) and disappeared mounds (2019). However, as large mounds were distributed homogeneously over the observatory, we assumed general suitability for mound construction all over the study site, and thus we analysed all mound categories with PCFs for homogeneous distributions (Getzin et al. 2008). *Boscia albitrunca* showed a highly heterogeneous distribution in the study site and most trees aggregated in the north-east. Nevertheless, as we also compared the distribution of *B. albitrunca* with different termite mound categories, we chose a PCF for homogeneous patterns to ensure comparability. Following the protocol of Grohmann et al. (2010), we analysed subsets of mound size classes (small ≤ 0.7 m, medium > 0.7–2 m, large > 2 m) and activity categories (active, inactive, remnant). Mound heights of 2007 were available only as height above the outwash pediment. We further analysed subsets of the year of appearance, also considering the activity over time (2007 and 2019; Table 1). We prepared the data for PCF analysis with the R packages 'maptools' (Bivand and Lewin-Koh 2019), 'sp' (Bivand et al. 2013) and 'rgdal' (Bivand et al. 2019). Then we used 'spatstat' (Baddeley et al. 2015) to apply the PCFs with the function 'PCF'. To consider boundary effects of the 1 km² observatory, we applied the default correction 'best', which provides the most accurate edge correction (Baddeley et al. 2015).

For spatial relationships between termite mounds of contrasting categories (height and activity; Table 2), we considered only total height measurements from 2019. We conducted all analyses with the mark connection function ($p_{ij}(r)$). p_{ij} can be interpreted as the conditional probability that points of mark j are found at exact distance r to points of mark i (Illian et al. 2008). To test our hypothesis of a self-thinning process between termite mounds, we chose a random labelling null-hypothesis to compare against the actual distribution patterns. Whilst such a self-thinning process can be regarded as an a posteriori assigning of marks to the mounds, the random labelling null-hypothesis shows the theoretical spatial correlation under assumption of random thinning (Goreaud and Pélissier 2003). Since the null hypothesis of random labelling is robust to environmental heterogeneity when both compared point patterns are created by the same point process (Wiegand and Moloney 2004), no further correction was made for it. The mark connection function was applied with the 'markconnect' command from 'spatstat' (Baddeley et al. 2015). We set rmax to 253 m according to the sensitive default. Isotropic edge correction was applied.

To explore the spatial relationships and test for independence between the point patterns of *B. albitrunca* trees and termite mounds, we used a bivariate cross PCF ('PCFcross' in

Table 2. Spatial relationships between contrasting mound categories in 2019. Relationships were explored with the mark connection function ($p_{ij}(r)$). Significant deviation from random labelling was assessed by visual inspection of ~99% envelopes, obtained from the 5th-lowest and 5th-highest value of 999 Monte Carlo simulations. Results in italics indicate a tendency to repulsion.

Mound category $p(i)$	Mound category $p(j)$	Relationship	Range $p_{ij}(r)$
Medium and large (> 0.7 m)	Small (≤ 0.7 m)	Random	
Large (> 2 m)	Small (≤ 0.7 m)	Repulsion	5–40 m
Large (> 2 m)	Disappeared (07–19)	Random	
Medium and large (> 0.7 m) and active	Small (≤ 0.7 m) and active	Random	
Large (> 2 m) and active	Small (≤ 0.7 m) and active	*Random*	*20–30 m*
Large (> 2 m) and active	Disappeared (07–19)	Random	
Long-term active (07 and 19)	New and active (19)	Repulsion	0–90 m
Long-term active (07 and 19)	Disappeared (07–19)	Random	

'spatstat' (Baddeley et al. 2015)). We implemented a random toroidal shift null-model to account for the original point patterns (Wiegand and Moloney 2014) with the default correction. The chosen toroidal shift had a radius of 500 m, to cover the whole 1 km² study site. *Boscia albitrunca* was only mapped in 2019, hence we only analysed the relationships to the different mound categories as recorded in 2019 (see above for the different mound categories). For all analysis types, we obtained significant bands of approximately 99% by using the 5th-lowest and 5th-highest value of 999 Monte Carlo simulations. For mark connection functions, coordinates were fixed and labels were randomly assigned (Getzin et al. 2008). More details about spatial point pattern analysis can be found in Ben-Said (2021).

Results

We recorded 388 mounds including remnant outwash pediments in 2007 and 344 mounds in 2019 (n_{pairs} = 485; Fig. 2). In 2019, 23 mounds (mean height (M) = 47.61 ± 11.69 cm) and 118 mound remnants of the 2007 mapping had completely disappeared (36.34%) and 97 new mounds had appeared (M = 83.9 ± 7.6 cm; Fig. 2, Supporting information). The overall density of mounds was 3.88 mounds ha⁻¹ in 2007 and 3.44 mounds ha⁻¹ in 2019, whilst active mounds only occurred in densities of 1.42 mounds ha⁻¹ (2007) and 1.63 mounds ha⁻¹ (2019).

Whilst active mounds in 2019 were on average 56.2 ± 7.24 cm higher than in 2007 (p < 0.001), inactive mounds in 2019 were 8.8 ± 6.1 cm smaller than in 2007 (p = 0.15). These differences include mounds that were recorded first in 2019. The extreme values were +320 cm height gain (new and active mound in 2019) and −360 cm height loss (eroded to a pediment by 2019). On average, new and active mounds (first recorded in 2019) were 99.6 cm high (± 10.27 cm).

The developmental trends of termite mounds between 2007 and 2019 (Fig. 3, Supporting information) showed that 91.47% (118/129) of remnant outwash pediments in 2007 remained remnant in 2019 or had disappeared. Almost half of the inactive mounds in 2007 were remnant or had disappeared in 2019 (57/117, 48.72%). In contrast, mounds mapped as active in 2007 tended to be also active in 2019 (81/142, 57.04%). Further, 65.98% (64/97) of the newly mapped mounds in 2019 were active. Mounds that were active both in 2007 and 2019 had average heights of 200.43 cm (± 9.49 cm) in 2007 and 218.95 cm (± 9.21 cm) in 2019 (Supporting information). On the other hand, active mounds of 2007 that were remnant or had disappeared in 2019 had an average height of 82.79 cm (± 21.03 cm) in 2007. Looking only at the active mounds in 2019 (n = 163), 39.26% (64) were new (first recorded in 2019), 49.69% (81) originated from mounds already active in 2007 and only 11.04% (18/163) were located on sites that were recorded as inactive or remnant mounds in 2007.

