Spatial Self-Organization of Ecosystems: Integrating Multiple Mechanisms of Regular-Pattern Formation

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Abstract

Large-scale regular vegetation patterns are common in nature, but their causes are disputed. Whereas recent theory focuses on scale-dependent feedbacks as a potentially universal mechanism, earlier studies suggest that many regular spatial patterns result from territorial interference competition between colonies of social-insect ecosystem engineers, leading to hexagonally overdispersed nest sites and associated vegetation. Evidence for this latter mechanism is scattered throughout decades of disparate literature and lacks a unified conceptual framework, fueling skepticism about its generality in debates over the origins of patterned landscapes. We review these mechanisms and debates, finding evidence that spotted and gapped vegetation patterns generated by ants, termites, and other subterranean animals are globally widespread, locally important for ecosystem functioning, and consistent with models of intraspecific territoriality. Because these and other mechanisms of regular-pattern formation are not mutually exclusive and can coexist and interact at different scales, the prevailing theoretical outlook on spatial self-organization in ecology must expand to incorporate the dynamic interplay of multiple processes.

INTRODUCTION

Regular spatial patterns—periodic distributions of features that share a characteristic cluster size (126), as opposed to random configurations of heterogeneously sized clusters—are common in natural systems and convey important information about those systems' structure and function. Accordingly, pattern formation has long been a focus of research in nearly every field of biology, at levels of organization ranging from cells (161) and organisms (82, 111) to entire landscapes (46, 81, 123, 146), as well as in branches of chemistry, mathematics, physics, geology, and the social sciences. In ecology, "the problem of pattern and scale" (94, p. 1943) and its implications for populations and ecosystems have been central since the inception of the field (70).

One of the most intriguing aspects of regular patterning is that the configurations that emerge at different spatiotemporal scales and levels of organization are often strikingly similar. For example, the stripes and spots of tigers and leopards have nanometer-scale analogs in the corneal coats of insects (15) and kilometer-scale analogs in the banded and dotted patterns of vegetation in many terrestrial ecosystems worldwide (40, 126), which are the focus of our review. These similarities invite the supposition of a common underlying mechanism. Indeed, much research across disciplines has been inspired by the discovery, in the 1950s, that the coupling of positive and negative feedbacks operating at different rates or spatial scales can reproduce many of the regular patterns found in natural systems (151).

However, the appeal of universal explanations must be tempered by recognition that myriad processes operate simultaneously in complex systems, more than one of which might promote or modulate the emergence of regular patterns at different scales. This is perhaps especially true for spatial patterns in ecosystems, which have attracted scientists of diverse backgrounds—including zoologists, ecosystem ecologists, physicists, and mathematicians—to study a problem that spans all their fields. In such cases, distinct disciplinary literatures and narratives may evolve in parallel with little exchange between them, and controversies may ensue when disciplinary perspectives clash over interpretations of the same phenomena.

Large-scale regular spatial patterning in vegetation and other sessile or semisessile organisms has been documented with increasing frequency over the past 15 years. These discoveries have spurred the development of a largely theoretical literature that views patterns as the self-organized emergent consequence of scale-dependent positive and negative feedbacks (SDF) between organisms and limiting resources; in the case of vegetation patterns, which are the primary focus of our review, such feedbacks are typically thought to occur between plants and water. However, equally long-standing (albeit less cohesive and visible) literatures in entomology and animal behavior suggest a different mechanism by which some of these same patterns can be produced—namely, competition for space among social insects and other territorial animals that physically engineer their environments in ways that affect plant growth. These previously nonintersecting literatures have recently collided in debates over pattern genesis that pit these two mechanisms as competing alternatives. However, these mechanisms are not mutually exclusive; to the contrary, it has recently been found that multiple mechanisms can co-occur and interact within ecosystems to generate complex multiscale patterns (16, 98, 140). Reconciling these viewpoints is of more than just academic importance, as different patterning mechanisms can have divergent implications for ecosystem functioning and robustness in the face of anthropogenic perturbations such as habitat destruction and climate change.

Here, we seek to bridge these literatures, underscoring their fundamental compatibility, and to advocate a research agenda that couples vegetation self-organization and faunal ecosystem engineering to explain more completely the multiscale regular patterns observed in nature. We focus on these two mechanisms because both are globally widespread and feature prominently in recent debates, but we emphasize that they are not the only mechanisms that can produce regular patterns. We restrict our review to biotically generated, self-organized patterns rather than those arising from preexisting geological or other abiotic templates (i.e., emergent rather than imposed, sensu 133) or from human activity, although these latter classes, too, can coexist and interact with the mechanisms discussed here and must ultimately be incorporated into any comprehensive theory of regular patterning in ecosystems. We begin by reviewing the literature on patterning induced by SDF and ecosystem engineers, respectively. We then discuss the relationships between these two mechanisms and the opportunities for integrating them into a more encompassing unified framework.

