### LETTER

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# **Resource availability and heterogeneity shape the self-organisation** of regular spatial patterning

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#### Abstract

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Explaining large-scale ordered patterns and their effects on ecosystem functioning is a fundamental and controversial challenge in ecology. Here, we coupled empirical and theoretical approaches to explore how competition and spatial heterogeneity govern the regularity of colony dispersion in fungus-farming termites. Individuals from different colonies fought fiercely, and inter-nest distances were greater when nests were large and resources scarce—as expected if competition is strong, large colonies require more resources and foraging area scales with resource availability. Building these principles into a model of inter-colony competition showed that highly ordered patterns emerged under high resource availability and low resource heterogeneity. Analysis of this dynamical model provided novel insights into the mechanisms that modulate pattern regularity and the emergent effects of these patterns on system-wide productivity. Our results show how environmental context shapes pattern formation by social-insect ecosystem engineers, which offers one explanation for the marked variability observed across ecosystems.

#### **KEYWORDS**

coupled human-natural systems, ecosystem engineers, emergent properties, rangeland management, self-organised spatial patterning, semi-arid African savannas, spatial heterogeneity, termite mounds, territorial interference competition

### **INTRODUCTION**

Regular spatial patterns are ubiquitous in nature across scales (Klausmeier, 1999; Rietkerk and van de Koppel 2008; Zhang & Sinclair, 2015; Pringle & Tarnita, 2017) and are frequently integral to the functioning of the systems in which they are embedded (Bonachela et al., 2015; Liu et al., 2014). Identifying the mechanisms underlying pattern formation is a longstanding goal in biology (Hutchinson, 1953; Turing, 1952), but clarity remains elusive for large-scale patterns. Because different ecological processes can theoretically generate identical patterns, pattern analysis alone cannot resolve underlying mechanisms (Pringle & Tarnita, 2017). This problem is compounded by the fact that many patterns develop over timescales of decadesto-centuries and length scales of tens to thousands of metres, which makes them impossible to manipulate experimentally. Integration of large-scale measurements, small-scale experiments, and mathematical modelling is needed to circumvent these obstacles (Pringle & Tarnita, 2017).

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One globally widespread class of large-scale patterns consists of evenly spaced (overdispersed), hexagonally distributed 'polka dots' in dryland vegetation (Deblauwe et al., 2008, Rietkerk and van de Koppel 2008, Pringle & Tarnita, 2017). These include spots or rings of vegetation on otherwise bare soil, clumps of woody thicket surrounded by grassland and patches of productive grass in an herbaceous matrix (Pringle & Tarnita, 2017). Often, the patches that make up these patterns are occupied by social-insect colonies (Juergens, 2013; Korb & Linsenmair, 2001; Pringle et al., 2010), and the overdispersion of such patches has been linked with ecosystem functioning (Pringle et al., 2010). However, the extent to which insects *cause* the spatial regularity of these patches, as opposed to inhabiting them after they form by other mechanisms, is disputed (Cramer & Barger, 2013; Ryti & Case, 1992; Schuurman & Dangerfield, 1997; Tarnita et al., 2017; Tschinkel, 2012). Many groundnesting social insects, such as fungus-farming termites (Macrotermitinae), act as ecosystem engineers in and around their nests (mounds) by modifying soil structure and nutrients in ways that alter productivity and species composition (Jouquet et al., 2006; Sileshi et al., 2010); similarly, by actively keeping their galleries and nest chambers moist, termites increase water availability, even during drought (Ashton et al., 2019; Bonachela et al., 2015). Moreover, ant and termite nests are frequently overdispersed, which has been hypothesised to arise from competition between neighbouring colonies (Darlington, 1982b; Darlington & Bagine, 1999; Korb & Linsenmair, 2001; Pomeroy, 2005). Consistent with this hypothesis, recent theoretical modelling has shown that aggressive territorial competition for resources-such that larger colonies kill smaller ones whenever territories meet (e.g., Darlington, 1982b; Jones & Trosset, 1991; Palmer, 2004; Thorne et al., 2003)-can generate regular hexagonal packing of colonies (Tarnita et al., 2017).

Yet uncertainty persists for several reasons. First, there are few data corroborating the role of competition in generating nest overdispersion (Korb & Linsenmair, 2001; Pringle & Tarnita, 2017), which is the fundamental premise of recent theory (Tarnita et al., 2017). Second, critics of this theory have argued that although competition may cause colony overdispersion, it cannot produce the spatial periodicity observed in the most regular spotted patterns that have been empirically documented to date (Getzin et al., 2019). Finally, the influence of underlying spatial heterogeneity on the emergent regularity of landscape patterns is poorly understood (Sheffer et al., 2013) and has not been incorporated in models of socialinsect self-organisation (Ryti & Case, 1992; Tarnita et al., 2017). Ecosystems differ in degree of substrate heterogeneity and, within ecosystems, different sources of heterogeneity predominate at different scales. Across geological gradients, for example, some areas may be more or less inhabitable by ground-nesting insects, which should disrupt the emergence of highly ordered patterns

at large scales (Davies et al., 2014; Muvengwi et al., 2018). At smaller scales, variation in soil-nutrient concentrations (and hence resource availability) could influence nest density; resulting variability in the distance between neighbours (colonies whose Voronoi cells share an edge) would likewise diminish the degree of regularity in point patterns.

We hypothesised that resource availability and heterogeneity interact with intraspecific competition to modulate the degree of regularity in social-insect nest distribution. To evaluate this hypothesis, we tested a series of predictions. First, if intraspecific competition is strong, then aggression between individuals from different colonies should be high. Second, if colonies compete for resources, then given a fixed resource level, a colony's foraging area (territory size) should constrain colony size. Third, and consequently, higher resource availability should result in smaller foraging areas for colonies of a given size. Fourth, because territory sizes should differ between resource-rich and resource-poor areas, resource heterogeneity should lead to heterogeneous territory sizes and thus diminished regularity of nest distribution. Importantly, because the size of nests relative to foraging areas constrains the possible location of nests within territories (and hence the distribution of possible neighbour distances), we expected that the ratio of nest:territory area would also modulate pattern regularity.

We tested these predictions using behavioural experiments, large-scale measurements, population-genetic analyses and a mathematical model inspired by fungusfarming termites in a well-studied focal systemsemi-arid savanna in Laikipia, central Kenya (Mpala Research Centre, MRC; Donihue et al., 2013; Fox-Dobbs et al., 2010; Porensky & Veblen, 2012; Pringle et al., 2010; Veblen, 2012; Veblen & Young, 2010). At MRC and elsewhere in East Africa, overdispersed *Odontotermes* spp. mounds occur on clay-rich 'black-cotton' vertisols (Fox-Dobbs et al., 2010; Pringle et al., 2010). Early debate over the origin of these mounds was resolved when excavations revealed termite nests (Darlington, 1985), yet the cause of their overdispersion has never been resolved and could conceivably reflect some cryptic template. Odontotermes mounds in these ecosystems have distinctive soil structure (Darlington, 2005; Jouquet et al., 2011), with elevated water infiltration and nutrient concentrations relative to the surrounding matrix (Franz, 2011). These properties elevate primary productivity, which attracts herbivores ranging from insects to elephants (Brody et al., 2010; Holdo & McDowell, 2004; Pringle et al., 2010). The black-cotton landscape is relatively homogeneous compared with other tropical savannas (Figure 1a-c), but resource heterogeneity is imprinted by human activity. Pastoralists and ranchers confine livestock in corrals at night, where animals deposit thick layers of waste (Veblen, 2012); after corrals are abandoned, they develop into nutrient-enriched 'glades' (typically



**FIGURE 1** Natural and anthropogenic spatial heterogeneity in primary productivity. (a) Aerial image of the black-cotton ecosystem at MRC, which is ecologically homogeneous in most respects but comprises local variability in understory productivity (higher greenness). Two neighbouring glades (darker green and treeless) are in the center of the image. (b) False-colour infrared Quickbird satellite image (2.4-m resolution). Termite mounds appear as small bright spots, indicating high primary productivity. Larger bright patch is a glade. (c) An *Odontotermes* mound (middle right) at MRC. (d) Decay in normalised difference vegetation index (NDVI) with increasing distance from glades. The black line is the mean across all sampled glades (coloured lines, n = 26), which varied in size and location across MRC (SI text, Figure SI). Line colours correspond to latitude, with red lowest (southernmost) and violet highest (northernmost). The peak at 150 m for the southernmost glade corresponds to the location of a nearby glade

0.25–1.0 ha; Figure 1a,b,d). Glades persist for decades by attracting dense aggregations of wild ungulates, which slows the decay of nutrient enrichment (Ford et al., 2014; Porensky & Veblen, 2012; Young et al., 1995). These productivity hotspots are irregularly distributed, creating an anthropogenic mosaic of resource-rich patches. We used this coupled human-natural system to explore how resource heterogeneity influences the distribution of *Odontotermes* mounds and how the interplay of heterogeneity and self-organisation affects system-wide productivity.

### MATERIALS AND METHODS

Detailed methods are in Appendix S1.

# Termite sample collection and spatial distribution of termite mounds

We surveyed mounds and collected termites for genetic analyses using a stratified sampling scheme. We divided the study area into a 1-km<sup>2</sup> grid and tried to collect termites from at least one mound near the centre of each grid cell and up to five mounds  $\leq 100$  m from that mound. We exhaustively sampled mounds within two 6.25-ha plots in the center and south of the study area. We also sampled all mounds within three glades and all mounds neighbouring those glades. In total, we sampled 336 mounds spanning 4000 ha (Figure S1), recording their locations with a GPS. Termites were stored in 90% ethanol. We measured the diameter of each mound and the mean distance to and size of all neighbouring mounds, including only those with distinctive vegetation and/or an active area >1-m diameter. We evaluated whether mean distance to neighbours was explained by mound size and proximity to nearest glade using generalised linear models and AIC-based model selection (Appendix S1a and Table S1).

### **Resource abundance**

We evaluated resource abundance on and around glades by quantifying the normalised difference vegetation index (NDVI), which correlates strongly with primary productivity in savannas, and mammalian herbivore dung density (termites eat both plant litter and dung). We calculated NDVI for each mound in a circle of diameter equal to the mound size, as well as for an annulus with diameter equal to that of the mound plus 7 m and a hole equal to mound diameter plus 2 m. We compared NDVI on- versus off-mound using a paired t test and evaluated NDVI as a function of distance to glades using linear mixed-effects models with glade identity as a random effect. We surveyed large-herbivore dung at a subset of mounds used for genetic sampling (n = 115), counting and identifying all piles within  $40 \text{-m} \times 1 \text{-m}$  transects centred on mound centres, and calculated the distance of each mound to the nearest glade edge; we then evaluated whether dung density declined with distance from glades using linear regression.

### Genetic analyses

To verify termite species identity, we extracted genomic DNA from termite head capsules. We sequenced mitochondrial 16S rRNA for comparison with published *Odontotermes* sequences (Darlington et al., 2008). We genotyped 3705 single nucleotide polymorphisms (SNPs) generated by double-digest restriction-site associated sequencing libraries prepared following a protocol modified from Peterson et al., (2012) (Appendix S1a).