The PCF identified a regular distribution of all mounds including remnants within the scale of 5–15 m for both 2007 and 2019 (Fig. 4, Table 1). However, in 2007, we also found tendencies for clustering at the scale of more than 40 m distance. Large mounds above 2 m, as well as all mounds above 0.7 m height, were regularly dispersed over the observatory (Fig. 5, Table 1). Within the active mounds, only long-term active (2007 and 2019) mounds were regularly dispersed in 2019. In contrast, new mounds and new active mounds (2019) occurred in clusters (Table 1). The latter were partially due to a cluster of 13 new active mounds in the west of the observatory (Fig. 2, 5c, 6a). Small mounds (≤ 0.7 m) were also distributed in clusters, with different clustering distances between 2007 (40–50 m) and 2019 (15–55 m; Table 1). Note that small mounds in 2007 comprised a larger size range, as heights in 2007 were recorded above the pediment. Inactive mounds showed a random distribution in both study years. In 2019, remnants, active mounds and medium sized mounds were also randomly distributed. Mound remnants (2007) and disappeared mounds (2019) occurred in clusters at the scale of ~ 40–80 m (Table 1). *Boscia albitrunca* occurred clustered, with a large proportion of trees located in the north-east of the observatory (Supporting information). Mound–tree associations were regularly distributed at small spatial scales up to 15 m, but showed clustering at larger scales of 60–70 m (Supporting information).

The results of the mark connection function $p_{ij}(r)$ (only applied for the total mound heights of 2019) showed that small mounds (≤ 0.7 m) were randomly distributed in relation to the group of medium and large mounds (> 0.7 m) but were underrepresented in close distances (5–40 m) to large mounds of more than 2 m height (Table 2, Fig. 5). New active mounds in 2019 were underrepresented within distances of up to 90 m to long-term active mounds (Table 2, Fig. 6). All small and active mounds showed a close to significant tendency to underrepresentation in the vicinity of large and active mounds in 2019, whilst being randomly distributed in relation to the group of medium and large
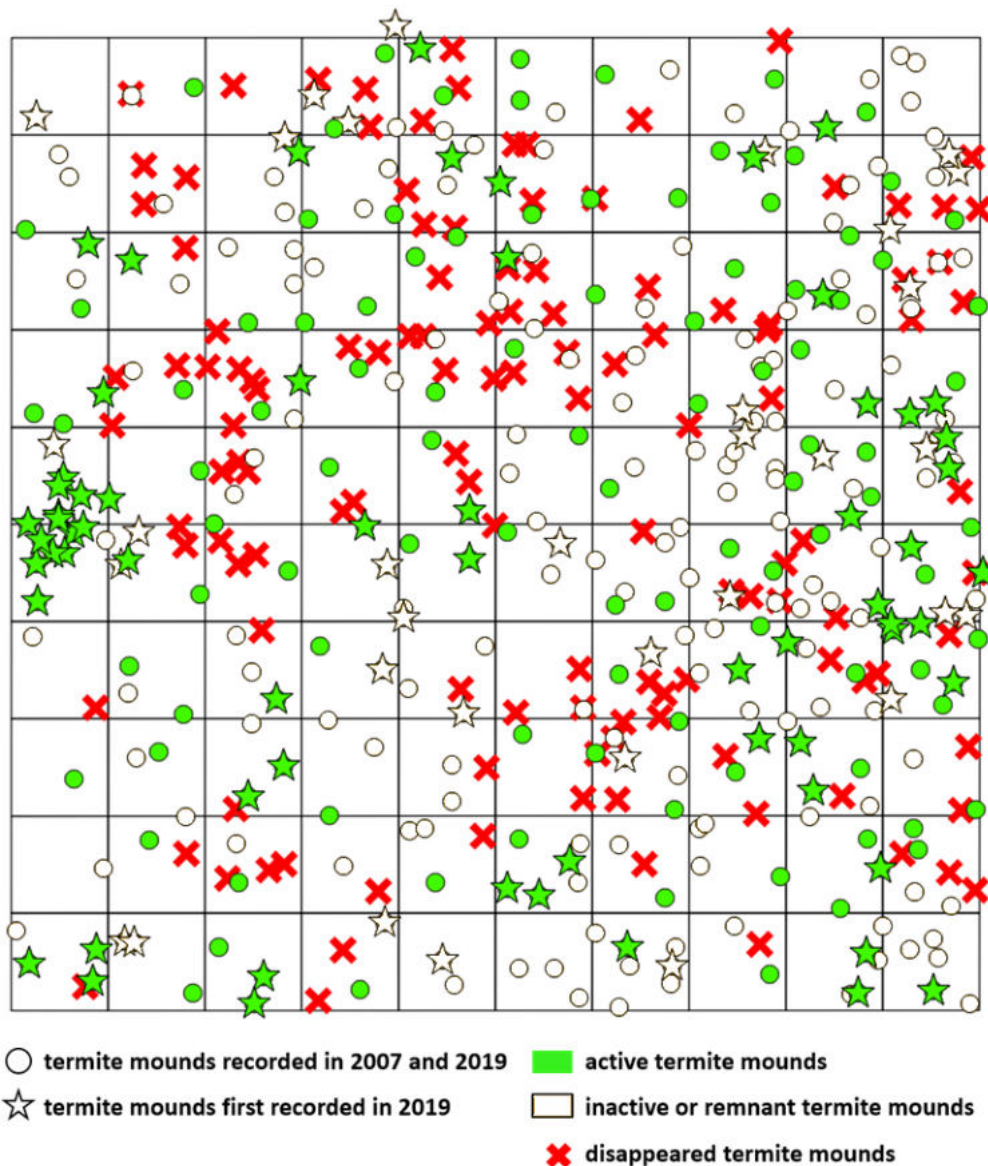
Figure 2. Map of all 485 termite mounds recorded in 2007 and 2019. Mounds that disappeared between 2007 and 2019 are marked with a red X. All active mounds in 2019 are coloured in green.

active mounds. Disappeared mounds (2007–2019) showed no significant spatial correlation to large or long-term active mounds (Table 2, Fig. 6).