THEORY OF REGULAR PATTERNING VIA SCALE-DEPENDENT FEEDBACKS

The increasing coverage and accessibility of high-resolution remotely sensed imagery during the 2000s, enormous quantities of which became freely available with the launch of Google Earth in 2005, has led to a rapid proliferation of studies reporting regular spatial patterns in terrestrial, freshwater, marine, and intertidal biomes (most frequently in tropical deserts and savannas, but also in subarctic peatlands, subtropical swamps, montane forests, Pacific reefs, and Atlantic mussel beds) (40, 126). The periodic patterns documented in these studies—including gaps, labyrinths, stripes, spots, and rings—can all be reproduced theoretically by models incorporating SDF. These models couple short-distance positive (activating) feedbacks with long-distance negative (inhibitory) feedbacks to explain emergent patterning in plants, mussels, corals, and fungi (7, 8, 41, 46, 63, 65, 81, 87–89, 106, 123, 124, 133, 141, 155). This activation-inhibition principle, famously invoked in Turing's (151) reaction-diffusion theory of morphogenesis, has long been central to models of pattern formation in both organismal (82, 111) and ecological contexts (93, 95), providing a rich mathematical foundation for SDF. In populations of sessile organisms, short-range positive feedbacks are produced by facilitation between neighboring individuals that benefit each other by increasing resource availability or ameliorating abiotic stress, whereas long-range inhibition results from resource competition between distant clusters of individuals. In drylands, the key resource is usually assumed to be water, which is locally concentrated by plants (e.g., via enhanced infiltration, reduced evaporation, or lateral-root transport) but becomes limiting as local plant biomass increases (65, 105, 106, 123). Similarly, mussels (*Mytilus* spp.) benefit locally from aggregation, which improves individual feeding efficiency and confers resistance to wave dislodgment; however, aggregation becomes costly at larger spatial scales owing to competition for food, which generates periodically distributed, characteristically sized clusters of individuals (98, 154, 155).

The SDF framework is seductively versatile and generalizable. Depending on the parameterization, SDF models can theoretically recapitulate most, if not all, of the large-scale spatial pattern morphologies discovered in ecosystems to date. Moreover, the key ingredients of competition, facilitation, and dispersal are ubiquitous in ecological communities, such that SDF models can be adapted to a wide range of contexts. Thus, SDF has been embraced as a unifying and arguably universal principle underlying large-scale self-organization in ecosystems—perhaps even "a necessary condition for self-organized patchiness to form" (124, p. 1928).

The potential generality of this framework notwithstanding, there is vanishingly little empirical support for the role of SDF in generating any of the large-scale patterns discussed above (17, 97, 100). This is due in part to the intractability of these patterns, which have wavelengths ranging from tens of meters to multiple kilometers and may take years, decades, or centuries to develop; definitive experimental manipulations of key processes are impossible over such scales. In lieu of such experiments, some investigators have gathered field data to validate assumptions and empirically measure parameter values (6, 46, 133, 153). Yet in many studies, evaluation of putative SDF-driven landscape patterning has been limited to matching model predictions with remotely sensed imagery, often without any ground truthing to verify that features in images are indeed what they are assumed to be. The resulting potential for misattribution has been a source of discomfort. Borgogno et al. (17) wrote, "A few major open issues emerge from this review: Most of the theories presented in this paper have not been quantitatively validated in the field. We are not aware of any conclusive experimental evidence that the vegetation patterns observed in many regions of the world are actually induced by mechanisms of symmetry-breaking instability" (p. 31).

This concern, coupled with skepticism about the assumptions and parameterization of some SDF models (79), suggests a need to evaluate alternative or complementary mechanisms associated with putative SDF-generated patterns. Indeed, studies over the past several years have revealed important nuances in the mechanistic interpretation of emergent regular patterns in nature (16, 21, 97–100), to which we return in the sections below.

HEXAGONAL SPACING OF ANIMAL TERRITORIES

Two years prior to the publication of Turing's (151) paper on reaction-diffusion morphogenesis, British geologist William Macfadyen provided an account of vegetation patterns in the semiarid desert plains of British Somaliland based on aerial reconnaissance (101). In it, he described "remarkable rhythmic patterns," including what he called "termitaria peppering" (p. 199) (**Figure 1*a***): a polka-dot pattern of overdispersed termite mounds "visible as pin points surrounded by bare ground" (p. 209) (101).

The extreme form of spatial overdispersion is a hexagonal lattice, which homogenously partitions area while maximizing distance between neighboring points (22, 142). This is expected under a model of spatial-pattern formation distinct from SDF: namely, interference competition within (and, perhaps, among) species of territorial animals. In 1968, Grant (61) calculated that male territories of Alaskan sandpipers (*Calidris melanotos*) were polygonal with boundary angles of ~120°, suggesting a honeycomb array of hexagonal territories. In this case, each individual should have six equidistant neighbors, with territory boundaries "set by a resolution of centripetal and centrifugal forces exercised by two neighbors" (61, p. 75). Grant hypothesized that such