To determine whether each mound housed a single colony of *O. montanus* (Darlington, 1985), we quantified inter-individual relatedness using Ritland's  $F_{ij}$  (Ritland, 1996). We assessed isolation by distance with Mantel tests (all mounds) and a generalised additive model (mounds  $\leq 150$  m apart) of genetic distance and geographic

distance among colonies using Nei's D (Nei, 1972). To determine whether neighbouring colonies were more related than non-neighbours at local scales ( $\leq 150$  m), we compared D using a null-model test of the analysis of variance (ANOVA) F statistic and 1000 random permutations assigning 'neighbour' or 'non-neighbour' to each pair of mounds. To determine whether mounds on glades were from the same colony or, if not, were more related to each other than to off-glade colonies at comparable distances, we compared mean  $F_{ii}$  among individuals collected from the same mound, individuals from different mounds on glades (all <60 m apart), and individuals from different mounds off-glades <60 m apart. We compared  $F_{ii}$  with a null-model test of the F statistic and 1000 random permutations of assignment to one of the categories described above (Appendix S1a and Table S2).

### **Behaviour experiments**

We collected termites from neighbouring and nonneighbouring mounds on and off glades. We constructed an observation arena from clear acrylic, leaving a ~5mm space to allow a layer of moist soil and enable termites to move freely. After at least 24 h of isolation, we introduced 20 termites (18 workers and 2 soldiers) from different containers to opposite ends of the arena and continuously recorded interactions in darkness for 24 h using infrared cameras. We also conducted control trials involving termites collected from the same mound at the same time (n = 2 mounds) and housed separately for 24 and 48 h (one trial at each interval for each replicate mound, n = 4 trials total). In total, we filmed and scored 20 trials (Appendix S1a). We recorded the types of interactions observed (aggressive, non-aggressive and no interaction) for each caste combination (worker-worker, worker-soldier and soldier-soldier). We defined aggression as attempted or actual biting and directional lunging (Jmhasly & Leuthold, 1999a; see Movie S1).

### **Theoretical model**

To further explore the relationship between colony size, resource availability and inter-mound distance, we used a theoretical model that builds on Tarnita et al., (2017) (details in Appendix S1b, Figures S4–S9 and Tables S3–S4). As a colony's size grows logistically, it requires more resources and, therefore, a larger foraging territory. If the borders of two territories meet, then the colonies fight (Thorne & Haverty, 1991); the winner is determined with a probabilistic rule that strongly favours the larger colony (Darlington, 1982b; Jones & Trosset, 1991; Palmer, 2004; Thorne et al., 2003). Colonies that exceed a certain size are considered 'established'; colonies below that threshold are 'incipient'. Only established colonies reproduce; their alates disperse randomly and found

incipient colonies. We incorporated effects of termites on vegetation by assuming enhanced plant growth on mounds (Jouquet et al., 2011; Pringle et al., 2010; Sileshi et al., 2010).

This model departs from Tarnita et al., (2017) in a fundamental way: it allows mound properties (e.g., size and location within territory), in addition to territory sizes, to emerge dynamically from colony dynamics. To do this, we incorporated three new assumptions. First, instead of assuming that mound size is proportional to territory area, we used data to estimate mound size as a function of colony size (Darlington 2000b,a, 2005; Darlington & Bagine, 1999). Second, instead of assuming that mound locations are fixed and determined by alate landing site, we assumed that growing mounds can shift towards the interior of the territory, such that the territory always fully contains the mound; nest movement is widespread in social insects (McGlynn, 2012) and we have observed it in Odontotermes at MRC (Appendix S1b). Although mounds must always be fully inside foraging territories, we do not constrain their location further (mound can be anywhere in the territory). Third, we included legacy effects (Darlington & Dransfield, 1987; Pomeroy, 2005): when colonies die, mounds do not instantly disappear but remain vacant and decay at a constant rate; abandoned but not yet fully decayed mounds can be re-colonised (Appendix S1b).

To evaluate effects of resource availability, we first assumed homogeneous resource distribution and explored four levels of resource density (a baseline of 250  $g \cdot m^{-2}$ , approximating standing understory biomass at MRC, and up to 3500  $g \cdot m^{-2}$ ; Appendix S1b). We then tested how mound distribution was affected by three types of resource heterogeneity, all of which exist at MRC: (i) large resource hotspot (e.g., glade) in an otherwise homogeneous resource background; (ii) continuous resource gradient (e.g., in rainfall); and (iii) discontinuous resource gradient (e.g., abrupt transition between soil types). Lastly, we quantified overall productivity of the modelled system with different human footprints: (i) no glades, with mounds on homogeneous resource background; (ii) randomly distributed glades; and (iii) regularly distributed glades. We compared the outcomes against those of 100 simulations in which mounds were randomly distributed. Because the interaction of mound and glade effects has not been studied, we assumed that productivity at any given point in the landscape is determined by either the nearest mound or the nearest glade, but not both (Appendix S1b and Figure S8).

Although we incorporated realistic assumptions and parameter values based on existing knowledge about *Odontotermes* and other Macrotermitinae, along with data for MRC from this study and previous publications (Appendix S1b), not all parameters are precisely measurable. Our model, however, is general, such that the mechanistic relationships among social-insect behaviour, environmental context, and emergent pattern formation are robust to system-specific parameterizations.

### RESULTS

#### **Genetic analyses**

The vast majority of the sampled mounds were inhabited by *O. montanus*; ~10% were occupied by the closely related taxon *O. anceps* (Darlington et al., 2008). Although genetically distinct, these termite taxa, their mounds and their local habitat effects were visually indistinguishable. Thus, we included all mounds when analysing the largescale mound distribution.

Mean relatedness among individuals within mounds was 0.48 (SD 0.1), consistent with full siblings (Figure S2a). Individuals within mounds were more related than those from different mounds, both on and off glades (Figure S2a and Table S2). Thus, all mounds represent distinct colonies, including neighbouring mounds and those inside glades. There was a shallow but significant positive relationship between genetic and geographic distance (Figure S2b), indicating isolation by distance at the scale of the study area (0-12 km). At local scales (0-150 m), however, mean genetic distance was high and constant with geographic distance ( $R^2 = -0.001$ , Figure S2b), and there was no significant difference in relatedness of neighbours versus non-neighbours (Figure S2c), indicating that neighbouring colonies are more likely to be distant relatives than highly related. Thus, most colonies are distantly related regardless of their proximity, but when closely related colonies do occur, they are invariably within 1 km-consistent with observations that alates rarely fly distances >1000 m (Hu et al. 2007).

### **Resource abundance**

Glades are resource hotspots and create resource gradients for both plants and animals. Mean NDVI was greater on than off mounds (t = 6.54, df = 108, p < 0.0001) and decreased with distance from nearest glade (Figure 1d). Similarly, large-herbivore dung density decreased with distance from glade ( $R^2 = 0.24$ ,  $F_{1,34} = 10.75$ , p = 0.002). We found termites in all dung types (Figure S3). Within glades, NDVI did not differ significantly on versus off mounds (t = -0.04, df = 14, p = 0.97), indicating that productivity of mounds in glades is comparable to that of glades themselves.

### Spatial relationships

Distance between neighbouring mounds ranged 3–124 m (mean 42 m, SD 22 m; Figure 2a). Neighbours were closer inside glades (mean 18 m, SD 7 m) than outside (mean 45 m, SD 22; t = -17.69, df = 170.52, p < 0.0001). Distance between neighbouring mounds was positively correlated with distance to nearest glade, which reflects resource availability (Figure 2b), and with mound diameter, which reflects colony size (Darlington, 2000a,b; Darlington &



**FIGURE 2** Distance between neighbouring mounds increased as functions of colony size and resource scarcity. (a) Frequency distribution of nearest-neighbour distances for mounds (n = 506 pairs) in glades (black) and off glades (grey). (b) Mean neighbour distance increased with distance from glade edge ( $R^2 = 0.16$ ,  $F_{1,199} = 38.77$ , p < 0.0001); thus, mounds were farther apart where resource availability was lower. Negative values on the *x* axis indicate mounds located inside a glade. (c) Mean neighbour distance increased with mean mound diameter, a proxy for colony size ( $R^2 = 0.29$ ,  $F_{1,199} = 83.97$ , p < 0.0001). (d) There was no correlation between mean mound diameter and distance from glade ( $R^2 = 0.002$ ,  $F_{1,199} = 1.472$ , p = 0.23), the independent variables used to predict neighbour distance. Each point in (b) and (c) shows measured values for a focal mound and its nearest neighbours. Distance from glade is the distance of the focal mound to the nearest glade edge, and mean neighbour distance the mean of the distance from the focal mound to each of its neighbours. Mean mound diameter is the mean size of the focal mound and each of its neighbours, as measured in the field

Bagine, 1999) and thus resource requirement (Figure 2c). Together, glade proximity and mound diameter (which were uncorrelated: Figure 2d) predicted inter-mound distance ( $R^2 = 0.37$ ,  $F_{2,198} = 60.81$ , p < 0.0001) better than either variable independently (Table S1). Thus, for a given resource level, larger colonies were more distantly spaced (suggesting larger foraging areas), but elevated resource availability enabled denser packing of mounds—consistent with our predictions.

### **Behaviour experiments**

Termites from different colonies (both interspecific and intraspecific) displayed aggression in 15 of 16 trials (94%). In contrast, four trials involving termites from the same colony yielded no evidence of aggression (Table 1), despite groups being held in isolation for 24 or 48 h to account for potential effects of isolation on kin recognition (Adams, 1991). In most trials, termites killed each other; in others, including the only between-colony trial without obvious aggressive behaviour, termites minimised encounters by clustering at opposite ends of the arena. Because termites from different colonies always fought in at least one trial, there was no trend relating aggressive behaviour to whether colonies were neighbours, were of the same or different species or occurred in glades (Table 1). We rarely encountered highly related colonies (Figure S2) so were unable to assess whether relatedness influenced aggressiveness.

