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LETTER

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

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Abstract

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 decades-to-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 ground-nesting 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 social-insect 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 fungus-farming termites in a well-studied focal system—semi-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

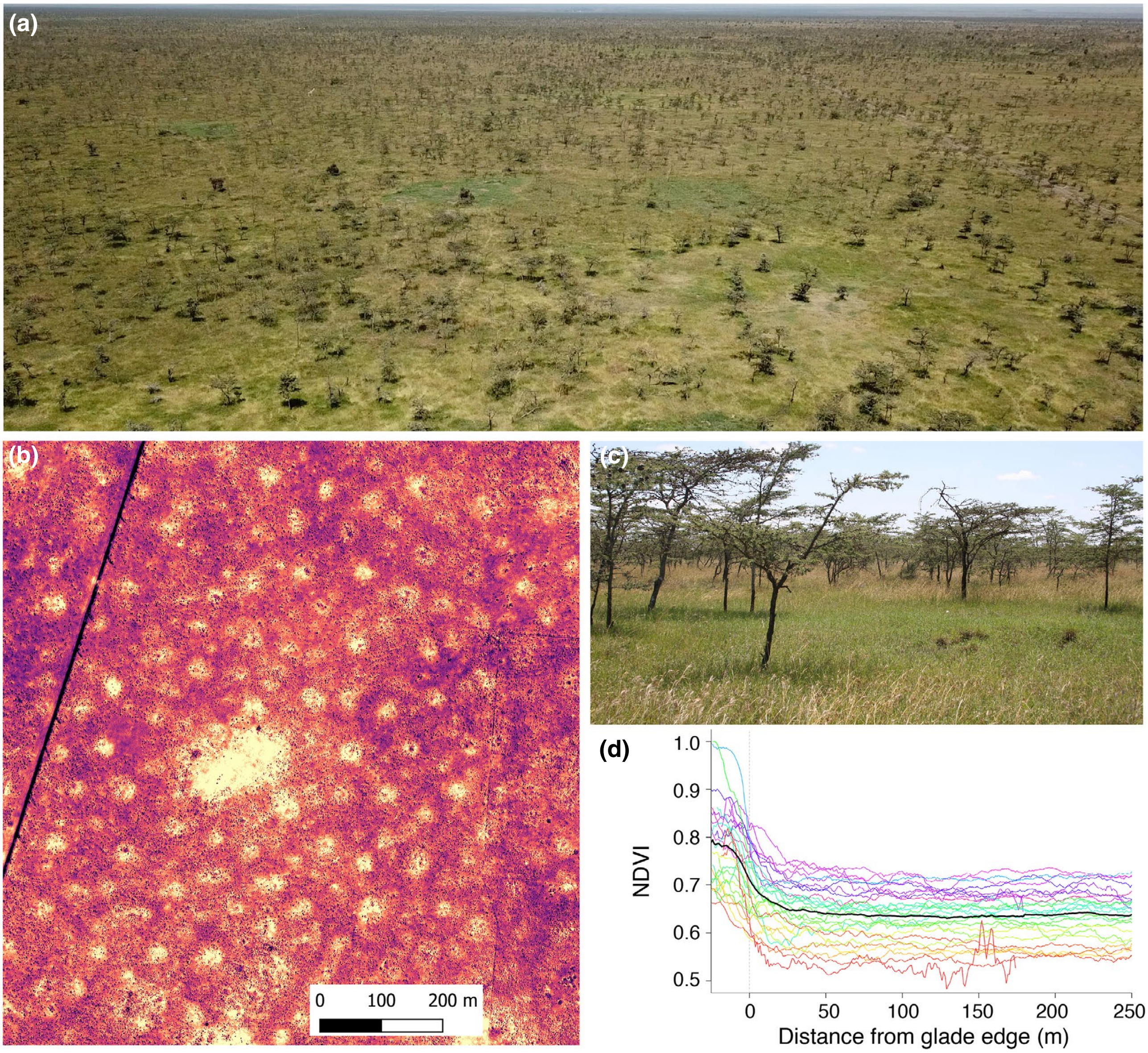

FIGURE 1 Natural and anthropogenic spatial heterogeneity in primary productivity. (a) Aerial image of the black-cotton ecosystem at MRC, which is ecologically homogeneous in most respects but comprises local variability in understory productivity (higher greenness). Two neighbouring glades (darker green 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 S1). 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^2 grid and tried to collect termites from at least one mound near the centre of each grid cell and up to five mounds ≤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-m × 1-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 ≤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 (≤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_{ij} 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_{ij} 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 non-neighbouring mounds on and off glades. We constructed an observation arena from clear acrylic, leaving a ~5-mm 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 large-scale 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 &