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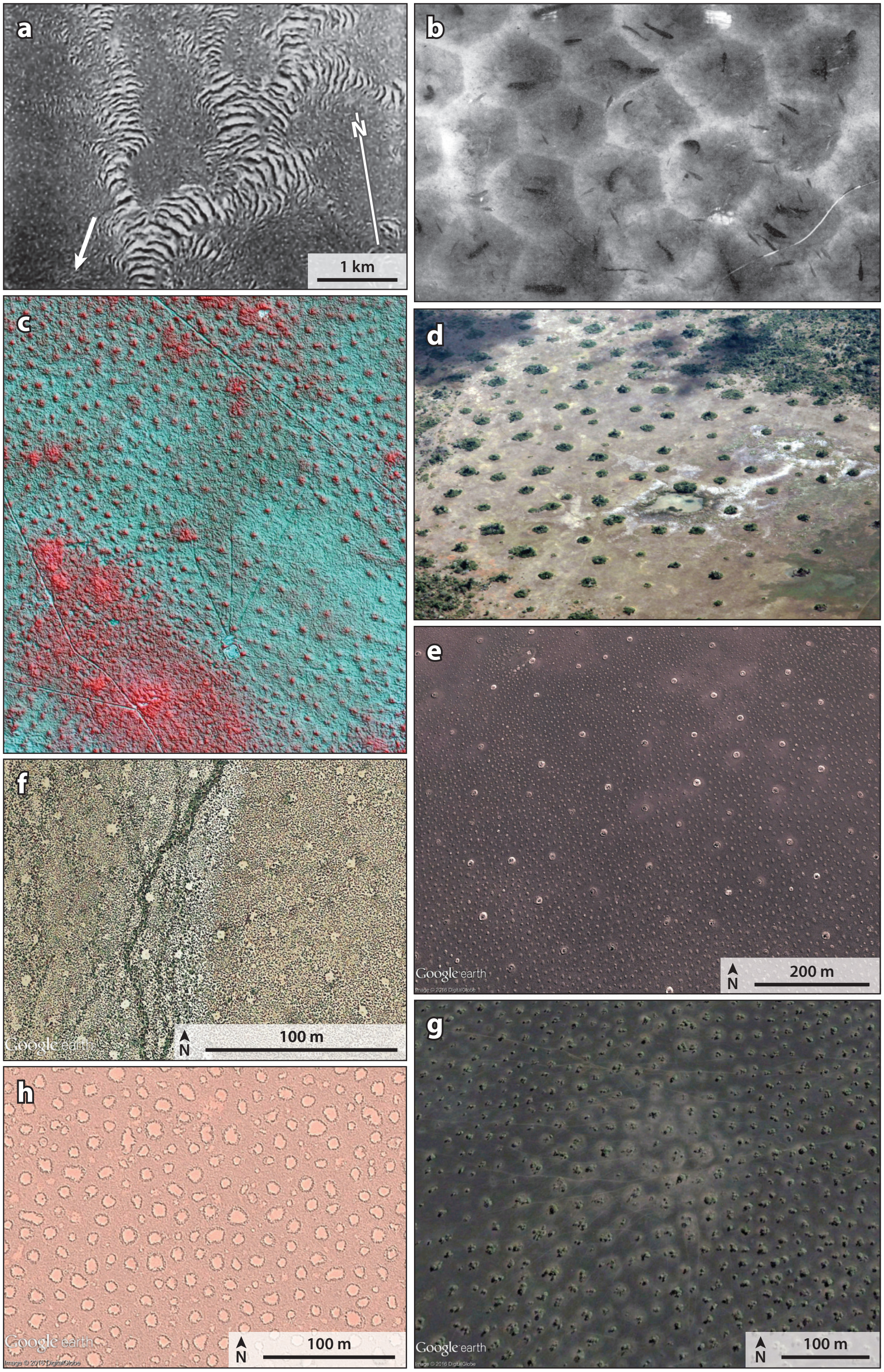
Figure 1

Examples of hexagonal spatial patterns created by animals (see Reference 140). (*a*) Macfadyen's (101) aerial photograph of "termitaria peppering" (*small white spots*) in Somalia; arrow indicates slope direction (adapted from Reference 101 with permission; permission conveyed through Copyright Clearance Center, Inc). (*b*) Hexagonal territories of male *Tilapia mossambica* fish (adapted from Reference 9 with permission from Elsevier). (*c*) False-color shaded-relief Pleiades (CNES/Astrium) satellite image of grass-covered *Odontotermes montanus* termite mounds (*small red bumps*) in savanna matrix at the Mpala Research Centre in Laikipia, Kenya (latitude: ~0.30, longitude: ~36.85); here, red color indicates areas of higher primary productivity as inferred from the red and near-infrared bands of the multispectral imagery (see Reference 120). (*d*) *Macrotermes* sp. termite mounds with associated woody-vegetation thickets in eastern Mozambique between Vilanculos and Gorongosa National Park (photo by R.M. Pringle). (*e*) Multiscale mound patterning, potentially created by two different social-insect species, in the Bangweulu floodplain, Zambia—an ecosystem described by explorer David Livingstone as "a world of water and anthills" (latitude: –11.113, longitude: 30.184). Imagery: Google, DigitalGlobe. (*f*) *Pogonmyrmex barbatus* ant nests in Arizona (latitude 36.255, longitude: –113.082) (138). Imagery: Google, DigitalGlobe. (*g*) Termite mounds with associated vegetation thickets in the Pantanal, Brazil (latitude: –11.943, longitude: −50.777). Imagery: Google, DigitalGlobe. (*h*) Fairy circles in Namibia (latitude: –24.996, longitude: 16.004) (see Reference 78).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hexagonal packing should occur for species with nonoverlapping territories in structurally homogeneous habitats but noted the logistical difficulty of mapping territory boundaries for most animal species.