### **Theoretical model**

### Resource abundance and inter-mound distance

All dynamic variables of interest—number of established mounds and average territory area, neighbour distance,

**TABLE 1** Summary of behavioural trials, including colony ID (numbers under A and B) and species for both colonies, whether colonies were neighbours, which of the two colonies were on glades, the number of trials in which aggressive behaviour was observed, the distance between mounds, and genetic distance between mounds quantified as Nei's D for *O. montanus* pairings

Type of pairing	Colony A	Colony B	Species A	Species B	Neighbours	Glade	Aggressive	Geographic distance (m)	Genetic distance (D)
Within Colony	1	1	O. montanus	O. montanus		_	0/2	0	0.000
Within Colony	2	2	O. montanus	O. montanus		A, B	0/2	0	0.000
Interspecific	6	7	O. montanus	O. anceps	No	_	1/1	83	_
Interspecific	8	9	O. montanus	O. anceps	No	_	1/1	4007	_
Interspecific	5	4	O. montanus	O. anceps	No	А	1/1	37	_
Interspecific	3	4	O. montanus	O. anceps	Yes	А	1/1	14	_
Intraspecific	10	12	O. montanus	O. montanus	No	_	2/2	108	0.075
Intraspecific	2	11	O. montanus	O. montanus	No	А	1/1	1145	0.071
Intraspecific	3	13	O. montanus	O. montanus	No	А	2/2	2389	0.072
Intraspecific	14	2	O. montanus	O. montanus	No	A, B	1/1	49	0.069
Intraspecific	10	11	O. montanus	O. montanus	Yes	_	1/1	52	0.076
Intraspecific	3	5	O. montanus	O. montanus	Yes	A, B	1/1	24	0.072
Intraspecific	8	2	O. montanus	O. montanus	Yes	A, B	1/1	27	0.070
Intraspecific	14	8	O. montanus	O. montanus	Yes	A, B	1/1	25	0.072
Intraspecific	15	16	O. montanus	O. montanus	Yes	A, B	1/2	10	0.075



**FIGURE 3** Greater resource density increases regularity, whereas background heterogeneity decreases regularity. (a–d) Pair correlation functions for homogeneous landscapes with varying resource levels, in units of grams per square meter of vegetation: (a)  $250 \text{ gm}^{-2}$ , (b)  $500 \text{ gm}^{-2}$ , (c)  $1000 \text{ gm}^{-2}$  and (d)  $3500 \text{ gm}^{-2}$ . (e) Enlargement of the pair correlation function in (a), the baseline case corresponding to typical resource density at MRC. (f–h) Pair correlation functions for different types of heterogeneous landscapes: (f) one resource hotspot (e.g., a glade), (g) continuous gradient and (h) discontinuous gradient. In all panels, grey shading represents significance envelopes (i.e., the range of values consistent with random expectation), and coloured shading represents 90% confidence intervals reflecting the variability of the pair correlation function reflects resource level (lighter shades indicate lower resources). N = 100 replicate simulations for (a) and (e), 50 for (b) and (c) and (f)–(h) and 15 for (d); the different number of replicates is justified by the fact that the number of mounds in the system (and thus statistical power) increased with resource density

colony size and mound size—reached stationarity (a well-defined value that did not vary with time except for small stochastic fluctuations) well before the maximum length of our simulations (all averaged over multiple

replicate runs). At stationarity, there is no empty space in the system: territories occupy the entire landscape, and short-lived openings created by colony deaths are filled almost immediately. Although incipient mounds exist in our simulations, most are quickly killed by competitors, and those that survive mature rapidly.

As predicted and consistent with empirical data (Figure 2b), we found that mean foraging area, and thus distance between neighbouring mounds, decreased as resource levels increased (Figure S4a). Because colonies reached nearly maximum size at stationarity regardless of resource level (Figure S4b) and because mound size was determined entirely by colony size, mounds also reached maximum size across all resource levels (Figure S4c). Thus, total number of mounds increased with resource availability (Figure S4d).

The emergent spatial distribution of mounds showed significant regularity at all four resource levels, as assessed by pair correlation functions: both the first peak (corresponding to the typical distance between neighbours) and the first valley (corresponding to the typical distance to the second-nearest neighbours, that is, Voronoi neighbours of neighbours) differed significantly from random expectation (Figure 3a-d). Height of first peak and depth of first valley increased with resource density, indicating enhanced regularity. For the baseline resource level, the nearest-neighbour distance indicated by the peak of the pair correlation function was  $\sim$ 47 m (Figure 3a), similar to the mean field-measured value of ~45 m (Figure 2a). The regularity of this configuration corresponded well with previously published analysis (Tarnita et al., 2017) of satellite imagery from a 1.2-km<sup>2</sup> subset of our study area (Figure S9; see also Figure S1). Higher resource levels led to peaks at successively smaller distances, which was also reflected in the mode of the probability distribution for nearest-neighbour distance (Figure S5a,d). The probability distribution for the number of sides per tile of a Voronoi diagram peaked at six neighbours (Figure S5b,e), and the mode of the distribution of angles with nearest neighbours was 50-60° (Figure S5c,f). Combined with the regularity of the pair correlation functions, these results show that modelled mounds were distributed in a hexagonal pattern.

### Mound-to-territory area ratio

At the baseline resource level, an average mound comprised only ~2% of its colony's territory area at stationarity (Figure S6a). This low mound-to-territory area ratio means that mounds of mature colonies can occur almost anywhere in the colony's territory and still be fully inside it. This increases variability in the location of mounds within territories, which contributes to the wide distribution of nearest-neighbour distances (Figure S5a,d) and the relatively small (albeit statistically significant) peak in the pair correlation function (Figure 3a). However, as resource level increased, regularity of mound distribution also increased (Figure 3a–d), and this increase coincided with an increase in mound-to-territory area ratio (Figure S6a). We expected that the increase in mound-to-territory area ratio, by decreasing the number of possible mound locations within the territory, reduced variability in the distribution of nearest-neighbour distances and contributed to the enhanced regularity.

To test this idea, we ran the model with the baseline resource level but modified one parameter-mean dry weight of fungal comb-which influences mound-toterritory area ratio without significantly affecting the number of colonies in the system (Appendix S1b and Equation 8). Modifying mean fungal biomass enables a close statistical comparison with the baseline-resourcelevel case, as both have similar mound densities. Decreasing this parameter by 15-fold increased moundto-territory area ratio by 16-fold, which increased the peak of the pair correlation function by ~40% without affecting the significance envelope (Figure S6b). This new peak was nearly indistinguishable from that achieved at the highest resource level (14-fold higher than baseline). Thus, increasing mound-to-territory area ratio, and thereby decreasing a key source of variability, vastly increased the regularity of the system.

### Resource heterogeneity

All three types of heterogeneity reduced regularity relative to the homogeneous case (Figure 3e–h). Although the first peaks of the pair correlation functions remained significantly different from random, heterogeneity brought them closer to the significance envelopes, and the first valleys of these functions ceased to fall outside the envelopes. Thus, these patterns had reduced regularity in terms of nearest neighbours, and the characteristic distance to secondnearest neighbours disappeared completely.

This reduction of regularity occurred because resource heterogeneity increased variability in territory size and therefore in the distance between mounds. In the case with one glade, colonies had access to much higher resource density inside the glade (Figure S7a), resulting in smaller territories (Figure S7b). This produced a nearly bimodal distribution of territory radii: different peaks arose from the distinct territory sizes inside versus outside the glade, and a gradient of territory sizes in the region surrounding the glade accounted for the remainder of the distribution. However, because the glade was small relative to the landscape, the distribution of nearestneighbour distances, while slightly wider, remained similar to that of the baseline (Figure S7c). The differences in nearest-neighbour distances relative to the baseline case were much more striking for the continuous (Figure S7d) and discrete (Figure S7e) gradient scenarios.

### Ecosystem productivity

Prior work has suggested that termites' local augmentation of productivity (plant and animal biomass) is



FIGURE 4 Spatial regularity of resource hotspots enhances ecosystem functioning. Comparison of mean average landscape productivity in a system with 250 g m<sup>-2</sup> of matrix vegetation under different templates of resource heterogeneity: no glades (homogeneous resources), randomly distributed glades (left inset), and regular (hexagonally distributed) glades (right inset). Red and black dots in insets indicate mature mounds and abandoned colonies, as in Figure 3. In all cases, we compared the productivity of a system with randomly distributed mounds (null model, white circle) against that of a system emerging from our dynamical model (black circle). Symbols represent mean landscape values among all replicates (n = 100), with whiskers extending up to the maximum and minimum productivity observed across replicates. Connecting letters above points indicate statistically significant differences in pairwise contrasts (Tukey's honestly significant difference [HSD]) from a  $2 \times 2$  factorial linear model of productivity as a function of mound regularity, glade regularity and their interaction (whole model  $R^2 = 0.65$ ,  $F_{3,396} = 250.2$ , p < 0.0001; main effect of glade regularity  $F_{1,396} = 345.9$ , p < 0.0001; main effect of mound regularity  $F_{1,396} = 357.5$ , p < 0.0001; interaction  $F_{1,396} = 47.2$ , p < 0.0001)

amplified by spatial patterning, such that the observed regular mound distribution boosts system-wide productivity more than simulated random distributions (Pringle et al., 2010). We predicted that the same should hold for additional heterogeneity imparted by anthropogenic resource hotspots—specifically, that regularly distributed glades should increase system-wide productivity more than randomly distributed glades. As expected, the regular mound distribution emerging from our model generated higher productivity than did random mound configurations (Figure 4). Relative to the homogeneous-resource case, glades increased productivity regardless of their distribution. With glades present, productivity was greatest when both mounds and glades were regularly distributed and lowest when both mounds and glades were randomly distributed (Figure 4). These results, which assumed a sigmoidlike decline in productivity with distance from mound/ glade, held qualitatively for other plausible functional forms (e.g., purely convex or concave declines; Appendix S1b).

### DISCUSSION

We used a blend of approaches to explore the mechanisms underlying spatial patterning in social-insect nests-a widely observed but incompletely explained phenomenon (Pringle & Tarnita, 2017). Behavioural trials showed that Odontotermes termites display high aggression (interference competition) towards non-nestmates (see also Darlington, 1982a; Jmhasly & Leuthold, 1999b on Macrotermes spp.), regardless of their geographic proximity or species identity. These results contrast both with the idea that competition/aggression should be strongest between neighbours and with the 'dear-enemy' hypothesis that territorial animals should respond less aggressively to neighbours than to strangers (Temeles, 1994). Although genetic relatedness might influence the degree of aggression between non-nestmates (Adams, 1991), we were unable to test this possibility because highly related colonies were so rare; even if aggression were lower between close relatives, the effect on mound spacing should be minimal given that neighbours were generally distantly related. The scarcity of close relatives on the landscape further suggests an extremely low probability of colony establishment and maturation, consistent with strong territorial competition and reflected in the quick death of incipient colonies in our simulations.

Our dynamical model of territorial interference competition produced overdispersed mounds, with nearestneighbour distances that were inversely correlated with resource availability (cf. Dibner et al., 2015). Empirically, we confirmed this prediction by comparing nearestneighbour distances of mounds on versus off resource hotspots. The inverse correlation between neighbour distances and resource density suggests that colonies can obtain adequate nutrition from smaller foraging areas when resources are abundant. Collectively, these findings support the hypothesis that inter-colony competition is the primary driver of overdispersion in fungus-farming termite mounds. The only previous study to experimentally probe the role of competition in driving this characteristic spatial pattern found that colonies were food-limited: colonies with supplemental food produced ~30 times more alates (Korb & Linsenmair, 2001). Although the replication of that experiment was limited (one colony in each of two years), the effect was enormous, and the result is consistent with our inferences. Future work could use resource-addition (or removal) manipulations to establish whether variability in resource levels causes contraction (or expansion) of foraging territories around focal mounds, as predicted by our model.

Two factors influenced the regularity of emergent nest distributions in our model: spatial heterogeneity in resource distribution and the area of mounds relative to the area of foraging territories. Both factors impacted regularity by affecting variability in nearest-neighbour distances, but via different mechanisms. Resource heterogeneity increased variability in nearest-neighbour

distances by increasing variability in territory sizes: resource-rich areas allowed for smaller territories, and vice versa. This result held for all types of heterogeneity: a resource hotspot, a continuous gradient and a discontinuous gradient. The ratio of mound-to-territory area impacted regularity by affecting the variability in nearest-neighbour distances directly, and not necessarily by affecting the variability of foraging territories. Specifically, low mound-to-territory area ratio increased the range of possible locations for mounds within territories, thereby increasing variability in nearest-neighbour distances. This inference could be generalised to comparisons among species/systems: given two species that require a similar foraging area to support a given colony size but build different-sized structures, the one with the larger nest size should generate more regular patterns.