The applied bivariate PCF revealed that *B. albitrunca* was significantly clustered very close to termite mounds (0–6 m). *Boscia albitrunca* further showed clustering with small, large and active mounds. We detected no clustering between *B. albitrunca* and remnant, disappeared and new mounds (Table 3, Supporting information).

Discussion

The extent of our spatio-temporal study on termite mounds provides novel insights and consolidation for common theories in development and spatial interactions of an important

ecosystem engineer. Whilst colony founding seems to be determined by availability and environmental conditions, successful colony establishment seems highly regulated by intra-specific competition and results in regular spatial patterns.

The recorded density of 3.44 mounds ha^{-1} underpins earlier published data of *Macrotermes* mound densities in comparable climatic regions, as they range from ~0.5 mounds ha^{-1} to ~5 mounds ha^{-1} (Lepage 1984, Meyer et al. 1999, Pomeroy 2005a, Grohmann et al. 2010, Davies et al. 2014). These studies furthermore reported densities of active termite mounds in the range of ~0.5 mounds ha^{-1} to ~3 mounds ha^{-1}, which is in line with the results of the present study, where active mounds occurred in the density of 1.63 mounds ha^{-1}.

Our results indicate temporal consistency of mound activity, as inactive and remnant mounds of 2007 were only reactivated in 16% of the cases in 2019 and 57%
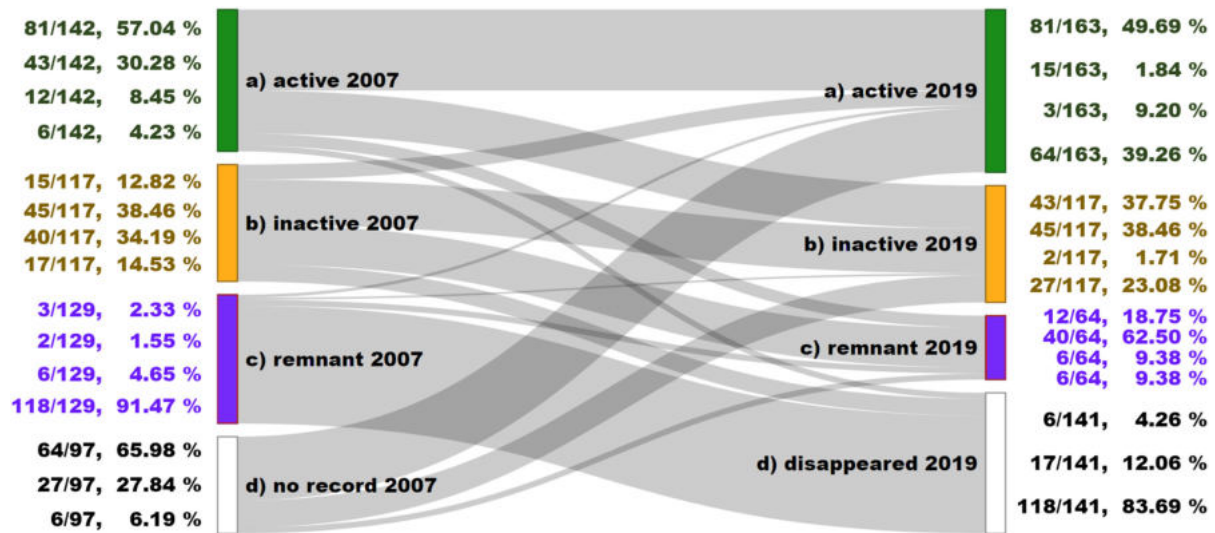
Figure 3. Change in termite mound activity over 12 years within the study observatory. Only 2.33% of the remnant mound sites in 2007 were reactivated in 2019.

of the active mounds of 2007 were also active in 2019 (Fig. 3). Active mounds that died within the study period were initially much smaller than those that were also active after 12 years. These findings reinforce previous studies which found that, once established, *Macrotermes* mound populations are stable (Pomeroy 2005b), whilst small and young colonies show high mortality rates (Pomeroy 1976, 2005a, b, Collins 1981, Lepage 1984). Korb and Linsenmair (1999) observed that only 20% of *M. bellicosus* mounds reached maturity in the savanna. As we neither recorded the genetic identity of the colonies nor monitored the mound activity regularly over the 12 years, we cannot determine whether the active colonies in 2019 were the same as in 2007. Although *Macrotermes* queens can reach ages up to 20 years (Keller 1998, Wisselink et al. 2020), median lifespans of only 6 years were observed for *M. bellicosus* reproductives

(Elsner et al. 2018). Therefore, our study interval of 12 years is too long to deduce a clear picture of colony demographics. Nevertheless, the extremely small number of mound reactivations within 12 years is remarkable. Especially for remnant mound sites that disappeared completely between 2007 and 2019 (n = 118/129, 91.47%), recolonisation within the 12 years can be considered unlikely. Only 3 out of 129 remnant mounds in the study area were newly colonised within the 12 years (2.33%). Another study on *M. bellicosus* mounds over 3 years showed low rates (8%) of recolonisation as well (Pomeroy 1976). Mugendi (2020) discovered even less recolonisation (2%) within 9 years for inactive *M. subhyalinus* mounds (study size: 292 mounds). Thus, neither our study nor other temporal studies support the theory that swarming alates prefer remnant mound sites over the matrix for new colonisations (Schuurman and Dangerfield 1996). This may be explained by the fact that
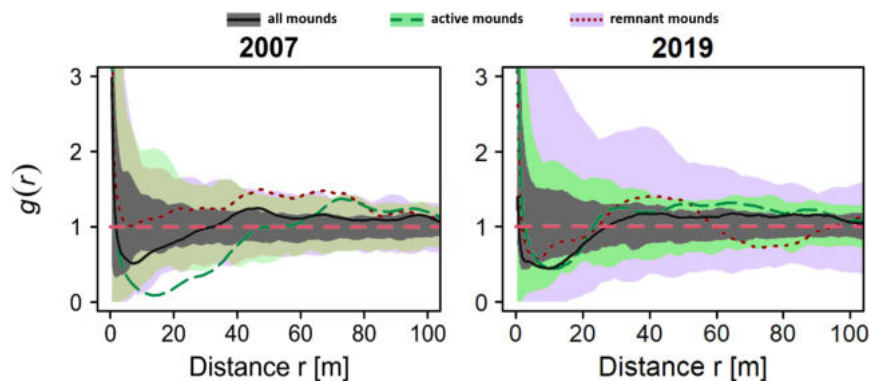