Indeed, there remain few documented examples of hexagonal territory spacing among vertebrate animals in nature. Males of the mouthbrooding cichlid fish *Tilapia mossambica* (which delineate and defend territories by excavating shallow pits in the sand, facilitating mapping) produced hexagonal patterns when kept in laboratory ponds at unnaturally high densities (**Figure 1*b***), although this pattern deteriorated when densities decreased (9). Buckley & Buckley (19) documented hexagonal packing in nests of royal terns (*Sterna maxima*) in the wild, which they attributed to extreme antipredator gregariousness (producing high densities) coupled with behavioral defense of individual space. Analysis of scent marking by wolves (*Canis lupus*) on snow-covered terrain in Minnesota suggested that territories had six neighbors (115), as did a radio-telemetry study of urban foxes (*Vulpes vulpes*) in England (44).

Theoretical arguments ranging from the geometry of optimal space packing to dynamical models of local movements and interactions predict that strong intraspecific agonism in dense populations occupying homogenous environments should promote hexagonal distributions (3, 25, 64, 74, 119, 139). However, all authors emphasize that variability in abiotic templates, resource distributions, population contiguity and density, interspecific interactions, and individual traits can relax or obscure these patterns. These factors may explain why such patterns have rarely been reported in wild vertebrate populations.

Patterns of territorial dispersion have been most extensively documented for social insects—especially ground-nesting, central-place-foraging ants and termites—which often exhibit the pronounced regular spacing described by Macfadyen (101). Examples exist from deserts, grasslands, savannas, and forests on all six continents where termites and ants occur (96). Moreover, many of the taxa involved are ecosystem engineers that dramatically alter plant growth, such that overdispersion of colonies generates corresponding patterns in the vegetation (or lack thereof) associated with nest sites. Although familiar to many entomologists, this phenomenon is neither well understood nor widely known within ecology more broadly; it has rarely been connected with the parallel literature on vertebrate territoriality (but see 3) and has largely been ignored in the theoretical literature on vegetation self-organization despite often producing spotted and gapped patterns similar to those predicted by SDF models (16, 24, 27, 80, 123, 140).

We next explore in more detail the mechanisms and global generality of regular patterning in social-insect nests. We then relate this phenomenon back to the broader literature, arguing that the development of more encompassing (i.e., multimechanism, multitrophic, multiscale) theories of spatial self-organization is a promising avenue of research in basic and applied ecology.

OVERDISPERSION IN SOCIAL-INSECT NESTS: MECHANISMS AND GENERALITY

Territorial agonism and competition between colonies is extremely common in ants and termites (67, 143, 144). Conflicts at territory boundaries often result in the death of individual workers and incipient colonies (33) and can even lead to the annihilation of large, mature colonies (13, 114). Strong intraspecific competition in densely packed, homogeneous environments can produce spatial overdispersion of colonies (127), and both geometric optimization models (2, 3, 85) and dynamical models of neighborhood competition (140) suggest that territory distributions in such cases should tend toward hexagonal arrays. The mechanisms and conditions underlying the emergence of regular patterning in these systems are similar to those revealed in the vertebrate studies above. However, competition-driven self-organization in termites and ants may be especially likely (and amenable to quantitative study) because colonies of many species (*a*) build large nest structures from which they radially forage, producing centrifugal force in all directions (and making territory centers and sometimes boundaries easy to map); (*b*) produce vast quantities of aerially dispersing reproductives (alates), thereby saturating habitats and minimizing "empty" space; (*c*) are long-lived and often relatively insensitive to predation at the colony level, allowing time for spatial order to emerge; and (*d*) often recolonize abandoned nest structures (37, 116), producing a legacy effect that reinforces pattern formation over successive generations. Moreover, because strong asymmetries in colony size often differentiate between conflict winners and losers, territories of colonies that survive conflicts are likely to be similarly sized, which enhances regularity. These considerations pertain especially to soil-nesting species in unfragmented landscapes that can (at least in principle) exhaustively partition two-dimensional space, whereas underlying patchiness of plants may obscure patterning in arboreal or cavity-nesting taxa (but see 18).

Most studies assume that nest spacing is maintained by direct aggression between workers of neighboring colonies. However, behavioral avoidance and/or exploitation competition may be more important in some contexts (60), and at least one modeling framework exists that could be used to assess nest distributions arising under different assumptions about foraging behavior and conflict costs (5). The difficulty of ascertaining competitive mechanisms, most of which are not mutually exclusive, is particularly acute in subterranean termites that forage (and thus encounter conspecifics from other colonies) within networks of underground tunnels (71, 147, 148). This is an area in need of continuing research.

The widely applicable conditions promoting nest overdispersion in social insects suggest that such patterns should be frequently observed, and indeed they are. In the only prior review, Levings & Traniello (96) assembled published reports of ant-nest distributions and found overwhelming evidence for the global generality of overdispersion. Of 157 instances reviewed, involving 136 ant species and spanning nearly all continents, latitudes, and biomes where ants occur, only 2 were significantly clumped and 2 others tended toward clumping. An additional 11 distributions were random. The remaining 134 cases (excluding 8 arboreal taxa) were either significantly overdispersed ($n = 64$) or tended toward overdispersion ($n = 70$).