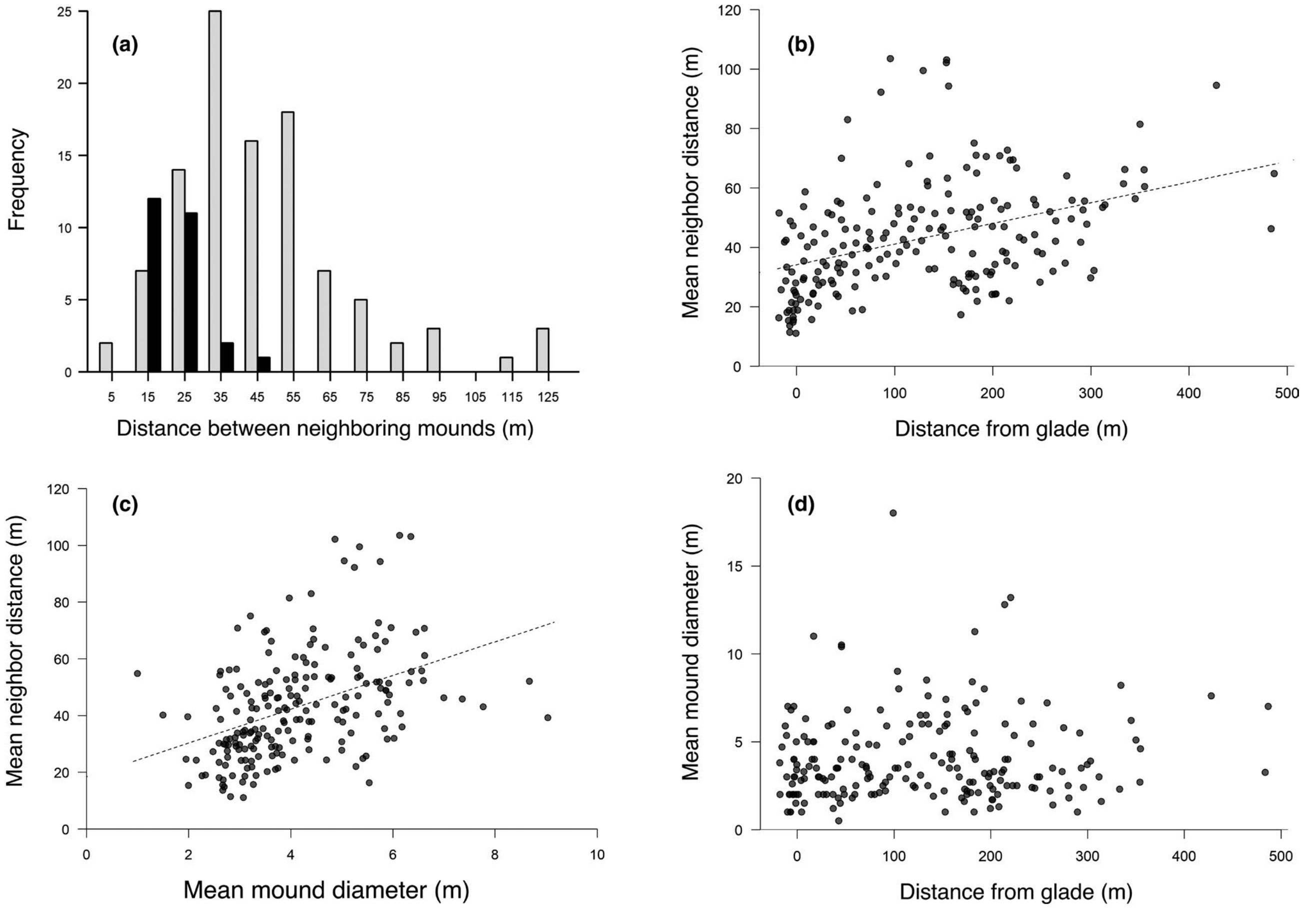

FIGURE 2 Distance between neighbouring mounds increased as functions of colony size and resource scarcity. (a) Frequency distribution of nearest-neighbour distances for mounds (n = 506 pairs) in glades (black) and off glades (grey). (b) Mean neighbour distance increased with distance from glade edge ($R^2 = 0.16$, $F_{1,199} = 38.77$, $p < 0.0001$); 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	A	1/1	37	–
Interspecific	3	4	*O. montanus*	*O. anceps*	Yes	A	1/1	14	–
Intraspecific	10	12	*O. montanus*	*O. montanus*	No	–	2/2	108	0.075
Intraspecific	2	11	*O. montanus*	*O. montanus*	No	A	1/1	1145	0.071
Intraspecific	3	13	*O. montanus*	*O. montanus*	No	A	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