Together, these two findings could help to explain the variation in nest regularity across disparate ecosystems and insect species (Getzin et al., 2019; Levings & Traniello, 1981; Netshifhefhe et al., 2020) and suggest that the most regular patterns should emerge in species and systems where substrates are homogeneous over extensive areas and nests are large relative to foraging territories. This finding has implications for debates over the mechanistic bases of spotted, gapped and mounded vegetation patterns (Cramer & Midgley, 2015; Gabet et al., 2014; Getzin et al., 2015; Getzin et al., 2019; Juergens, 2015; Tarnita et al., 2017; Zangerlé et al., 2016). Specifically, we show that the degree of regularity in a point pattern cannot be used to exclude faunal activity as a potential mechanism (Getzin et al., 2019), because social insects can in theory produce patterns that range from nearly random to extremely ordered depending on both intrinsic (e.g., behaviour towards conspecifics, mound area required to house a colony of a given size) and extrinsic (e.g., resource heterogeneity) attributes. There is a need for empirical research to test the mechanisms implicated by our model. In particular, the role of nest-to-territory area ratio is a novel and potentially general factor that, to our knowledge, has not been explored.

Last, we explored how the interplay between termiteinduced patterning and resource heterogeneity influenced ecosystem-wide productivity. Termites enhance local productivity by enriching soils and watering their nests and galleries (Sileshi et al., 2010), and previous theoretical (Bonachela et al., 2015) and empirical (Ashton et al., 2019) studies show that these actions can mitigate the impact of drought on ecosystems. Statistical extrapolation of the local productivity boost around individual termite mounds suggests that mound overdispersion enhances net landscape-level production (Pringle et al., 2010). Our process-based model reproduced this effect and showed that the presence of anthropogenic nutrient hotspots (glades in abandoned cattle corrals) further increased overall productivity-especially when glades were also regularly distributed. Increasingly, studies have explored feedbacks among livestock, vegetation and wildlife in African savannas (Augustine et al., 2003; Donihue et al., 2013; Veblen, 2012; Young et al., 2005); recognition that glades influence the foraging behaviour of large herbivores (Augustine et al., 2003) has prompted property managers in East Africa to consider how these resource hotspots could be used to synergise livestock production and ecotourism (Ng'weno et al., 2019). Our results show that strategic placement of cattle corrals in regular arrays should yield greater positive impacts on landscape productivity than the prevailing haphazard approach-and that this outcome emerges through the direct and indirect influences of glades on the distribution of termites, which themselves influence the foraging behaviour of herbivores (Brody et al., 2010; Holdo & McDowell, 2004). This finding has immediately implementable relevance for the management of semi-arid rangelands.

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### AUTHOR CONTRIBUTIONS

All authors contributed to study design. J. A. C. V. and C. C. M. B. collected field data. J. A. C. V. analysed empirical data. J. A. B., R. M. P. and C. E. T. performed modelling work. J. A. B. performed model simulations and analysis. J. A. C. V., J. A. B., C. E. T. and R. M. P. drafted the manuscript. All authors contributed to revisions.

#### PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13822.

#### DATA AVAILABILITY STATEMENT

All data, including raw sequences, will be made available with appropriate accession codes, unique identifiers and web links upon manuscript acceptance.

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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- 1 Supporting Information for
- Resource availability and heterogeneity shape the self-organization of regular spatial
   patterning
- 3 patteri 4
- 5 Jessica A. Castillo Vardaro<sup>1,2\*§</sup>, Juan A. Bonachela<sup>3§</sup>, Christopher C. M. Baker<sup>1,4</sup>, Malin L.
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- 20 Appendix S1
  21 Legends for Movie S1
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- 24 Other Supporting Information for this manuscript include the following:
- 25 Movie S1
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### 27 APPENDIX S1

### 28 A. Empirical Data Collection and Analyses

### 29 Site description

30 We conducted fieldwork at the Mpala Research Centre (MRC) in Laikipia, Kenya, between October 2015 and July 2017 (Fig. S1). MRC is a low-latitude (0°N), high-elevation (1800 m), semi-arid ecosystem in 31 central Kenva. We focused on the 'black-cotton' soils, which occupy a high-clay, poorly drained, 32 topographically uniform plateau (1) in the southwestern quadrant of MRC. The black-cotton savanna is 33 34 characterized by a few dominant species of bunchgrass and a single tree species, Acacia drepanolobium, which comprise  $\sim 90\%$  of understory and 97% of tree cover, respectively (2). This relatively homogeneous 35 36 savanna is scattered with several glades (abandoned cattle corrals) ranging from ~40 to ~130 m in diameter (3). Glades have elevated soil nutrients and are visibly greener than surrounding areas (3). Rainfall increases 37 from north to south across MRC owing to the rain-shadow effect of Mt. Kenya (4); our study area comprises 38

the southern half of this gradient, but we lack rainfall data corresponding to our specific sampling locations.

### 40 *Odontotermes* termite mounds

Odontotermes spp. (Blattodea: Isoptera, Termitidae, Macrotermitinae) termites form large, lenticular 41 42 mounds (typically < 1 m tall) in black-cotton soils throughout East Africa. Typical mature mounds exceed 10 m in diameter, and some can reach up to 30 m in diameter (5). Mounds consist of a nuptial chamber 43 typically with a single reproductive king and queen, and many surrounding chambers containing sponge-44 like fungal combs (6). Mound size is correlated with colony size, as inferred from the number of active 45 fungal combs (6-10), such that colony size increases linearly with mound area (see Eq. 7 below). However, 46 colony size may fluctuate from year to year as a result of seasonal and inter-annual variation in precipitation 47 and, accordingly, resource abundance (10). We sampled mounds  $\geq 1$  m diameter. Worker termites forage 48 for plant material, including plant letter and herbivore dung (5, 11, 12), which they consume and then 49 50 deposit as fecal pellets on the fungal comb. Basidiomycete fungus, *Termitomyces* spp. (Agaricales: Lyophyllaceae), grows in the fecal pellets and produces vegetative nodules which are then consumed by 51 the termites (13). This central-place foraging behavior and resulting competition for food resources has 52 been proposed as the mechanism driving overdispersed patterning in Odontotermes mounds (5, 7). 53

### 54 Spatial arrangement of termite mounds.

55 Previous studies of Odontotermes mounds at MRC have reported an overdispersed spatial arrangement with 56 an average of six neighbors and distances among neighboring mounds of 40-80 m (14-16). These observations were made from multispectral satellite imagery in which large, established mounds are easily 57 detectable owing to their characteristically elevated greenness. For this study, we calculated distances to 58 59 neighboring mounds, including small/incipient mounds that may not appear in satellite imagery. We recorded the location of each mound with a Trimble<sup>™</sup> GeoXT handheld GPS unit and processed the data 60 using Differential Correction in GPS Pathfinder<sup>®</sup> Office v5.85, resulting in horizontal precision of <1 m. 61 62 For each mound, we measured the diameter with a field tape and calculated mean distance to all neighboring mounds in R. 63

To evaluate whether mean distance to neighbors (i.e., the average distance to all neighboring mounds)depends on mound size and resource abundance, we used a generalized linear model with the function:

### 66 *Mean neighbor distance ~ Mound size\*Distance to nearest glade*

67 where mound size is the mean diameter of the focal mound and all neighboring mounds. We compared the

- resulting 5 models (factorial model, additive model, each predictor independently, null intercept-only
- 69 model) based on  $\triangle AIC_c$  using the *MuMIn* (17) package in R. The additive model with mound size and

- distance to glade, with no interaction, best explained distance between neighboring mounds (Table S1),
- while both mean mound diameter ( $R^2 = 0.29$ , p < 0.0001) and distance to nearest glade ( $R^2 = 0.16$ , p < 0.0001) had a significant positive trend with neighbor distance.

### 73 Quantification of resource abundance

74 We evaluated resource abundance on and around glades by quantifying vegetation greenness and large 75 mammalian herbivore dung abundance. We calculated greenness as the normalized difference vegetation index (NDVI) using ArcMap 10.3.1 (ESRI, Redlands California) and Ouickbird Pléiades 1 multispectral 76 satellite imagery collected on 23 May 2013. For each mound, we calculated mean NDVI within a circle of 77 78 diameter equal to the mound size, as well as for an annulus with diameter equal to the mound radius plus 79 7m and a hole equal to the mound radius plus 2m. We compared NDVI values on versus off mounds using 80 a paired *t*-test. NDVI was significantly higher on mounds than off mounds (t = 6.54, df = 108, p < 0.0001), but not for mounds on glades (t = -0.04, df = 14, p = 0.97). 81

We also evaluated NDVI as a function of distance to glade edge, for 26 glades, by applying a linear mixed
effects model with glade ID as a random effect using the *lme4* packages in R:

84 
$$NDVI \sim distance + (1 + distance | gladeID)$$

B5 Distance from glade edge was negative for values on the glade itself and both distance and NDVI were scaled to the mean value across all glades. We then compared the full model to a null model including only the random effect with a likelihood ratio test. NDVI decreased as distance from glade increased ( $\chi^2_{df=1} =$ 25.28, n < 0.0001, Figure 1D)

88 25.38, p < 0.0001, Figure 1B).

We counted all large-herbivore dung within  $40 \times 1$  meter strips centered on mound centers (i.e., extending 89 90 for 20m in two directions away from the mound; n = 36 mounds) and calculated the distance from each mound to the nearest glade edge. Dung density decreased as distance from glade increased ( $R^2 = 0.24$ ,  $F_1$ ) 91  $_{34} = 10.75$ , p = 0.002, Figure S3A). This trend was strongest for zebra (*Equus quagga* and *Equus grevyi*,  $R^2$ 92 93 = 0.23,  $F_{1,34}$  = 10.3, p = 0.003), which were also the most abundant dung species (61%). The negative relationship between dung abundance and distance to glades was also significant for antelopes ( $R^2 = 0.15$ , 94  $F_{1,34} = 5.96, p = 0.02$ ), but not for elephant (Loxodonta africana,  $R^2 = 0.01, F_{1,34} = 0.38, p = 0.54$ ), which 95 comprised 5% of total dung, or for African buffalo/cow (Syncerus caffer and Bos indicus,  $R^2 = 0.01$ ,  $F_{1,34}$ 96 = 0.50, p = 0.49), which comprised 19% of total dung. Antelope dung, which comprised 8% of all dung, 97 98 included impala (Aepyceros melampus), hartebeest (Alcelaphus buselaphus), steenbok (Raphicerus 99 campestris), Grant's gazelle (Nanger granti), and eland (Tragelaphus oryx), and unidentified dung possibly from oryx (Oryx beisa). Other dung included in the overall analyses were reticulated giraffe (Giraffa 100 camelopardalis reticulata, 6%) and common warthog (Phacochoerus africanus, 1%). We surveyed 192 101 dung piles for signs of termite activity and positively identified termite signs in 41%, including 100% of 102 elephant, 40% of zebra, and 39% of antelope dung (Figure S3B). We found termite signs in  $\geq$ 25% of dung 103 104 for all species encountered. Of the dung with positive termite sign, 29% were definitively O. montanus or 105 O. anceps while 46% only included distinctive termite mudding and were from unknown species.