We are unaware of any comparable review for termites but provide our own (noncomprehensive) list of published instances of overdispersion in termites spanning 10 countries on three continents, including deserts, grasslands, savannas, woodlands, and tropical rainforests (**Table 1**). Although our list is incomplete and does not include studies reporting only random or aggregated patterns in termites (23, 107, 118, 131), it is sufficient to establish that overdispersion in termite nests is globally widespread and common. According to Pomeroy (116), "It seems likely that all colonies of mound-building [termite] species are territorial, leading to a regularity of dispersion which is pronounced at high densities" (p. 336).

Although there has not (to our knowledge) been a single conclusive experimental demonstration that intraspecific competition causes these patterns in social insects, this interpretation is consistent with theory (2, 85, 127, 140), biological intuition, and multiple lines of empirical evidence. Large nests are often farther apart than, and suppress the growth and survival of, small ones (116, 117). Closer neighbors compete more intensively (4, 66), and nest densities increase with food-resource availability, or proxies thereof (12, 38, 91). Experimental food supplementation in one study also vastly increased termite alate production, suggesting resource limitation (84). In one of the only experiments to manipulate colony spacing, frequency of competitive brood raids was greater in clumped than in hexagonally distributed fire ant (*Solenopsis invicta*) colonies (4), although this only slightly increased the regularity of the surviving incipient colonies over two months, suggesting that the reported spatial regularity of mature colonies was a longer-term product of

Table 1 Studies reporting regular spatial overdispersion of termite mounds

Year	Country	Continent	Habitat	Termite taxon	Evidence	Reference
1959	Tanzania	Africa	Savanna	Unspecified	Qualitative (photographic)	69
1964	Kenya	Africa	Savanna	*Odontotermes* sp.	Qualitative (drawing)	58
1977	Mozambique	Africa	Savanna	*Macrotermes* spp.	Qualitative (aerial imagery and verbal)	145
1984	Ivory Coast	Africa	Multiple	*Macrotermes bellicosus*	Quantitative (dispersion coefficient)	90
1985	Kenya	Africa	Savanna	*Odontotermes* spp.	Qualitative (verbal)	31
1986	Ghana	Africa	Savanna	Various Termitidae spp.	Quantitative (Morisita's I_s)	11
1986	Australia	Australia	Woodland	Various Termitidae spp.	Quantitative (various metrics)	137
1987	Kenya	Africa	Savanna	*Macrotermes michaelseni*	Qualitative (verbal)	37
2000	Kenya	Africa	Grassland	*Odontotermes montanus*	Quantitative (nearest-neighbor distances)	32
2001	Ivory Coast	Africa	Savanna	*Macrotermes bellicosus*	Quantitative (Clark-Evans R)	84
2005	Kenya	Africa	Savanna	*Odontotermes montanus*	Quantitative (intermound distances)	34
2005	Kenya	Africa	Savanna	*Macrotermes* spp.	Quantitative (Clark-Evans R)	116
2007	Kenya	Africa	Savanna	*Odontotermes fulleri*	Qualitative (verbal)	35
2010	Namibia	Africa	Savanna	*Macrotermes michaelseni*	Quantitative (pair correlation function)	62
2010	South Africa	Africa	Savanna	*Macrotermes* spp.	Qualitative (LiDAR hillshade imagery)	91
2010	Kenya	Africa	Savanna	*Odontotermes montanus*	Quantitative (Ripley's L)	120
2011	French Guiana	South America	Rainforest	*Anoplotermes banksi*	Quantitative (Ripley's L)	18
2014	South Africa	Africa	Savanna	Multiple genera, including *Macrotermes* and *Odontotermes* spp.	Quantitative (Ripley's K)	38
2015	Brazil	South America	Caatinga	*Syntermes dirus*	Qualitative (satellite imagery)	50
2015	Namibia	Africa	Savanna	*Macrotermes michaelseni*	Quantitative (various point-pattern metrics)	80

sustained/iterative interactions. Finally, in another experiment, elimination of ant colonies led to shifting and reorganization of territory boundaries to occupy the newly available space (2).

What Explains Instances of Clumped or Random Colony Distributions?

Competition-driven regularity of nest spacing thus appears to be a widely prevailing condition in social insects, but it is not universally observed; moreover, the notion that competition leads to overdispersion or that overdispersion results from competition is not a foregone theoretical conclusion (127). These issues have contributed to the accumulation of equivocal results in the literature and to persistent uncertainty (and skepticism) about both the generality of nest overdispersion and its mechanistic basis (4, 29, 55, 131).

Instances of randomness or aggregation reported for termites (107, 118, 131, 137) have been attributed to the same factors thought to obscure regularity in vertebrate territories—notably, low colony densities, interspecific interactions, and environmental heterogeneity (116). In their review of ants, Levings & Traniello (96) suspected observer error in three of the four cases of clumpy distribution. However, Ryti & Case (127) subsequently noted that both publication bias and limited statistical analysis in the original studies may have contributed to the preponderance of studies reporting regularity.