Figure 4. Pair correlation functions (PCFs) for all mapped termite mounds in the study observatory in 2007 and 2019 (all mounds: solid line, grey envelope; active mounds: dashed line, green envelope; remnant mounds: dotted line, red envelope). Envelopes (~99%) were obtained by using the 5th-lowest and 5th-highest value of 999 Monte Carlo simulations. All mounds were regularly distributed. Active mounds were regularly distributed in 2007 and randomly distributed in 2019. Remnant mounds were clustered at ~60–75 m in 2007 but did not deviate significantly from the Poisson distribution in 2019.
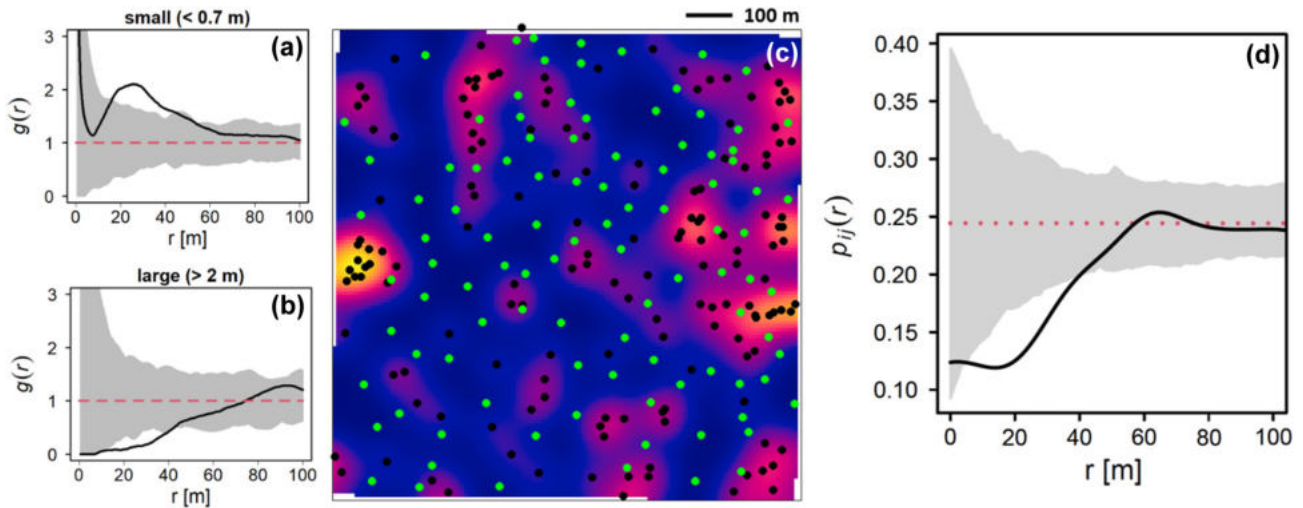
Figure 5. Envelopes (~99%) for (a) all small mounds (< 70 cm) and (b) all large mounds (> 200 cm) in 2019. The pair correlation function (PCF) for small mounds indicates clustered spatial patterns, whilst the PCF for large mounds indicates regular patterns. (c) Density map of all small mounds (black dots) in 2019 (sigma = 40). Colour gradient indicates clustering corresponding to bright yellow. Large mounds are indicated with green dots. (d) Mark connection function $p_{ij}(r)$ of all large mounds versus all small mounds in 2019. Black line: $p_{ij}(r)$. Significant bands (~99%) of 999 Monte Carlo simulations of random labelling in grey. $p_{ij}(r)$ shows underrepresentation of small mounds within the radius of 5–40 m around large mounds.

swarming *Macrotermes* alates prefer sheltered areas under leaves and litter for nest choice (Mitchell 2007) but termite mounds tend to be sparsely vegetated (Glover et al. 1964). Nevertheless, high *Macrotermes* survival rates when recolonising abandoned mound sites (Pomeroy 1976, 2005b) and mound site ages over thousands of years (Erens et al. 2015) show that mounds indeed are recolonised. We suggest that new colonisation of remnant mound sites occurs over larger time scales than the investigated 12 years of our study. However, further comprehensive spatio-temporal data sets might clarify patterns of new colony establishment.

The mound spatial patterns in this study complement past findings on termite mounds that reported overall regular distributions (Davies et al. 2014, Mujinya et al. 2014) and a combination of regularity within large mounds and aggregations within small and new mounds (Korb and Linsenmair 2001, Grohmann et al. 2010, Hagan et al. 2017). This phenomenon is assumed to be caused by intraspecific competition, as competitively strong, large colonies with high foraging demand occupy a certain territory and thus organise themselves in high regularity (Korb and Linsenmair 2001, Pomeroy 2005a, Grohmann et al. 2010). Our study further supports this assumption by showing regular spatial patterns within long-term active mounds (2007 and 2019), whereas inactive and remnant mounds occurred clustered or randomly distributed. We considered mounds as long-term active if they were recorded as active in 2007 and 2019, knowing that the mounds might have been uninhabited and reactivated in the meantime (above). Nevertheless, this scenario remains negligible when assessing the impact of intraspecific competition as a pattern-building factor, as activity by different inhabiting colonies would have a more competitive impact on surrounding colonies than no termite

activity at all. This supposition is supported by the highly regular spatial patterns of these 'long-term' active mounds. It is remarkable that all active mounds in 2019 were distributed randomly (Fig. 4). However, this can be explained by the strong clustering of new active mounds in 2019. This illustrates the fact that regular patterns caused by intraspecific competition are consolidated over time, whereby clusters of young stages are often the starting pattern (Korb and Linsenmair 2001, Getzin et al. 2008).