### 106 DNA extraction and 16S sequencing

107 We extracted genomic DNA from termite head capsules using DNeasy Tissue Kits (Qiagen Inc.) according

to manufacturer's instructions. To identify individuals to species, we produced 450 bp 16s ribosomal RNA

109 sequences (primers 16SAr:GCCTGTTTAACAAAAACAT, 16SBr:CCGGTCTGAACTCAGATCACGT)

and compared sequences to published *Odontotermes* sequences (18). PCRs were carried out in 12.5  $\mu$ L

reactions containing: 10mM Tris-HCl, 50mM KCl, 2.5 mM MgCl<sub>2</sub>, 200 µM each dNTP, 0.1 mg/mL BSA,

4% DMSO, 0.2 μM each primer, 0.5U *Taq* DNA polymerase (New England Bio Labs; Ipswich, MA), and

113 1 µL of DNA extract. Cycling parameters were an initial denaturing at 95°C for 5 min, followed by 35

114 cycles of 94°C for 45s, 50°C for 45s, and 72°C for 45s, with a 10-min final extension at 72°C. PCR products

were visualized on a 1.5% agarose gel containing GelRed (Biotium; Fremont, CA) and cleaned with

116 ExoSAP-IT (Applied Biosystems; Waltham, MA). Cleaned PCR products were sequenced on an ABI 3730

- by GENEWIZ (South Plainfield, NJ). Sequences were then edited, analyzed, and compared using Geneious
- 118 V9.0.5 software (Biomatters Ltd.).
- 119 The 16S sequences matched published sequences from Darlington et al. (16) by >99% sequence identity.
- 120 We identified two species of *Odontoterms* on the black-cotton. Approximately 90% of the mounds sampled
- 121 contained *O. montanus*, with the remaining 10% containing *O. anceps*. Unique sequences were uploaded
- to GenBank (accession numbers MZ126676-MZ126681).

### 123 Library preparation and RAD sequencing

We prepared double-digest RAD-sequencing (ddRADseq) libraries following a protocol modified from 124 125 Peterson et al. (19). We quantified DNA extractions (same as used for 16S sequencing) using PicoGreen (Thermo Fisher Scientific, Waltham, MA) and a SpectraMax M3 Microplate Reader (Molecular Devices; 126 Sunnyvale, CA, USA), then standardized the concentrations to 5 ng/ $\mu$ L. DNA extracts were digested in 50 127 128 µL reactions using 20 U each of PstI and EcoRI restriction enzymes and 150 ng DNA for 4hr at 37°C. 129 Digested samples were then cleaned with AMPure beads (Beckman Coulter; Brea, CA, USA) to remove small DNA fragments and remaining proteins. Cleaned digestions were quantified again using PicoGreen 130 131 and a plate reader and then grouped into pools of 48 samples according to DNA quantity. The DNA concentrations were then standardized within each pool for ligation of P1 adapters containing unique 6-132 133 nucleotide barcodes and a P2 forked adapter. Ligations took place in 30  $\mu$ L reactions at room temperature  $(\sim 25^{\circ}C)$  for 1.5 hrs then heat killed at 65°C for 10 min followed by a decrease in temperature of 2°C every 134 90s until achieving room temperature. Ligated samples were pooled and cleaned twice with AMPure beads, 135 then size selected to 477bp using the "tight" setting on a Pippin Prep (Sage Science; Beverly, MA). The 136 remaining fragments were then amplified with PCR using Illumina indexed primers designed to only 137 amplify DNA with both P1 and P2 adapters. PCR products were then cleaned using AMPure beads, 138 quantified using Qubit Fluorometric Quantitation (Thermo Fisher Scientific; Walkham, MA, USA), and 139 pooled in 10 nM libraries. Each of two libraries contained 8 pools of 48 individuals barcoded with a unique 140 141 pool-individual barcode combination, for a total of 384 individuals per library. We sequenced single-read, 150-bp length fragments on an Illumina HiSeq 2500 at the Princeton University Sequencing Core Facility. 142 Raw sequence reads for each sample were archived in the NCBI SRA (Accession PRJNA726729). 143

144

## 145 Bioinformatics and SNP genotyping

146 Sequence reads from pooled libraries were demultiplexed by Illumina index using a Python script adapted 147 from FASTX Barcode Splitter in the FASTX toolkit programs (20). Sequenced reads were further 148 demultiplexed by barcode and cleaned using process radtags in STACKS v.1.4 (21). We called SNPs separately for each species using the *denovo map* program in STACKS. We determined optimal STACKS 149 parameter values by running a subset of individuals through the *denovo map* pipeline, including duplicate 150 151 individuals sequenced in both libraries, for a range of minimum stack depth (m = 2 to 4), maximum distance 152 between stacks (M = 2 to 4), and maximum distance between catalog loci (n = 1 or 2). We chose the parameters that resulted in the greatest proportion of shared alleles between duplicate samples, calculated 153 using the Adegenet package in R (22). We ran the *denovo map* program again for all individuals using the 154 155 optimal parameters (m = 4, M = 4, n = 2). We included 1 SNP per RAD locus, and removed loci typed in <60% of individuals, with a minor allele frequency of <0.01, and those fixed in >95% of termite colonies. 156 157 We tested loci for significant deviations from Hardy-Weinberg proportions across all samples, as well as within termite mounds that had more than 10 individuals typed. Additionally, we removed individuals typed 158 at <50% of loci. After filtering individuals and loci, we retained 3,705 loci for further analyses in 634 159 160 individuals for O. montanus and 4,922 loci in 80 individuals for O. anceps.

### 161

### 162 **Population-genetic analyses**

163 We quantified genetic relatedness among individuals from the RADseq SNP genotypes using Ritland's 164 kinship coefficient, F<sub>ii</sub> (23) and among colonies using Nei's distance, D (24). We calculated metrics using the Adegenet (22) and Related (25) packages in R. For colony-based analyses, we removed termite colonies 165 that had fewer than 2 individuals genotyped. To avoid biasing the F<sub>ii</sub> calculation due to uneven sampling 166 among mounds, we subsampled no more than four individual termites per mound 10,000 times, calculated 167 F<sub>ii</sub> from each subsample, and averaged over the pairwise estimates. We evaluated the presence of isolation 168 169 by distance using Mantel tests from the *ecodist* package in R. There was a significant, positive relationship between D and geographic distance among O. montanus termite colonies (Mantel R = 0.17, p < 0.001) and 170 a negative relationship with  $F_{ii}$  (Mantel R = -0.17, p < 0.001), indicating the presence of an isolation by 171 172 distance pattern (Fig. S2B). There was a similar isolation by distance trend with O. anceps among 173 populations (Mantel R = 0.19, p < 0.01) and individuals (Mantel R = -0.33, p < 0.001). We evaluated the relationship between D and geographic distance at the local scale, <150m, using a generalized additive 174 model (GAM) and found no evidence for isolation by distance ( $R^2 = -0.001$ , p = 0.66). To assess whether 175 neighboring mounds are on average more related than non-neighboring mounds of similar distances, we 176 compared D with ANOVA followed by a null model test of the observed F statistic and the distribution of 177 178 F statistics derived from 1000 random permutations of group assignment (neighbor vs non-neighbor). We calculated a p-value as the proportion of simulated F statistics that were as large or larger than the observed 179 value (Fig. S2C). There was no significant difference in mean relatedness among neighboring mounds and 180 non-neighboring mounds <150m apart (p = 0.09). 181

182

183 To determine whether mounds on glades were more related to each other than mounds off-glades of comparable distance, we compared F<sub>ii</sub> among the following groups: individuals collected from the same 184 mound, individuals from different mounds on glades, individuals from different mounds off-glades less 185 than 60 m apart (Fig. S2A). We compared F<sub>ii</sub> with ANOVA followed by a null model test, as described 186 above. Termites from different mounds on glades were significantly less related than termites from the 187 188 same mound and not significantly different than termites from different colonies off glades less than 60 m apart (Table S2). Relatedness among individuals within mounds was consistent with full siblings (mean 189  $0.48 \pm 0.1$  s.d., Fig. S2A). The observed range in within-mound relatedness may be the result of multiple 190 191 founding individuals (lower relatedness) or inbreeding among secondary, neotenic reproductives (higher relatedness). Multiple founding individuals have been observed within the Termitidae (26), including in the 192 193 closely related Macrotermes (27), while replacement reproductive are common within the Macrotermitinae 194 (28). Termites from different mounds on glades were therefore not from the same genetic colony, or highly related colonies. 195

196

### **197** Behavior experiments

198 We collected termites from the field and brought them back to the MRC lab for behavioral assays. Termites 199 were kept in plastic containers with moist soil and fungal comb for a period of at least 24 hours prior to trials, including for the control trials. We continuously recorded the interactions in the dark for 24 hours 200 using infrared cameras connected to a DVR. In total, we filmed and scored a total of 20 behavior trials, 201 202 including 16 inter-mound trials and four intra-mound control trials (two for each of two mounds, once after 203 24 h and once after 48 h). We reviewed videos in a serious of short observation periods and noted the 204 presence of different types of interactions observed within each period: aggressive, non-aggressive, or no interaction, for each caste combination: worker-worker, worker-soldier, and soldier-soldier. The first 205 observation period began when the termites from different mounds first came in contact with each other 206 207 within the arena and lasted ten minutes. The remaining observation periods were one minute every ten 208 minutes for the first hour, then one minute every hour for eight hours, for a total of 13 observation periods

and 22 minutes per trial. We defined aggressive behavior as attempted or actual biting and directional
lunging at another termite (29, 30).

In some trials, fighting was so intense that nearly all the termites were killed during the first ten minutes, reducing aggressive behavior in subsequent observation periods by either reducing the overall number of encounters among termites, reducing the number of individuals in one colony disproportionately to the other, or a combination of both. Aggressive behavior frequently occurred between workers (worker-worker: 36 observation periods, worker-soldier: 36, and soldier-soldier: 12), indicating that aggression is not exclusive to the soldier caste. However, soldiers appeared to be more efficient at wounding and/or killing workers than other workers were (Supplementary Movie S1).

218

### 219 **B. MODEL DESCRIPTION**

GLOSSARY OF TERMS USED IN MODEL DESCRIPTION

Active mound: Mounds that belong to a colony.

Abandoned mound (AB): Mound that belonged to a colony that is now dead.

**Partial occupation of an AB:** When the territory of an expanding colony overlaps with parts of an AB. In that case, no part of the AB can be claimed by any other expanding colony.

Full occupation of an AB: When the territory of an expanding colony fully covers an AB.

**Reuse of an AB:** When a colony's mound is indistinguishable from the AB, which can happen because i) the founding alates landed on any part of the AB; ii) the center of the colony's mound moved and overlapped with any part of the AB. In both cases, the AB itself disappears.

**Overlap:** When any pixel of object X matches a pixel of object Y (objects can refer here to a colony's territory or an AB).