Indeed, several statistical issues in pattern analysis affect the degree of regularity inferred from point-distribution data, including edge effects, sample size (power), and scale of sampling (116, 131). For example, analyses of nearest-neighbor distances yield different interpretations depending on the size and configuration of the area sampled: Complexes of social-insect nests may be locally overdispersed but will appear aggregated within larger, patchy landscapes that include areas with few or no nests, as also observed for pit-digging non-social insects (39, 136) and burrowing mammals (130). Increased recognition of this effect led to a shift away from simple nearest-neighbor indexes such as the R statistic (22) used in early quantitative studies (other early studies provided only verbal or pictorial descriptions) to functions such as Ripley's K and L that account for scale dependence (43, 62, 120) (**Table 1**). Although the *number* of neighbors has rarely been quantified, the few studies that have done so suggest that overdispersed colony distributions do indeed tend to be hexagonal (80, 140). Future studies should employ multiple metrics simultaneously to better characterize territory geometry (29, 55, 80).

There is, however, another crucial social-insect-specific factor that has influenced both researchers' perceptions and quantitative analyses of pattern regularity—namely, the effects of colony age/size. Old/large nests are consistently more overdispersed than are young/small ones (which are often aggregated), and inclusion of the latter in analyses can result in spatial randomness (4, 84, 116). This discrepancy can be explained under the competitive model outlined above: Because hexagonal territories exhaustively partition space, most new colonies arise on territory already occupied by larger colonies and are quickly killed (140). When a mature colony dies, its former territory is quickly filled by a cluster of nascent colonies, which will persist until one eventually outcompetes all the others. These young colonies will be clustered not just spatially, but also temporally, as synchronous reproduction of colonies following heavy rains leads to the simultaneous initiation of new cohorts (62). However, because they are small and short-lived, these nascent colonies will have limited effect on vegetation patterning and ecosystem functioning. For this reason, analyses of colony dispersion based on remotely sensed data (38, 43, 80, 91, 120) primarily detect large nests and tend to reveal cleaner signals of regularity than do analyses derived from ground mapping.

Effects of Social Insects as Ecosystem Engineers

The effects of ground-nesting termites (14, 30, 68, 73, 77, 135, 158) and ants (86, 102) on soils and vegetation are well documented. Bioturbation, foraging, and (in some species) N_2 fixation and fungus farming by these animals alters soil nutrient content, texture, and porosity (and, hence, bulk density, aeration, and hydrology), all of which influence plant productivity, biomass, species composition, and functional traits. Direct effects of insects on plants include consumption of roots, foliage, seeds, and other tissues.

These engineering activities—which vary among and within species, and even within populations, depending on local environmental conditions (83)—contribute to a wide range of vegetation syndromes associated with social-insect nests. These effects are most pronounced among species that create huge underground structures, such as seed-harvesting ants, fungus-farming leaf-cutter ants, and Old World fungus-farming termites (Macrotermitinae, including *Macrotermes* and *Odontotermes* spp.). For example, *Macrotermes* and *Odontotermes* nests in Africa are often islands of woody plants within a more sparsely vegetated matrix (75, 76, 132) (**Figure 1*d***) or islands of highly productive and compositionally distinct grasses within savanna-woodland matrices (31, 36, 48, 120) (**Figure 1*c***). They may also be bare-soil domes or cathedrals measuring 5 m or more in height (83) or flat discs of bare soil within patchy or continuous vegetation (35), as is also the case for many seed-harvesting ant species (43, 47) (**Figure 1*f***). Thatch ants (*Formica obscuripes*) often induce distinct rings of vegetation surrounding their nests (10); similarly, the sand termite *Psammotermes allocerus* is thought to induce the formation of so-called fairy circles in the Namib Desert (78) (**Figure 1*h***).

Due to such soil and vegetation engineering, social-insect nests are often conspicuous in high-resolution remotely sensed imagery (38, 47, 91, 92, 120), appearing as vegetation spots, bare gaps, or rings (**Figure 1**). When nests are hexagonally overdispersed, as described above, the vegetation and microtopography associated with nests have the same arrangement, creating patterns that are virtually identical to those predicted by certain SDF model parameterizations. These similarities have led to disputes over the mechanistic basis of several types of regularly patterned landscape features (27, 55, 80), which we review below.

CONTROVERSIES OVER PATTERNING MECHANISMS

Among the regular vegetative and microtopographic patterns whose origins remain debated or incompletely resolved are fields of earth mounds known locally as *heuweltjies* in South Africa (28, 29, 49, 109, 110), Mima mounds (52, 72) and burrow mounds (121, 130) in western North America, *surales* in the Orinoco Llanos (59, 162), and *murundus* in Brazil (51, 103, 108, 112), along with the aforementioned fairy circles (bare-soil discs surrounded by rings of perennial grasses) in southwestern Africa (26, 54, 55, 78–80, 149, 150, 156, 160) and Australia (56, 57, 157).