When assuming intraspecific competition as a pattern-building factor, it is inherent that young and small colonies with low foraging demand are only able to establish in unoccupied patches between the regularly distributed large colonies (Grohmann et al. 2010). However, our analysis of small mounds and their spatial relationship to all remaining larger mounds yielded a random pattern. Earlier studies on spatial relationships between small and larger *Macrotermes* mounds (> 0.7 m height (Grohmann et al. 2010); > 2.5 m diameter on basalt and > 10.8 m on granite (Muvengwi et al. 2018)) partly found small mounds closer to larger mounds than expected by chance. This contradicts the expectation that small mounds show a repulsion from larger and competitively stronger colonies. However, whilst Grohmann et al. (2010) and Muvengwi et al. (2018) only compared small mounds to all remaining larger mounds, we also compared the contrasting height categories of small (≤ 0.7 m) versus large mounds (> 2 m) whilst excluding medium-sized mounds. In fact, this analysis revealed a significant repulsion of small mounds within 40 m of diameter around large mounds (Fig. 5). This finding is supported by Korb and Linsenmair (2001), who found that small *Macrotermes* mounds were only distributed in clusters when larger mounds were present. Nests of the soil-feeding termite *Anoplotermes banksi* Emerson (1925)
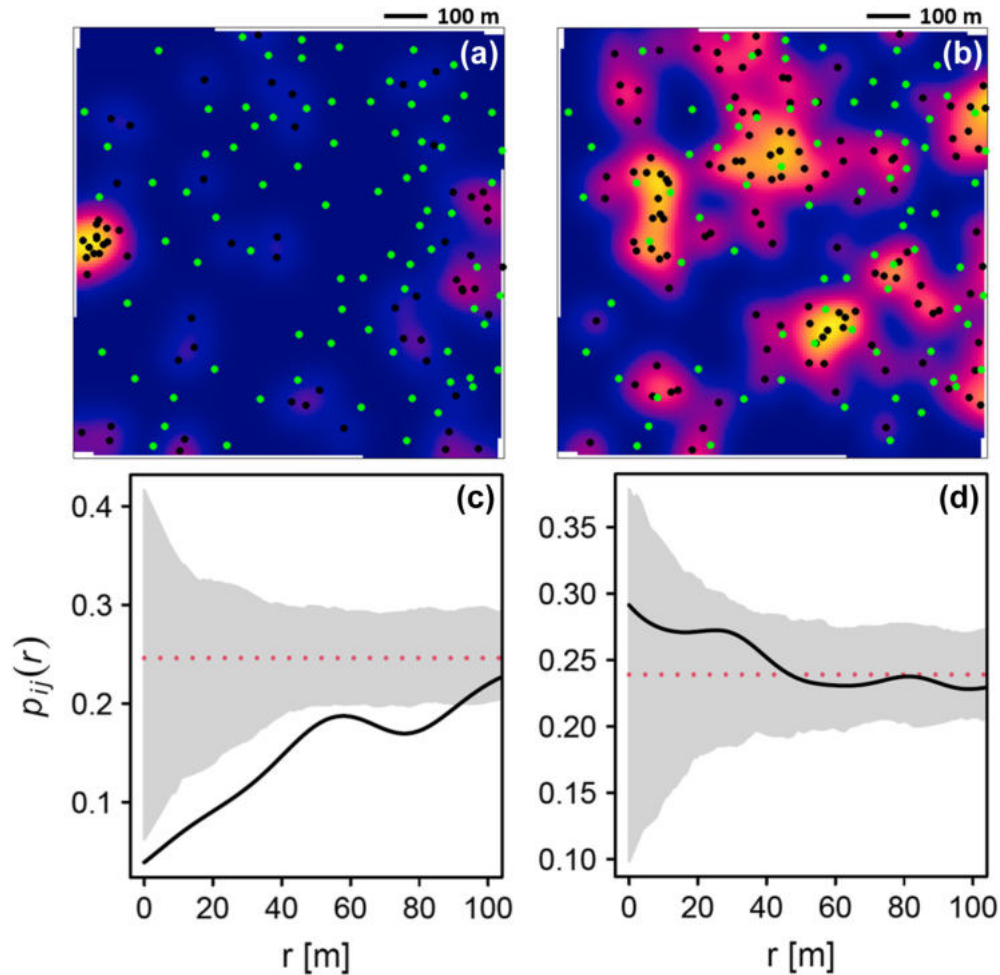
Figure 6. Density maps and Mark connection function $p_{ij}(r)$ of (a, c) new active mounds and (b, d) disappeared mounds in 2019 versus long-term active mounds (2007 and 2019; green dots, sigma = 40). Black line: $p_{ij}(r)$. Significant bands (~99%) of 999 Monte Carlo simulations of random labelling in grey. $p_{ij}(r)$ shows underrepresentation of new active mounds within the range of 0–90 m around long-term active mounds.

show similar patterns, as young colonies are clumped and negatively associated with large colonies (Bourguignon et al. 2011). Additionally, we analysed the spatial relationship between new versus established *Macrotermes* mound activity for the first time. Active new mounds (first recorded in 2019) in our study showed a repulsion to long-term active colonies (active in 2007 and 2019) within a radius of 90 m (Fig. 6). Similarly, newly founded *Macrotermes* colonies showed higher survival rates if located further apart from existing colonies in a 6.5-year study by Pomeroy (2005b). Thus, we overall provide strong support that small and newly established colonies are limited to the gaps between large and well-established colonies. In a well-fitting result, we found that all mounds that completely disappeared within the study period (2007–2019) were distributed in a random relationship to large and long-term active mounds (Fig. 6). Likewise, dying *Anoplotermes banksi* nests were randomly associated with large colonies and showed a positive association with areas of high nest densities (Bourguignon et al. 2011). We interpret this as another indicator that successful establishment of new and small colonies

is only possible at a 'safe' distance to large and well-established colonies – otherwise failure is likely.