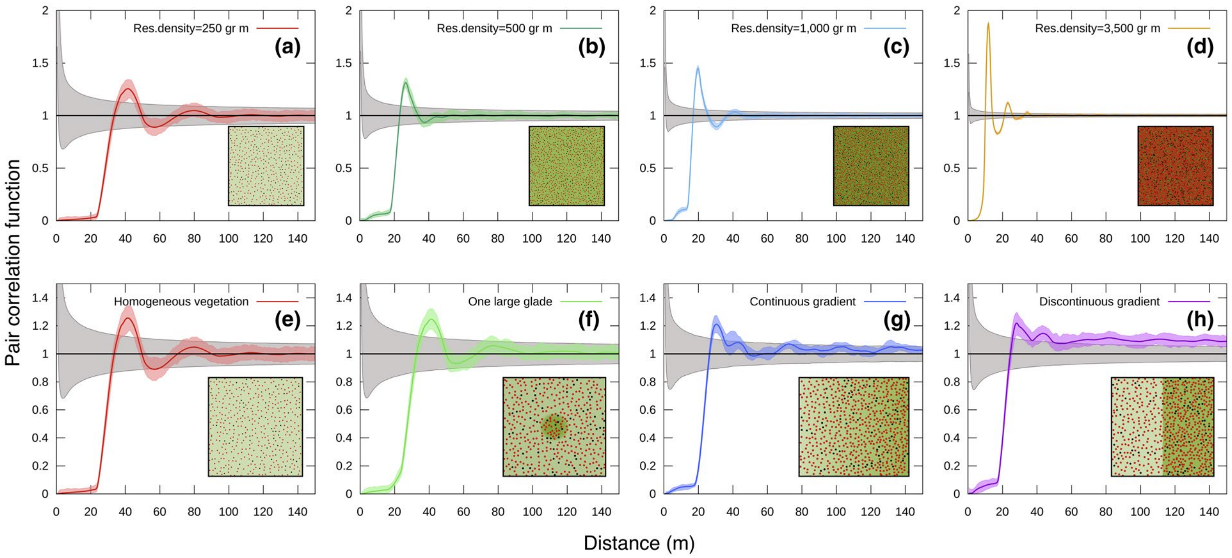

FIGURE 3 Greater resource density increases regularity, whereas background heterogeneity decreases regularity. (a–d) Pair correlation functions for homogeneous landscapes with varying resource levels, in units of grams per square meter of vegetation: (a) 250 g m^{-2}, (b) 500 g m^{-2}, (c) 1000 g m^{-2} and (d) 3500 g m^{-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 across simulated replicates (see SI appendix). Insets show the landscape; red dots indicate mature mounds, black dots indicate abandoned mounds, and intensity of green coloration 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 ~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^2 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-to-territory 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-resource-level case, as both have similar mound densities. Decreasing this parameter by 15-fold increased mound-to-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 second-nearest 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 nearest-neighbour 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

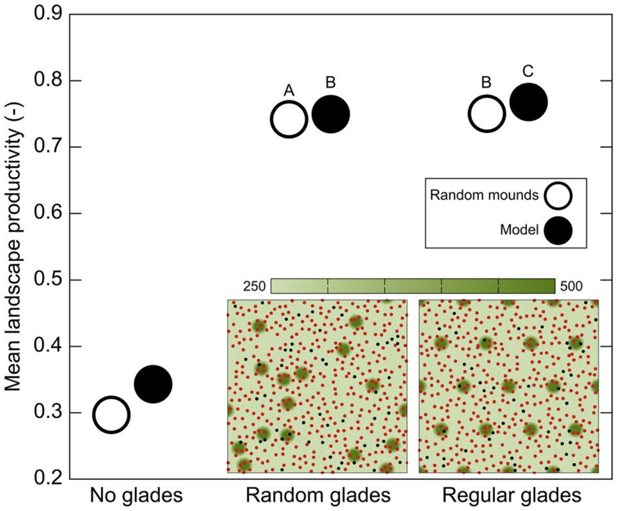

FIGURE 4 Spatial regularity of resource hotspots enhances ecosystem functioning. Comparison of mean average landscape productivity in a system with 250 g m^{-2} of matrix vegetation under different templates of resource heterogeneity: no glades (homogeneous resources), randomly distributed glades (left 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 × 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 sigmoid-like 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 nearest-neighbour distances that were inversely correlated with resource availability (cf. Dibner et al., 2015). Empirically, we confirmed this prediction by comparing nearest-neighbour 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 termite-induced 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.

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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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