The patterning mechanisms invoked to explain these formations fall predominantly into three broad categories: (*a*) abiotic processes (e.g., freeze-thaw and shrink-swell cycles, aeolian deposition and erosion, seismic activity), (*b*) faunal activity (e.g., social insects, earthworms, and burrowing mammals such as pocket gophers and kangaroo rats), and (*c*) vegetation self-organization via SDF, perhaps in a positive-feedback loop with abiotic processes such as differential soil deposition and erosion. These possibilities are often presented and debated as alternatives, and because the available data do not allow conclusive direct tests, many studies attempt to proceed by elimination: Negative (often indirect or circumstantial) evidence against certain hypotheses is more central in these arguments than is positive evidence in favor of any other hypothesis (27, 29, 54, 55, 80). Although the potential for polygenesis by multiple interacting mechanisms has been acknowledged in some cases (72, 104), the literature has not yet fully internalized this possibility (see also next section).

Momentum has built behind SDF as a potentially unifying mechanism involved in initiating these and other regularly patterned formations, especially in water-limited environments (27, 42, 54, 56, 160). Whereas faunal hypotheses are locally contingent and particular and therefore easily problematized (it is sometimes not even clear which among several animal species is the agent most likely responsible for a given feature), SDF is a flexible and theoretically well-developed framework that does not require complex assumptions about which species are present in a local community or how those species behave in different contexts. If "faunal genesis is appealingly simple and direct" (29, p. 16), then SDF is appealingly generalizable and parsimonious (albeit vexingly difficult to test empirically). The appeal to parsimony is sometimes explicit: According to one study on the periodic vegetation patterns of Sudan, "self-organization of vegetation can be regarded as more realistic than models invoking feedback loops between vegetation and termite nest building. . .since the latter hypotheses do not predict the complete range of observed morphologies nor their sequence along environmental gradients" (42, pp. 990–91). Others argue that "it is unlikely that central-feeding termites. . .could generate the enormous sizes of the tessellations and the mounds"

(29, p. 23) and point to the absence of a mathematical theory of faunal genesis analogous to the body of work supporting SDF (20, 53, 55).

Such assertions overlook a century of theory predicting the emergence of hexagonal formations (3, 25, 64, 85, 139, 142) and also underestimate the frequency of overdispersion in social-insect nests (16, 36, 43, 62, 80, 84, 91, 96, 116, 120)—oversights abetted by the poor statistical and geometrical characterization of insect-generated patterns in prior work, especially in early studies that lacked the benefit of sophisticated computational tools and globally available high-resolution satellite imagery. These arguments also fail to acknowledge an important shortcoming of the SDF models applied in terrestrial ecosystems to date, namely that none has been fully parameterized using in situ field measurements from the specific ecosystems where the patterns are found. Little has yet been published on this deficiency (but see 79).

It is therefore inappropriate to conclude from the "'aggregated knowledge' provided in aerial images" that "vegetation self-organisation is very well known to ultimately cause" regular patterning (55, p. 674). Such conflation of theory and reality whitewashes the scarcity of mechanistic empirical data. The same caveat applies to all theoretically plausible patterning mechanisms, especially when invoked in isolation from other potentially compatible mechanisms and divorced from ecological context. Explanations for any new patterns identified in remotely sensed imagery must include ground truthing, manipulative experimentation, careful scholarship (especially toward older and less-visible literature, where antecedents of many current debates can be found), and theoretical consideration of multiple, potentially complementary mechanisms and their interactions at different scales (16, 17, 98–100, 140).

INTEGRATING MULTIPLE PATTERNING MECHANISMS

That multiple mechanisms can in theory induce equivalent patterns does not mean that these mechanisms are mutually exclusive, as has been implied in the disputes reviewed above. To the contrary, it seems likely that the concurrent operation of multiple mechanisms leads to accumulation of evidence for all of them, thus providing fodder for arguments on all sides.

Indeed, recent literature has increasingly acknowledged the potential for interactions and feedbacks among multiple mechanisms, both self-organized and exogenous. Cramer & Barger (27) were skeptical of faunal mechanisms as the origin of *heuweltjies*, *murundus*, and Mima mounds; their favored explanation involves interactions among SDF, differential erosion, and aeolian deposition. Although this interpretation may be correct, it would be difficult to rule out the possibility that faunal activity interacts with an emerging SDF template to shape pattern development. For example, banded vegetation, which results from SDF models on sloping substrates in semiarid ecosystems (134, 141, 159), is positively correlated in space and time with the densities of ants, termites, and other soil biota (45). Termite foraging activity in and around vegetated areas increases soil porosity and can enhance infiltration rates by an order of magnitude (45); in turn, differential infiltration and runoff promotes band formation. Insects and SDF may thus interact in a positive-feedback loop to determine the distribution of vegetation (45, 141, 152).

Research in seasonally flooded South American savannas provides other examples of interaction among multiple mechanisms to create and reinforce spatial patterns over centuries. There, the template was exogenously imposed by pre-Columbian human farmers, who created dense raised fields of earth mounds to protect crops from flooding. After humans abandoned the fields, ants, termites, and earthworms reengineered and stabilized the mounds by creating soil aggregates resistant to erosion (104, 122). Recent studies of Mima mounds in Northern California likewise suggest that mounded landscapes are polygenetic and best explained by "combined bioturbation, seasonal frost action, and erosion processes, with occasional eolian inputs" (72, p. 135).