220

To study the effects of resource heterogeneity on the spatial arrangement of termite mounds and the fraction of the territory they occupy, we built on a previous theoretical model describing the basic competition and foraging behavior of termites (16). The modified version we present here also includes the changes to location and size of termite mounds resulting from the dynamics of the colony population biomass, resource needs, and surroundings. In addition, we considered in this new version potential legacy effects. To enable comparison with our empirical work, we focus here on the termite genus *Odontotermes*.

227 *Landscape*. As in (16), we considered a regular lattice with  $N \cdot N$  pixels of horizontal size dx and vertical 228 size dy=dx. In addition, we defined a minimum mound and foraging territory sizes,  $A_{Mmin}$  and  $A_{min}$ , 229 respectively, which represent minimum thresholds for detectability but also help avoid technical issues 230 related to the discretized space. Time *t* is also discretized, as colonies are updated on an annual basis.

The presence of mounds will affect the vegetation (see *Ecosystem engineering* section below). However, first we discuss the background vegetation in the absence of mounds. Vegetation was assumed to be at a homogeneous baseline level  $V_0$ . To explore the effects of resource heterogeneity, we considered two departures from this baseline:

i) *Glades*, nutrient-rich areas with higher vegetation biomass. We assumed glades to be circular, centered at  $x_G$  with radius r. Note that x represents a vector, as the system is in 2D. We implemented their effects via the following improvement function:

$$G(\mathbf{x}) = \begin{cases} E_G & \text{for } |\mathbf{x} - \mathbf{x}_G| \le r/2 \\ 1 + 2(E_G - 1)(1 - |\mathbf{x} - \mathbf{x}_G|/r) & \text{for } r/2 < |\mathbf{x} - \mathbf{x}_G| \le r \\ 1 & \text{for } |\mathbf{x} - \mathbf{x}_G| > r \end{cases}$$
(1)

where  $E_G$  represents the maximum enhancement factor for growth occurring on top of glades (see Tables S3,4 for symbols and units). The availability of resources at any location within the system is provided by the function:

$$V(\boldsymbol{x},t) = G(\boldsymbol{x})V_0 \tag{2}$$

ii) *Resource gradient*, which we implemented in two different ways:

*continuously*, with a progressive change in resource availability along the horizontal axis, using the following improvement function:

$$F(x) = \frac{(E_{\nabla} - 1)}{N \, dx} x + 1, \tag{3}$$

where *x* represents the horizontal coordinate of the position within the 2D system and  $E_{\nabla}$  represents the maximum improvement at the rightmost side of the system (i.e.  $F(dxN) = E_{\nabla}$ ). Thus, resources increase from left (no improvement, i.e. F(0)=1) to right, but remain constant in the vertical direction. This function aims to capture rainfall and/or resource gradients.

• *discontinuously*, i.e. an extreme form of the continuous gradient in which the left half of the 2D system sees no improvement (i.e.  $F(\mathbf{x})=I$ ), and there is a fixed improvement on the right half of the system (i.e.  $F(\mathbf{x})=E_{\nabla}$ ).

Regardless of the gradient, the availability of resources at any location within the system is provided by the function:

$$V(\mathbf{x},t) = F(\mathbf{x})V_0 \tag{4}$$

253

The vegetation landscape remains unchanged throughout the simulation, as we assume that the dead vegetation consumed by termites (see below) is naturally replenished annually. Vegetation does not carry over from year to year, i.e. unused vegetation during one year does not accumulate for the following year.

In the absence of resource heterogeneity F(x) = G(x) = 1, so that  $V(x, t) = V_0$  everywhere.

Colonies. A colony *i* is characterized at each time *t* by the biomass of its population,  $B_i(t)$ , the area of the mound that hosts such a population,  $A_{Mi}(t)$ , and the area of the associated foraging territory,  $A_i(t)$ . We assumed that termites forage for resources outwardly from the center of their mound, and that their exploration is only constrained by the presence of other colonies or by their own physiological limit. The latter was modeled by assuming a maximum foraging distance  $R_{max}$  from the center of the colony.

As in (16), we assume a logistic growth for the population biomass,  $B_i(t)$ :

$$\frac{dB_i(t)}{dt} = \mu \left( 1 - \frac{B_i}{B_{max}} \right) B_i - mB_i \tag{5}$$

- where  $\mu$  is the population growth rate, *m* is the worker natural mortality rate, and  $B_{max}$  is the carrying capacity (see parameter units and values in Table S4). The latter is never reached, as natural mortality imposes a saturation level equal to  $B_{max}(1-m/\mu)$ . Note that we assumed a constant individual biomass,  $B_{ind}$ , which means that Eq.(5) also allows us to track the dynamics of the number of individuals within the colony. Depending on their biomass level, colonies are either "mature" (those for which their biomass surpasses a certain level,  $B_i > B_{mat}$ ) or, otherwise, "incipient".
- Foraging territory. As the population grows, so does the need for resources to sustain this growth. Specifically, we assumed the amount of resources needed to support a given population level,  $\rho_i^{need}$ , to be:

$$\rho_i^{need}(t) = \frac{1}{c} B_i(t),\tag{6}$$

where c is the termite assimilation efficiency, i.e. how much termite biomass is produced per unit of resource biomass. Therefore, in order for a colony to grow, its foraging territory needs to contain at least the level of resources indicated by Eq.(6).

The total resources available to a colony, on the other hand, are given by the dead vegetation accumulated throughout the year within its foraging territory. Thus, if  $m_V$  represents the vegetation mortality rate, which we assumed to be constant throughout the system, the total resource available each year for a colony *i* was

277 we assumed to be constant throughout the system, the total resource available each year for a colony *i* was 278 given by:

$$\rho_i(t) = \int_{A_i(t)} m_V \int V(x, t') dt' dx \tag{7}$$

279 This available-resource level was compared at the beginning of the year with the level of resources needed to support population growth. If  $\rho_i^{need} > \rho_i$ , the foraging territory was expanded to meet the resource 280 requirements, using to that end any free space available (i.e. space not claimed by other colonies). If, on the 281 contrary,  $\rho_i^{need} < \rho_i$ , the foraging territory was reduced preferentially from the farthest points of the territory, 282 as the individuals can afford to stay closer to the nest and still fulfill the resource requirements set by Eq.(6). 283 284 The balance between available and needed resources was computationally sought following a series of 285 territory expansions and contractions, although some margin of error was allowed to avoid infinite computational loops. If resource needs could not be matched, the population growth was consequently 286 arrested and  $B_i(t)$  grew only as much as could be supported by the available resources. 287

288 Mounds. The center of a mound is originally placed at the landing site of the founding alates (see Reproduction section below) and the mound grows circularly outward. Termites expand the colony's 289 290 foraging territory also circularly outward from this landing site but, depending on the available space, the 291 territory may be able to expand more in certain directions than in others. Unlike in the model we developed 292 in (16), where we assumed that the mound area was a fraction of the territory area, here we allowed these 293 two variables to be decoupled: a colony *i* with a given biomass required not only a certain resource level, but also a certain mound size,  $A_{Mi}^{need}(t)$  (e.g., a certain number of fungal comb chambers for the fungus growing termites (6-10)). Increases in population biomass occurred only if the updated territory could host 294 295 the mound of area  $A_{Mi}^{need}(t)$  required by the updated population (i.e. the mound could fit within the foraging territory,  $A_{Mi}^{need}(t) < A_i(t)$ ). Unlike the foraging territory, which can take any contiguous shape, we required that the mound remain circular. Consequently, mound growth attempts may be precluded by the proximity 296 297 298 299 of the mound to the territory border, which could happen if, e.g., the territory is not circular. In these cases, 300 in order for the colony to achieve as much mound growth as possible, we included the possibility that mounds can move slightly towards the interior of the territory; nest movement occurs in many social-insect 301 302 taxa (31), and we have observed it in Odontotermes at MRC (after constructing an experimental rain shelter 303 above a mound, the mound shifted  $\sim 2$  m to the south, so that it was just outside the shelter. We implemented

this movement through an iterative process: the mound traveled away from the border by moving the center from nearest neighbor pixel to nearest neighbor pixel in the direction that takes the mound farthest from such a border; as long as the distance that a mound travels per year does not surpass a specific limit,  $v_M$ , the process is repeated until either (i)  $A_{Mi}^{need}(t)$  is realized, or (ii) no additional step grants any increase in allocated mound area. Whenever the updated mound area accommodated within the foraging territory remained below the needs of the colony, i.e.  $A_{Mi}^{need}(t) > A_{Mi}(t)$ , the growth of the population was arrested and  $B_i(t)$  was set to the population biomass that can fit into the realized mound area. Any consequent excess of resources was eliminated via territory shrinking (see above).

The mound area needed to host a colony of a given population biomass,  $A_{Mi}^{need}(t)$ , was given by the expression:

$$A_{Mi}^{need}(t) = \frac{B_i(t)}{n \, w_c w_{ratio}},\tag{8}$$

where *n* represents the number of chambers per unit area,  $w_{ratio}$  represents the ratio of sterile termites to fungus comb dry weight,  $w_c$  the dry weight for a typical comb (see Table S4). Here we assumed one single comb per chamber. As described in section *Odontotermes termite mounds* above, in order to obtain this expression we fitted available data on the number of chambers per mound as a function of the mound area (6-10) using linear regression and assuming that the curve goes through (0,0) (i.e. zero-area mounds have zero chambers). Thus, *n* was the only remaining parameter to be derived. The entire factor multiplying  $B_i(t)$ in Eq.(8) represents the mound area required to host a gram of termite.

- Eq.(8) and rules in this section were applied every time there was an increase in the colony's population biomass, as the population reassessed the need for space. On the other hand, a sudden decrease in the population led to unused parts of the mound (i.e.  $A_{Mi}^{need}(t) < A_{Mi}(t)$ ), which degrade slowly. To reflect this degradation, the area of the mound shrunk from the border towards the center at a rate  $r_{sh}$  until the discrepancy between mound area needed and mound area occupied disappeared.
- In this model, we also differentiated between two types of mounds: active mounds (i.e. mounds that belongto a colony) and abandoned mounds (mounds that belonged to a colony that is now dead). The rules above
- thus applied for the former, whereas the latter led to legacy effects (see below).
- 329 *Reproduction*. Reproduction is a discrete event that happens once a year (consistent with the fact that in most systems reproduction happens annually after the rainy season). Only mature colonies reproduce. 330 During reproduction events, a fraction of the population that represents alates flies away in pairs to try to 331 332 start a new settlement. The alates fly at random in every direction. For simplicity, we assumed that the 333 dispersal kernel for alates is larger than the simulated landscape, and that the number of alate pairs per 334 colony is large enough to potentially cover the available free space. For a pair of alates to successfully start 335 an incipient colony, their landing place had to fulfill three conditions: (a) it must not be part of the territory of another colony, nor coincide with any part of an abandoned mound that is partially or fully occupied by 336 337 a colony's territory; (b) the available surrounding space must be sufficiently large to fit an initial territory 338 of circular area  $A_{min}$ ; and (c) it must be at a minimum distance  $R_{set}$  from any mature colony (in other words, if we draw a circle of radius  $R_{set}$  around the landing location, it should not intersect the territory of any 339 340 mature colony; see Table S4 for values used for these parameters). These three conditions reflect the harsh 341 conditions faced by starting colonies.
- 342 *Colony mortality.* Mature colonies are subject to natural mortality, which we assumed happened at a rate 343 *D.* Incipient colonies are subject to other multiple sources of mortality (alate settlement constraints
- discussed above, competition for resources discussed below) that supersede natural mortality.