Boscia albitrunca trees and termite mounds showed a strongly clustered co-occurrence at short distances over a few metres (0–6 m). Various *Boscia* Lam. (1804) species are commonly associated with termite mounds (Muvengwi et al. 2013). Considering the finding that mound-associated trees, in particular the evergreen *B. albitrunca*, have strong facilitative effects on growth and activity of the investigated *Macrotermes* mounds (Wildermuth et al. 2021), we could assume that mound spatial patterns are rather shaped by the distribution of beneficial trees. Nampa and Ndlovu (2019) indeed suggest that *Trinervitermes trinervoides* mounds are preferentially built under the protecting canopy of associated trees. However, since *B. albitrunca* occurred clustered in the clayey north-east of the observatory, but large mounds were distributed regularly all over the study site, Wildermuth et al. (2021) considered it unlikely that spatial patterns of termite mounds are predominantly shaped by beneficial trees. In turn, it is more likely that the density of *B. albitrunca* increases

Table 3. Spatial relationships between all *Boscia albitrunca* trees above 1.50 m height and mound categories in 2019. Relationships were explored with the bivariate pair correlation function 'PCFcross' ($g_{ij}(r)$). Significance and ranges were assessed by visual inspection of ~99% envelopes, obtained from the 5th-lowest and 5th-highest value of 999 Monte Carlo simulations with implemented random toroidal shift of r = 500 m.

p(i)	Mound category p(j)	n	Relationship	Range $g_{ij}(r)$
Boscia albitrunca	Total	345	Cluster	0–6 m
n = 334	Small (≤ 0.7 m)	154	Cluster	0–3 m
	Medium (0.7–2 m)	107	Random	
	Large (> 2 m)	100	Cluster	0–4 m
	Active	163	Cluster	0–8 m
	Inactive	117	Cluster	0–4 m
	Remnant	82	Random	
	Long-term active (07 and 19)	81	Cluster	0–8 m
	New (19)	98	Random	
	New and active (19)	64	Random	
	Disappeared (19)	141	Random	

around the mounds, as observed similarly for lowland trees in a South African savanna (Davies et al. 2016). Our results provide further support for this assumption, as *B. albitrunca* occurred clustered together with active and large colonies, but did not show significant clustering with remnant, disappeared and new (active) mounds. This illustrates the long-term advantages of tree-associated colonies. Wildermuth et al. (2021) suspect a self-reinforcing cycle of both profiting 'partners'. We conclude that the advantages of tree-associated *M. michaelseni* mounds reflect within the intraspecific self-thinning process, as Wildermuth et al. (2021) showed that mound-tree associations are regularly distributed.

Despite the sparsely settled riverbed and the inhomogeneous soilscape, regularly distributed large mounds indicate suitability for settlement across the whole observatory. However, smaller mounds showed significant inhomogeneity across the observatory. Thus, we suggest that abiotic suitability for colony settlement and mound construction might affect the distribution of young mounds (Davies et al. 2014, Muvengwi et al. 2016, Jamilu Bala Ahmed et al. 2019). Nonetheless, self-organisation of termites through inter-colony competition shows remarkable persistence, as shown by our study and Davies et al. (2020) in different land-use systems with partially high degrees of disturbance. This highlights the ability of termites to boost ecosystem productivity, heterogeneity and robustness through competition-driven regularity (Pringle et al. 2010, Bonachela et al. 2015).

The temporal aspect of our study sheds new light on life histories and spatial pattern-building mechanisms of termite mounds. Against the initial assumption, previously inhabited mound sites are relatively unlikely for new settlement. Intraspecific competition creates regular spatial patterns of large and long-term active mounds, whilst small and young mounds occur clustered in unoccupied patches. Beneficial trees showed to be of advantage but remained a pattern-building factor of secondary importance. In sum, this study underlines the importance of termite mounds as a scalable and global example for competition-driven spatial self-organisation.

Author contributions

Benjamin Wildermuth: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Software (supporting); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Jens Oldeland**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (supporting); Writing – review and editing (equal). **Carsten Arning**: Conceptualization (supporting); Formal analysis (equal); Methodology (equal); Software (equal); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Felicitas Gunter**: Conceptualization (supporting); Funding acquisition (supporting); Methodology (supporting); Validation (supporting); Writing – review and editing (equal). **Ben Strohbach**: Data curation (supporting); Funding acquisition (supporting); Investigation (supporting); Project administration (supporting); Resources (supporting); Visualization (supporting). **Norbert Juergens**: Conceptualization (equal); Data curation (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Validation (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06306>.

Data availability statement

Data are available from the PANGEA: <https://doi.pangaea.de/10.1594/PANGAEA.931642> (Wildermuth et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Abe, S. S. et al. 2009. Physicochemical and morphological properties of termite (*Macrotermes bellicosus*) mounds and surrounding pedons on a toposequence of an inland valley in the southern Guinea savanna zone of Nigeria. – Soil Sci. Plant Nutr. 55: 514–522.

Arshad, M. A. 1982. Influence of the termite *Macrotermes michaelseni* (Sjöst) on soil fertility and vegetation in a semi-arid savannah ecosystem. – Agro-Ecosystems 8: 47–58.

Baddeley, A. et al. 2015. Spatial point patterns: methodology and applications with R. – Chapman and Hall/CRC Press, <www.crcpress.com/Spatial-Point-Patterns-Methodology-and-Applications-with-R/Baddeley-Rubak-Turner/9781482210200/>.

Ben-Said, M. 2021. Spatial point–pattern analysis as a powerful tool in identifying pattern–process relationships in plant ecology: an updated review. – Ecol. Process. 10: 1–23.

Bignell, D. E. and Eggleton, P. 2000. Termites in ecosystems. – In: Abe, T. et al. (eds), Termites: evolution, sociality, symbioses, ecology. Netherlands, pp. 363–387.

Bivand, R. and Lewin-Koh, N. 2019. maptools: tools for handling spatial objects. – R package ver. 0.9-5. <https://CRAN.R-project.org/package=maptools>.