Concurrent patterning mechanisms need not operate at the same scales. Recent work on mussel beds shows that distinct mechanisms can produce superficially similar regular patterns (97, 100, 155), that patterns can arise from processes other than SDF (97, 99), and that self-organization occurs simultaneously at distinct spatial scales (98). At small scales of centimeters and days, reticulate clusters form as a result of density-dependent movements of individuals, a recently identified driver of ecological patterning based on the physical principle of phase separation (99); at larger scales of meters and months, banded patterns arise from the interplay of facilitation and resource depletion (98). Similarly, we (16) have proposed that social-insect and vegetation self-organization coexist and interact in a semiarid Kenyan savanna landscape. There, a large-scale pattern of hexagonally overdispersed vegetation hotspots (**Figure 1*c***) created by termite mounds (120) coexists with fine-grained (centimeter-scale wavelengths) regular spatial patterning of herbaceous vegetation in the matrix between mounds. This small-scale pattern was reproduced by a modified version of a widely used SDF model (125) under stochastic rainfall. We find similar small-scale regularity in the matrix vegetation between Namibian fairy circles, and by coupling a dynamic model of territoriality-driven self-organization in termites with SDF-driven plant-water feedbacks, we can reproduce both the large-scale hexagonal overdispersion of spots and gaps and the previously unrecognized regularity of matrix vegetation (140). Because simple models based on single mechanisms cannot simultaneously produce patterns at multiple scales (98, 113, 126), the existence of complex multiscale patterns strongly suggests the co-occurrence of multiple processes.

FUNCTIONAL IMPLICATIONS OF MULTIPLE PATTERNING MECHANISMS

The development of SDF theory was propelled in part by the insight that regular spatial patterns may be intimately linked to key ecosystem functions. In SDF models of dryland vegetation, decreasing (or increasing) rainfall induces transitions along a predictable sequence of locally stable, regularly patterned states with decreasing (or increasing) total vegetation biomass. Starting from a homogeneously vegetated state, reducing rainfall leads to hexagonally overdispersed gaps, then to labyrinths, then to hexagonally overdispersed spots, and lastly to a sudden collapse in which all vegetation is lost—a catastrophic shift between alternative states (124, 126, 128, 129). It is difficult to recover vegetation from such desertified systems because associated soil erosion and water runoff inhibit the reestablishment of vegetation (129). Theoretically, then, pattern morphology could be used as a leading indicator of potentially irreversible ecosystem degradation (but see 105).

Importantly, however, the predicted relationship between pattern and function is sensitive to assumptions about the type and number of patterning mechanisms involved. In contrast to vegetation spots generated by SDF, spots associated with termite mounds (**Figure 1*d***) may confer robustness in the face of increasing aridity, because plants can persist on resource-enriched mounds long after matrix vegetation has collapsed and can subsequently act as a source of propagules to reseed the matrix. Thus, the aridity threshold required to induce total desertification is greater in systems where termites act as ecosystem engineers (16). Moreover, the hexagonal overdispersion of termite mounds further enhances system-wide productivity and resilience by minimizing the average distance of points in the landscape to the nearest mound (120); this should facilitate recovery in drought scenarios by reducing the distance propagules must travel to reach any given point in the matrix.

Likewise, various mechanisms thought to promote regular patterning in mussel beds have divergent functional implications. When large-scale banded patterns arise because high mussel densities reduce the rate of loss from disturbance (154, 155), then such patterns enhance productivity and hasten recovery time following a disturbance. In contrast, when large-scale patterns result from increased feeding efficiency atop hummocks of other mussels, the emergent effects on ecosystem functioning are minor (100). As hypothesized for semiarid savanna systems, multiscale and multimechanism patterning in mussel beds increases the robustness of these ecosystems (98).

CONCLUSIONS

Recent increases in scientists' ability to detect and quantify the spatial organization of ecosystems have confirmed the surprising frequency and geographic extent of emergent regular patterning in diverse biomes, providing fertile grounds for theoretical development. However, the superficial similarity of many of these patterns likely conceals underlying complexity and nuance that will require further research to elucidate. The importance of a multidisciplinary and pluralistic approach to this problem is illustrated by enduring controversies over the origins of patterned landscapes: When examining the same satellite image, a field biologist might see evidence of termite activity; a theoretician might see evidence of SDF; a geologist might conjecture about sedimentation and erosion; and an archaeologist might see evidence of prehistoric human activity. And they all could be correct—or not. Only by bringing these perspectives together, and by combining mathematical models, remote sensing, observational fieldwork, and (crucially) manipulative experimentation, are we likely to achieve a robust understanding of regular spatial patterns in ecosystems.

We believe that the recent work reviewed in the preceding two sections provides a foundation for an emerging research agenda that focuses not on competing alternative hypotheses or a single universal theory, but rather on the dynamic interplay of multiple mechanisms at multiple spatiotemporal scales. Manipulative experimental approaches—and the development of more experimentally tractable model systems for testing theoretical predictions (39, 99, 136)—are sorely needed, as is collective insistence upon rigorous standards for field-based model parameterization and validation. An expanded effort along these lines will confer a greater degree of generality and predictive power and will provide fresh insights into the ways in which self-organized biogenic patterns govern community properties and ecosystem functioning.

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