Competition for resources. Colonies expand their foraging territories as dictated by their need for resources. However, neighboring territories can constrain this expansion. When this happens, we assumed that conflicts ensue with a certain probability that depends on the size of both colonies (and thus on their need to grow). Following the previous model, we assumed that the probability for colony *i* to enter in conflict with a neighboring colony *j* is given by:

$$P(i \text{ and } j \text{ conflict}) = P(i \text{ seeks conflict}) \cdot P(j \text{ seeks conflict})$$
(9)

350 where:

$$P(i \text{ seeks conflict}) = \frac{1}{1 + e^{-\beta_2(1 - \alpha_2 S_i(t))}}, \qquad S_i(t) = \frac{B_i(t)}{B_{max}}$$
(10)

We assumed conflict resolution to also be probabilistic and dependent on the relative sizes of the fighting colonies: thus, colony *i* defeats colony *j* with probability:

$$P(i \text{ defeats } j) = \frac{1}{1 + e^{-\beta \left(1 - \alpha S_j(t) / S_i(t)\right)}}, \qquad (11)$$

353 If i does not defeat j, the probability for j to defeat i is given by P(j defeats i) and, with the remaining probability, the two colonies coexist. In the latter case, neither colony is able to expand in the direction 354 355 where the conflict arose. Otherwise, the loser is eliminated, whereas the winner, say colony *i*, remains alive with a population that is decimated due to the conflict in proportion to the biomass of the losing colony: 356  $B_i'(t) = B_i(t)(1 - B_i(t)/B_i(t))$ . If the winner happens to have a smaller population than the loser, its population 357 358 is reduced to a fixed fraction q, i.e.  $B_i'(t) = q B_i(t)$ . Either way, the winner's area is reduced according to Eq.(6) (using the average level of resources per unit area within the territory to transform biomass reduction 359 into area). 360

Colonies that are fully surrounded by one colony (e.g., in cases where a colony expanded its territory and engulfed a smaller neighboring colony) are assumed to be killed instantly. Clusters of such colonies, however, do not disappear instantaneously, as the engulfing colony needs to fight each one of them

364 individually.

Legacy effects. Unlike in the model we developed in (16), here we assumed that when a colony dies its mound does not immediately disappear, and thus can potentially be reused by other colonies (32, 33). We excluded from this rule colonies that, for any reason, fall below the detectability limit,  $A_{min}$ . Abandoned mounds that are not reused and transformed into an active mound degrade with time and, as a consequence, shrink starting with the edges of the mound. Thus, we assumed that abandoned mounds reduce their radius at a rate  $r_{sh}$ , until they are reused by a colony or until their area falls below  $A_{Mmin}$ .

The territory of an expanding colony can overlap with an arbitrary number of such abandoned mounds. For simplicity, we assumed that abandoned mounds can only overlap, however, with the territory of one single expanding colony at a time. Therefore, if an abandoned mound is partially or fully overlapping with the foraging territory of an expanding colony, no other expanding colony is able to invade any part of the abandoned mound (which is consistent with a system with antagonistic intraspecific interactions).

We considered that an abandoned mound is reused by a colony (and therefore becomes its *active* mound) under two circumstances: (i) the landing place for a pair of alates is any part of an available abandoned mound, in which case the center of the abandoned mound becomes the founding site for the incipient colony; (ii) in its search for more space, an active mound that is "traveling" to the interior of the territory overlaps so much with the abandoned mound that the center of the active mound enters any part of the abandoned mound. In the latter case, we considered that the active and abandoned mounds become almost indistinguishable and, consequently, we assumed the abandoned mound to be completely and instantaneously (i.e. within one time step, which is equivalent to the span of one year) overtaken by the active one. In both cases, if the colony's population requires an area smaller than the inherited one, i.e.  $A_{Mi}^{need}(t) < A_{Mi}(t)$ , we assumed that the mound continues to degrade and shrink until the population growth catches up with the mound size (see *Mounds* section). The parts of the abandoned mound that overlap with the new mound are used and maintained by the new colony, which therefore prevents such parts from degrading over time.

When a colony is killed, it leaves behind a newly abandoned mound and "frees" any abandoned mound that existed on its foraging territory. Any existing overlap between the newly abandoned mound and previously abandoned mounds is resolved in favor of the newcomer, on account of those overlapping parts being maintained by its colony until it was killed, and therefore following its same fate.

*Ecosystem engineering.* Because here we focused on *Odontotermes*, we assumed that the presence of the termites and their ecosystem engineering on the mound (increase in water infiltration due to gallery excavation and increase in soil fertility due to accumulation of dead organic matter in the galleries) lead to an overall improvement of the growth conditions for vegetation. Akin to our implementation for glades, we implemented such improvement effectively using:

$$H(\mathbf{x},t) = \begin{cases} E_M & \text{for } |\mathbf{x} - \mathbf{x}_M| \le r/2 \\ 1 + 2(E_M - 1)(1 - |\mathbf{x} - \mathbf{x}_M|/r) & \text{for } r/2 < |\mathbf{x} - \mathbf{x}_M| \le r \\ 1 & \text{for } |\mathbf{x} - \mathbf{x}_M| > r \end{cases}$$
(12)

Where  $x_M$  is the center of the mound, r is the mound radius, i.e.  $\sqrt{A_{Mi}(t)/\pi}$ , and  $E_M$  is the maximum enhancement on the mound.

Based on empirical measurements, we assume that the plant growth improvement on glades exceeds that on mounds; specifically, we assumed that glades improve vegetation growth as much as 100%, and termite engineering as much as 50%, which sets the values for  $E_G$  and  $E_M$ , respectively (see Table S4). There are no available data for the combined effect of glades and mounds (i.e. when mounds are within the glades); in that case, we conservatively assume that the glade effect supersedes the mound effect. Consequently, in a landscape that has both mounds and glades, the vegetation density is given by:

$$V(\mathbf{x},t) = \max(G(\mathbf{x}), H(\mathbf{x},t))V_0, \tag{13}$$

that is, plant availability at location x is enhanced by the presence of glades *or* mounds, and remains unchanged otherwise.

408 In a landscape without glades but with mounds, plant availability is given by  $V(\mathbf{x}, t) = F(\mathbf{x})H(\mathbf{x}, t)V_0$ .

Initial conditions and parametrization. As initial conditions, we considered one single colony of territory size  $A_{min}$  formed by two individuals (a queen and a king) placed at a randomly selected point of the system. The system is composed of 2048·2048 pixels, and our chosen resolution dx = dy = 0.5m leads to a system size of 1024·1024 meters, i.e. similar in size to our field grid (see main text). We parameterized the vegetation components accordingly to our focal system (black-cotton savanna at the Mpala Research Center, Laikipia, Kenya). In addition, we parameterized the termite components by drawing on existing

415 knowledge of *Odontotermes*, when available, and from the sister genus *Macrotermes* otherwise. See

416 parameters in Table S4.

### 417 The effect of regularity on net productivity

- 418 Both mounds and glades enhance productivity (i.e., plant and animal biomass); this effect is greatest on the
- 419 mound or glade itself, but also extends beyond the borders of the mound/glade and diminishes with distance
- 420 (3, 14, 34, 35). The exact functional forms of these diminishing effects on productivity have not been 421 quantified, but available data suggest that they are qualitatively similar for mounds and glades (14, 34).
- 422 Accordingly, to study the effect of regularity on productivity we assumed the same functional form linking
- 423 productivity and distance to mounds and/or glades: productivity is highest on the mound/glade and declines
- 424 beyond the edge with a change in convexity (i.e., a sigmoid-like function) until no effect is perceptible. The
- 425 results were qualitatively equivalent if, instead, we assumed a convex or concave decline. We further
- 426 assumed the maximum productivity on glades to be double that of mounds, and that the distance at which
- 427 glade effects completely attenuate (80m; (3, 34) is double than that of mounds (40m; (14)).
- Because the interaction effect between mounds and glades has not been empirically quantified, we conservatively assumed that a given point in the landscape is influenced by the feature that has the strongest effect at that point (either the nearest mound or the nearest glade), but not by both. Thus, at a location x at distance  $r_{\bullet}(x) = |x - x_{n\bullet}|$  from the nearest mound/glade (where  $\bullet$  is a placeholder index for either m, in the case of mounds, or g, in the case of glades), the net productivity is:

$$prod(\mathbf{x}) = max\left(f_m(r_m(\mathbf{x})), f_g(r_g(\mathbf{x}))\right)$$
(14)

433 where the productivity function is given by

$$f_{\bullet}(y) = f_{MAX,\bullet} \cdot e^{-a y^2}, \qquad \text{where} \quad a = \frac{\log \log \left( f_{MAX,\bullet} / f_{MIN} \right)}{r_{MAX,\bullet}^2}$$
(15)

434  $f_{MAX,\blacksquare}$  represents the maximum productivity (which we take to be 1 on mounds and 2 on glades),  $f_{MIN}$ 435 represents the minimum value for the function (negligible, but not exactly zero for technical reasons —see 436 equations above— taken to be the same for both mounds and glades), and  $r_{MAX,\blacksquare}$  represents the maximum 437 range for the function, i.e. distance from the center of the mound/glade beyond which productivity is 438 minimal (40m for mounds and 80m for glades, see above). Fig. S8 shows two examples of the productivity 439 landscapes resulting from these functions.

440

### **FIGURES**



**Figure S1.** Map of study area within Mpala Research Centre showing sampled mounds of *O. montanus* (white circles) and *O. anceps* (yellow triangles). Glades are shown in red. Yellow bounding box shows the area where mounds were mapped using Pleiades-1 satellite imagery of Kenya copyright 2013 CNES/Astrium (GeoTIFF file supplied by Apollo Mapping, Boulder, Colorado, USA) to produce the pair-correlation function in Fig. S9 (corresponding to the 'Kenya 2' region in (16).



Figure S2. Average relatedness between termite colonies is not predicted by geographic distance at the local scale. (A) Inter-individual relatedness  $(F_{ii})$  for termites from different mounds <60m apart not on glades (blue), from different mounds on glades (all <60m apart, purple), and within the same mound (green). Vertical lines indicate means. Termites from different mounds on glades were significantly less related than termites from the same mound, and there was no significant difference in relatedness among individuals from mounds on glades as compared to mounds off glades of similar distances (Table S2). (B) Genetic distance (Nei's D) between termite colonies (mounds) plotted against geographic distance for all mounds (main plot) and mounds <150m apart (inset); points represent all pairwise comparisons between sampled mounds, where larger D indicates lower relatedness. Red lines show the predicted values (derived from a generalized additive model, GAM) (C) Genetic distance (Nei's D) among mounds up to 150 m apart, representing the range of observed distances between nearest neighbors, for neighboring mounds (pink) and non-neighboring mounds (blue). Vertical lines indicate means. There was no significant difference between relatedness among neighbors and non-neighbors at distances <150m (p = 0.09). Overall, genetic distance increased slightly with distance for mounds up to ~1000 m and then leveled out for distances >1000 m, with a significant isolation by distance pattern when all distances are included (Mantel R = 0.17, p < 0.001); at the smaller scale, there was no significant relationship between genetic and geographic distances on average (GAM R<sup>2</sup> = -0.001, p = 0.66). However, the small minority of closely related colonies (D < 0.05) were all <1000 m apart, and the four most closely related pairs (D <(0.025) were nearest neighbors <50 m apart. Thus, although most dispersal occurs at scales <1000 m and the most related mounds were neighbors, neighboring mounds are more likely to be unrelated than highly related.