Bivand, R. et al. 2019. rgdal: bindings for the 'geospatial' data abstraction library. – R package ver. 1.4-4. <https://CRAN.R-project.org/package=rgdal>.

Bivand, R. S. et al. 2013. Applied spatial data analysis with R, 2nd edn. – Springer, <www.asdar-book.org/>.

Bonachela, J. A. et al. 2015. Termite mounds can increase the robustness of dryland ecosystems to climatic change. – Science 347: 651–655.

Bourguignon, T. et al. 2011. Are the spatio-temporal dynamics of soil-feeding termite colonies shaped by intra-specific competition? – Ecol. Entomol. 36: 776–785.

Collins, N. M. 1981. Populations, age structure and survivorship of colonies of *Macrotermes bellicosus* (Isoptera: Macrotermitinae). – J. Anim. Ecol. 50: 293–311.

Dangerfield, J. M. et al. 1998. The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. – J. Trop. Ecol. 14: 507–520.

Darlington, J. P. E. C. 1990. Populations in nests of the termite *Macrotermes subhyalinus* in Kenya. – Insectes Soc. 37: 158–168.

Darlington, J. P. E. C. and Dransfield, R. D. 1987. Size relationships in nest populations and mound parameters in the termite *Macrotermes michaelseni* in Kenya. – Insectes Soc. 34: 165–180.

Davies, A. B. et al. 2014. Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. – Ecography 37: 852–862.

Davies, A. B. et al. 2016. Termite mounds alter the spatial distribution of African savanna tree species. – J. Biogeogr. 43: 301–313.

Davies, A. B. et al. 2020. Resistance of mound-building termites to anthropogenic land-use change. – Environ. Res. Lett. 15: 094038.

Elsner, D. et al. 2018. Longevity and transposon defense, the case of termite reproductives. – Proc. Natl Acad. Sci. USA 115: 5504–5509.

Erens, H. et al. 2015. The age of large termite mounds – radiocarbon dating of *Macrotermes falciger* mounds of the Miombo woodland of Katanga, DR Congo. – Palaeogeogr. Palaeoclimatol. Palaeoecol. 435: 265–271.

Erpenbach, A. et al. 2017. The contribution of termite mounds to landscape-scale variation in vegetation in a West African national park. – J. Veg. Sci. 28: 105–116.

Fox-Dobbs, K. et al. 2010. Termites create spatial structure and govern ecosystem function by affecting N2 fixation in an East African savanna. – Ecology 91: 1296–1307.

Getzin, S. et al. 2008. Heterogeneity influences spatial patterns and demographics in forest stands. – J. Ecol. 96: 807–820.

Glover, P. E. et al. 1964. Termitaria and vegetation patterns on the Loita Plains of Kenya. – J. Ecol. 52: 367–377.

Goreaud, F. and Pélissier, R. 2003. Avoiding misinterpretation of biotic interactions with the intertype K_{12}-function: population independence vs. random labelling hypotheses. – J. Veg. Sci. 14: 681–692.

Grohmann, C. et al. 2010. Multi-scale pattern analysis of a mound-building termite species. – Insectes Soc. 57: 477–486.

Hagan, J. G. et al. 2017. Long-term livestock grazing increases the recruitment success of epigeal termites: insights from a >75-year grazing experiment in the Karoo, South Africa. – Afr. J. Range Forage Sci. 34: 123–132.

Illian, J. et al. 2008. Statistical analysis and modelling of spatial point patterns. – Wiley.

Jamilu Bala Ahmed, I. I. et al. 2019. Multi-criteria evaluation of suitable sites for termite mounds construction in a tropical lowland. – CATENA 178: 359–371.

Jmhasly, P. and Leuthold, R. H. 1999. Intraspecific colony recognition in the termites *Macrotermes subhyalinus* and *Macrotermes bellicosus* (Isoptera, Termitidae). – Insectes Soc. 46: 164–170.

Jones, C. O. et al. 1994. Organisms as ecosystem engineers. – In: Samson, F. B. and Knopf, F. L. (eds), Ecosystem management. Springer, pp. 130–147.

Joseph, G. S. et al. 2011. Large termitaria act as refugia for tall trees, deadwood and cavity-using birds in a miombo woodland. – Landsc. Ecol. 26: 439–448.

Joseph, G. S. et al. 2013. Termite mounds as islands: woody plant assemblages relative to termitarium size and soil properties. – J. Veg. Sci. 24: 702–711.

Jouquet, P. et al. 2006. Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. – Appl. Soil Ecol. 32: 153–164.

Jouquet, P. et al. 2016. Termites: the neglected soil engineers of tropical soils. – Soil Sci. 181: 157–165.

Juergens, N. et al. (eds) 2010. Biodiversity in Southern Africa. – Klaus Hess Publishers.

Juergens, N. et al. 2012. The BIOTA Biodiversity Observatories in Africa – a standardized framework for large-scale environmental monitoring. – Environ. Monit. Assess. 184: 655–678.

Keller, L. 1998. Queen lifespan and colony characteristics in ants and termites. – Insectes Soc. 45: 235–246.

Khan, M. A. and Ahmad, W. (eds) 2018. Biology, social behaviour and economic importance. – Springer.

Kirchmair, I. et al. 2012. Biodiversity Islands in the Savanna – analysis of the phytodiversity on termite mounds in Northern Benin. – Flora Veg. Sudano-Samb. 15: 3–14.

Konaté, S. et al. 1999. Influence of large termitaria on soil characteristics, soil water regime and tree leaf shedding pattern in a West African savanna. – Plant Soil 206: 47–60.

Korb, J. and Linsenmair, K. E. 1999. Reproductive success of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) in two neighbouring habitats. – Oecologia 118: 183–191.

Korb, J. and Linsenmair, K. E. 2000. Thermoregulation of termite mounds: what role does ambient temperature and metabolism of the colony play? – Insectes Soc. 47: 357–363.

Korb, J. and Linsenmair, K. E. 2001. The causes of spatial patterning of mounds of a fungus-cultivating termite: results from nearest-neighbour analysis and ecological studies. – Oecologia 127: 324–333.