Figure S3. (A) Mammalian herbivore dung density decreases as distance from glade edge increases. Open circles represent all taxa combined. The "Other" category includes African buffalo, reticulated giraffe, and common warthog. See text above for species included in the Antelope category. (B) Proportion of dung surveyed that contained termite signs (shaded). Numbers on top of bars are the sample sizes of dung piles examined for each large-herbivore species.



**Figure S4.** Temporal behavior of the system: (A) mean territory radius, (B) mean number of termites per colony, (C) mean mound radius, and (D) total number of mature colonies (equivalently, mounds) for four levels of resource density. Note that "effective radius" refers to the radius calculated from the area by assuming that the territory is circular, i.e. as  $(\operatorname{area}/\pi)^{1/2}$ . The number of replicates used was 100 for the lowest density level, 15 for the highest, and 50 for the intermediate levels; the diversity of replicates is justified as the number of mounds (and therefore the statistical power) in the system increased with resource density.



**Figure S5.** (A-C) Probability distributions for spatial indicators for the baseline resource density level,  $V_0=250 \text{ gr}\cdot\text{m}^{-2}$ . (D-F) Comparison with other resource levels. A) and D) probability distribution for the distance between nearest neighbors; B) and E) probability distribution for the number of nearest neighbors per mound; and C) and F) probability distribution for the angle between nearest neighbors. For a-c, the shaded area represents confidence intervals. Throughout, lines represent the kernel density (i.e. smoothed version of the histogram), obtained with the R function "density".



**Figure S6.** (A) Probability distribution for mound-to-territory area ratio for four different resource levels. (B) Comparison between two different outputs of the model with different mound-to-territory area ratios, obtained by decreasing the comb weight from wc=75gr/comb (red curve) to wc=5gr/comb (purple curve). The resource level is the same (baseline, 250g/m2) in both cases. The colored shad-ed regions represent 90% confidence intervals; the light grey shaded area represents the significance envelope for the red curve; the darker grey curves are the limits of the significance envelope corresponding to the purple curve (in other words, the two significance envelopes overlap).



Figure S7. (A) Within-colony resource availability and (B) territory area for colonies as a function of the distance to the center of the glade. Each red dot represents one colony. The points with negligible resource density or territory area correspond to abandoned mounds. (C-E) Nearest-neighbor distributions for different types of heterogeneity shown relative to the baseline case: (C) one large glade; (D) continuous gradient; (E) discontinuous gradient.



**Figure S8.** Measuring productivity. (A) The productivity at each location of a landscape resulting from our model with baseline homogeneous resources. (B) The productivity at each location of a landscape resulting from our model with heterogeneity introduced by regularly distributed glades and baseline resource level in between the glades. Insets show 200x200m zooms; the color bar reflects the productivity level (red = highest productivity; blue = lowest) and is the same in both (A) and (B).



**Figure S9.** Pair correlation functions obtained with the model (orange) and published data from Tarnita et al. (16) (their 'Kenya 2', blue). The latter area was a  $\sim 1.2 \text{ km}^2$  subset of the focal area in the present study (Fig. S1). Nearest-neighbor distances vary across our study area (Figs. 2A and S1) and differed by 17 m between the model output and the mapped subregion; here the distance (horizontal) axis is normalized to facilitate comparison of degree of regularity. Light gray indicate the significance envelopes for the model, and dark grey the outer boundaries for those of the Kenya 2 site.

### TABLES

(Intercept)	Distance to Nearest Glade (m)	Mean Mound Diameter (m)	Interactio n	df	$\mathbb{R}^2$	logLik	AICc	ΔAIC c
5.15	0.05	7.64		4	0.37	- 823.47	1655.1	0.00
1.91	0.08	8.46	-0.007	5	0.37	- 823.11	1656.5	1.40
7.35		8.70		3	0.29	836.21	1678.5	23.41
34.13	0.07			3	0.16	- 853.70	1713.5	58.39
43.03				2		- 871.59	1747.2	92.11

**Table S1.** Generalized linear models and AIC model selection criteria for predictors of the distance between neighboring mounds.

**Table S2.** Summary of ANOVA and null model test results for comparison of genetic relatedness ( $F_{ij}$ ) among individuals within a mound (mound), among mounds on glades (glade), and among mounds off-glades within 60 m apart (0 – 60 m). P values are the proportion of simulated *F* values, out of 1,000, that were as large or larger than the observed.

Comparison	df	F value	p value
mound : glade	1, 191	2100	0
mound : 0 - 60 m	1, 315	3262	0
glade : 0 - 60 m	1, 218	1.63	0.18

Symbol	Description	Units
$B_i(t)$	Population biomass for colony <i>i</i>	g (termite)
$\rho_i(t)$	Resource available within colony <i>i</i> territory	g (vegetation)
$\rho_{i}^{\mathrm{need}}\left(t\right)$	Resource requirement for colony <i>i</i>	g (vegetation)
$R_i(t)$	Largest radius of colony <i>i</i> 's foraging territory	m
$A_i(t)$	Foraging area for colony <i>i</i>	$m^2$
$A_{Mi}^{need}(t)$	Mound area needed to host colony <i>i</i>	$m^2$
$A_{Mi}(t)$	Realized mound area for colony <i>i</i>	$m^2$
$S_i(t)$	Fraction of the maximum possible biomass for a colony	-
$V(\boldsymbol{x},t)$	Live vegetation biomass at location $\boldsymbol{x}$	Kg $m^{-2}$
$f_p(r)$	Productivity function, where $r$ is distance to mound	-

**Table S3:** List of variables for the termite model. Note that only  $B_i(t)$  is an *independent* variable, as the rest of the variables in this table can be calculated using either  $B_i(t)$  or V(x,t) using the equations above.

Table S4: List of parameters for the model, and associated sources for their value.

Symbol	Description	Value Units		Source
R <sub>max</sub>	Maximum foraging radius	40	m	Estimate from sister genus, <i>Macrotermes</i> (36)
B <sub>max</sub>	Maximum possible colony biomass (carrying capacity)	$B_{ind} \times (2 \times 10^6)$	g (termite)	Estimates for other Rhinotermitidae species from diverse habitats include >300,000 (37), >800,000 (38), to >2 and >3 million (39).
B <sub>mat</sub>	Maturity/reproduction threshold	$B_{max} \times 0.5$	g (termite)	Chosen as half $B_{\text{max}}$ (40). This choice does not influence results qualitatively.
B <sub>ind</sub>	Biomass of individual termite	1×10 <sup>-3</sup>	g (termite) individual <sup>-1</sup>	Based on dry weights for individuals of <i>O. montanus</i> (18).
R <sub>set</sub>	Exclusion distance from mature colonies for settlement of alates	$0.15 \times R_{mat}$	m	Conservative assumption based on own observations. This choice does not influence the results qualitatively.
с	Biomass conversion factor	0.06	g(termite) g <sup>-1</sup> (res)	Plausible value of termite dry biomass production per plant biomass consumed in a semi-arid savanna, based on data for termite species in Sahelian savanna (41).
μ	Colony population birth rate	6.00	year-1	Growth rate such that max size reached in 3 years (assumed to be smaller than that of largest colony species (40)).

т	Per capita worker natural mortality rate	1.00	year <sup>-1</sup>	We assume the maximum lifetime of neuters $\approx 1$ year (42).
D	Death rate of mature colonies	0.04	year-1	Based on lifespan of ~25 years, which falls within the cross-taxa range for termites (42).
α	Reference value, conflict outcome probability	1.05	-	Unknown. Chosen to ensure that wars result in
β	Shape factor for conflict outcome probability	150.00	-	coexistence only when colonies have very similar sizes (based on the assumption that the war is a "war of attrition" (43-45)).
$\alpha_2$	Reference value for conflict probability	2.25	-	Unknown. Chosen to accentuate the difference in
$\beta_2$	Shape factor for conflict probability	10.00	-	expansionistic tendencies as a function of colony size.
q	Shrinking factor for small winning colonies	0.1	-	Unknown. Chosen to be small but does not affect qualitative behavior.
<i>r</i> <sub>sh</sub>	Mound degradation and retracement rate	5%	year-1	Unknown.
$v_M$	Maximum distance that a mound can move per year	2	m	Conservative estimate based on own observations.
Wratio	Ratio sterile termite biomass to fungal comb dry weight	0.47	g (termite) g <sup>-</sup> <sup>1</sup> (comb)	Based on estimates from <i>O</i> . <i>montanus</i> (7).
Wc	Mean fungal comb dry weight	75	g (comb)	Chosen within the range $161\pm107.68$ ; range obtained from averaging data in (6-10).
п	Number of combs per unit area (assuming one comb per chamber, and that all combs are alive)	0.000107	chambers m <sup>-2</sup>	Obtained from fitting data from (6-10) relating the number of chambers of a mound versus mound diameter.
$E_M$	Termite engineering improvement factor for vegetation growth	50%	-	Field measurements, Oct. 2018
$E_G$	Glade improvement factor for vegetation growth	2 (i.e., 100% improvement)	-	Based on data indicating ~ twofold higher aboveground net primary production in glades vs. non-glade sites at MRC across years (46).
$E_{ abla}$	Glade improvement factor for vegetation growth (gradient case)	2 (i.e., 100% improvement)	-	Maximum improvement at the rightmost side of the system in the gradient case (46).
$A_{min}$	Minimum viable area for a colony territory	$\pi \times 0.75^{2}$	m <sup>2</sup>	Taken equal to the minimum area of a detectable mound.
$A_{Mmin}$	Minimum area for termite mounds	-	m <sup>2</sup>	Calculated from defining the minimum distance from center to border for the first

				mound, at the initial condition for the simulation.
$V_0$	(Constant) vegetation density	Varied	Kg m <sup>-2</sup>	Characteristic of arid and semi-arid environments (47).
$m_V$	Vegetation mortality	0.05	year <sup>-1</sup>	Unknown.
r <sub>MAX,m</sub>	Maximum range prod. function for mounds	40	m	Chosen to be smaller/larger than the typical mature colony territory radius and consistent with (14).
f <sub>MAX,m</sub>	Maximum value prod. function for mounds	1	-	Chosen for the sake of generality
r <sub>MAX,g</sub>	Maximum range prod. function for glades	80	m	Chosen to be smaller/larger than the typical mature colony territory radius and consistent with (3, 34).
f <sub>MAX,g</sub>	Maximum value prod. function for glades	2	-	Chosen for the sake of generality
$f_{MIN}$	Minimum value productivity function	10-3	-	Chosen for mathematical convenience
Ν	Lateral grid size	2048	sites	Chosen for computational convenience.
dt	Integration time step	1	year	
dx, dy	Mesh sizes	0.5	m	Chosen for computational convenience.

Movie S1 (separate file). Video illustrating experimental setup for behavioral trials and examples of observed behaviors.

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