Leitner, M. et al. 2020. Termite mounds create heterogeneity in invertebrate communities across a savanna rainfall gradient. – Biodivers. Conserv. 29: 1427–1441.

Lepage, M. 1984. Distribution, density and evolution of *Macrotermes bellicosus* Nests (Isoptera: Macrotermitinae) in the north-east of Ivory Coast. – J. Anim. Ecol. 53: 107–117.

Meyer, V. W. et al. 1999. Distribution and density of termite mounds in the northern Kruger National Park, with specific reference to those constructed by Macrotermes Holmgren (Isoptera: Termitidae). – Afr. Entomol. 7: 123–130.

Meyer, V. W. et al. 2000. Intracolonial demography of the mound-building termite *Macrotermes natalensis* (Haviland) (Isoptera, Termitidae) in the northern Kruger National Park, South Africa. – Insectes Soc. 47: 390–397.

Mitchell, J. D. 2007. Swarming and pairing in the fungus-growing termite, *Macrotermes natalensis* (Haviland) (Isoptera: Macrotermitinae). – Afr. Entomol. 15: 153–160.

Moe, S. R. et al. 2009. Mound building termites contribute to savanna vegetation heterogeneity. – Plant Ecol. 202: 31–40.

Muche, G. et al. 2018. SASSCAL WeatherNet: present state, challenges and achievements of the regional climatic observation network and database. – Biodivers. Conserv. 6: 34–43.

Mugendi, D. G. 2020. Temporal patterns in *Macrotermes* mound occupancy in a savanna ecosystem. – MSc thesis, Norwegian Univ. of Life Sciences, Norway.

Mujinya, B. B. et al. 2014. Spatial patterns and morphology of termite (*Macrotermes falciger*) mounds in the Upper Katanga, D.R. Congo. – CATENA 114: 97–106.

Muvengwi, J. et al. 2013. Termite mounds may not be foraging hotspots for mega-herbivores in a nutrient-rich matrix. – J. Trop. Ecol. 29: 551–558.

Muvengwi, J. et al. 2016. Pulsing hydrology and topography determine the structure and spatial distribution of Cubitermes mounds in a savanna ecosystem. – CATENA 145: 99–106.

Muvengwi, J. et al. 2018. Geology drives the spatial patterning and structure of termite mounds in an African savanna. – Ecosphere 9: e02148.

Nampa, G. and Ndlovu, M. 2019. Association benefits between harvester termites (*Trinervitermes trinervoides*) and num-num plants (*Carissa bispinosa*) in a semi-arid savanna setting. – J. Arid Environ. 171: 104005.

Okullo, P. and Moe, S. R. 2012. Termite activity, not grazing, is the main determinant of spatial variation in savanna herbaceous vegetation: herbaceous species composition in savannas. – J. Ecol. 100: 232–241.

Pomeroy, D. E. 1976. Studies on a population of large termite mounds in Uganda. – Ecol. Entomol. 1: 49–61.

Pomeroy, D. E. 2005a. Dispersion and activity patterns of three populations of large termite mounds in Kenya. – J. East Afr. Nat. Hist. 94: 319–341.

Pomeroy, D. E. 2005b. Stability of termite mound populations in a variable environment. – J. East Afr. Nat. Hist. 94: 343–361.

Pringle, R. M. and Tarnita, C. E. 2017. Spatial self-organization of ecosystems: integrating multiple mechanisms of regular-pattern formation. – Annu. Rev. Entomol. 62: 359–377.

Pringle, R. M. et al. 2010. Spatial pattern enhances ecosystem functioning in an African Savanna. – PLoS Biol. 8: e1000377.

Schuurman, G. and Dangerfield, J. M. 1996. Mound dimensions, internal structure and potential colony size in the fungus growing termite *Macrotermes michaelseni* (lsoptera: Macrotermitinae). – Sociobiology 27: 29–38.

Schuurman, G. and Dangerfield, J. M. 1997. Dispersion and abundance of *Macrotermes michaelseni* colonies: a limited role for intraspecific competition. – J. Trop. Ecol. 13: 39–49.

Sileshi, G. W. et al. 2010. Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns: termite-induced heterogeneity in African savanna vegetation. – J. Veg. Sci. 21: 923–937.

Støen, O.-G. et al. 2013. Termites facilitate and ungulates limit savanna tree regeneration. – Oecologia 172: 1085–1093.

Strohbach, B. J. 2019. Vegetation of the Thornbush Savanna of central Namibia: baseline description of the present vegetation at Farm Erichsfelde, Otjozondjupa Region. – Namib. J. Environ. 3A: 17–36.

Traoré, S. et al. 2008a. Impact of *Macrotermes termitaria* as a source of heterogeneity on tree diversity and structure in a Sudanian savannah under controlled grazing and annual prescribed fire (Burkina Faso). – For. Ecol. Manage. 255: 2337–2346.

Traoré, S. et al. 2008b. Macrotermes mounds as sites for tree regeneration in a Sudanian woodland (Burkina Faso). – Plant Ecol. 198: 285–295.

Wiegand, T. and Moloney, K. A. 2004. Rings, circles and null-models for point pattern analysis in ecology. – Oikos 104: 209–229.

Wiegand, T. and Moloney, K. A. 2014. Handbook of spatial point-pattern analysis in ecology. – CRC Press.

Wildermuth, B. et al. 2021. A beneficial relationship: associated trees facilitate termite colonies (*Macrotermes michaelseni*) in Namibia. – Ecosphere 12: e03671.

Wildermuth, B. et al. 2022. Data from: Spatial patterns and life histories of *Macrotermes michaelseni* termite mounds reflect intraspecific competition: insights of a temporal comparison spanning 12 years. – PANGEA, <https://doi.pangaea.de/10.1594/PANGAEA.931642>.

Wisselink, M. et al. 2020. The longevity of colonies of fungus-growing termites and the stability of the symbiosis. – Insects 11: 527.

Wood, T. G. 1988. Termites and the soil environment. – Biol. Fertil. Soils 6: 228–236.