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Key Points:
- Regular spatial patterns are common in ecology, but highly ordered patterns with spatial periodicity like fairy circles (FCs) are rare
- Based on 25 data sets worldwide, we show that typical termite and ant nest patterns in drylands are systematically less ordered than the FCs
- We identify termites in drylands as an unlikely cause for periodic FC patterns and discuss plant self-organization as an alternative cause

Supporting Information:
- Supporting Information S1

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(*continued*)

Contrasting Global Patterns of Spatially Periodic Fairy Circles and Regular Insect Nests in Drylands

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Abstract Numerical analysis of spatial pattern is widely used in ecology to describe the characteristics of floral and faunal distributions. These methods allow attribution of pattern to causal mechanisms by uncovering the specific signatures of patterns and causal agents. For example, grassland-gap patterns called fairy circles (FCs) in Namibia and Australia are characterized by highly regular and homogenous distributions across landscapes that show spatially periodic ordering. These FCs have been suggested to be caused by both social insects and competitive plant interactions. We compared eight Namibian and Australian FC patterns and also modeled FCs to 16 patterns of social insect nests in Africa, Australia, and America that include the most regular termite mound patterns known. For pattern-process inference, we used spatial statistics based on both nearest-neighbor analysis and neighborhood-density functions. None of the analyzed insect-nest distributions attain the spatially periodic ordering that is typical of FCs. The inherently more variable patterns of termite and ant nests are commonly attributable to well documented aspects of the faunal life-history. Our quantitative evidence from drylands shows that the more variable insect-nest distributions in water-limited environments cannot explain the characteristic spatial signature of FCs. The analysis demonstrates the interpretation of scale-dependent neighborhood-density functions and that it is the identification of unique spatial signatures in regular patterns that need to be linked to process. While our results cannot verify a specific hypothesis, they support the hypothesis that FCs in these drylands are more likely an emergent vegetation pattern caused by strong plant competition for water.

1. Introduction

Self-organized spatial pattern is common globally, requiring only the existence of positive feedbacks to destabilize uniform states to produce abiotic periodic patterns such as aeolian sand ripples, longitudinal dunes, ocean swells, and cloud streets (Lämmel et al., 2018). These generally linear abiotic patterns are similar to some biotic ecological patterning that is also approximately linear and periodic (e.g., banded tiger bush; Lefever & Lejeune, 1997). There is, however, a great diversity of biotic patterning, with many patterns departing from these linear formations and being better represented as spot or gap patterns in otherwise uniform vegetation states (Barbier et al., 2008; Couteron & Lejeune, 2001; Meron, 2018; Rietkerk & van de Koppel, 2008). Indeed, self-organizing biotic spatial spot or gap patterns are common worldwide. Examples include termitaria (Martin et al., 2018), savanna tree spacing (Moustakas et al., 2008), mima mounds (Cramer & Barger, 2014), and fairy circles (FCs; Getzin et al., 2015a). For some of these biotic examples (e.g., termitaria and savanna trees), the causal biotic process operates currently wand is generally indisputable. For other formations that might be very old (e.g., mima mounds and FCs), the causal mechanisms are not clear, and they are subject to ongoing controversy (Sahagian, 2017). These structures may result from long-term development, making experimental manipulation of pattern formation difficult to achieve (Tschinkel, 2015). As a consequence, several authors have resorted to numerical modeling techniques to uncover the detailed structure of the patterning (Getzin et al., 2015a, 2015b, 2019) and to relate the patterning to mechanistic causes (Grabovsky, 2018; Zelnik et al., 2015). Spatial pattern analysis can be used to contrast alternative theories for causal agent behavior and thus for understanding the drivers of self-organized biological systems (Grimm et al., 2005; McIntire & Fajardo, 2009).

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Identification of pattern signatures that characterize a system at multiple scales (Grimm & Railsback, 2012) is necessary for depicting the fundamental scales of organization in an ecosystem (Levin, 1992; Wiegand et al., 1998). The use of computationally simple nearest-neighbor statistics such as the Clark-Evans index (Clark & Evans, 1954) or Voronoi tessellations (Dacey, 1964; Miles, 1970) describing nearest-neighbor distributions ignores long-range spatial correlations in point patterns and has been superceded by scale-dependent neighborhood-density functions (Wiegand et al., 2013). One such statistic, the pair-correlation function (or g function), can uncover spatial periodicity and is the most consistent and robust descriptor of patterns at a range of scales (Perry et al., 2006). Here we used these statistics to analyze several patterns globally to test the potential similarities of the patterns and to uncover the significant details in interpretation of the statistics.

Social-insect nests are often regularly distributed (overdispersed); hence, they show a lack of nearby neighbors, for instance, due to territorial interference competition. Long known examples include termitaria in Australia (Noble et al., 1989; Spain et al., 1986) and in Africa (Darlington, 1985), as well as vegetation gaps created by harvester ants in North America (Crist & Wiens, 1996; Ryti & Case, 1986; Wiernasz & Cole, 1995). This pattern regularity requires a relatively homogeneous environment, but the degree of regularity of faunal patterns is commonly constrained by other factors, such as the manner of dispersal of the fauna (Blanco-Moreno et al., 2014). For example, winged insects may disperse relatively far from the parent colony in the right wind conditions, breaking the closest possible packing arrangement or aggregated dispersal around parent nests may typically lead to a lowering of spatial regularity at small neighborhood scales (Grohmann et al., 2010). For instance, Lepage (1984) found little or no deviation from a random distribution (seven of nine cases) for *Macrotermes bellicosus* even at high densities. Similar results have also been found in many other studies of intraspecific territoriality (Holt & Easey, 1985; Muvengwi et al., 2016; Schuurman & Dangerfield, 1997). Thus, while it is certain that fauna generate regular spatial patterns, it is informative to understand the specific characteristics of that pattern and the constraints on its regularity.

FCs probably represent the most spectacular example of regular ecological patterning and serve as an important benchmark example of the generation of regular pattern (Figure 1a, 1b). FCs are roughly circular barren patches occurring in a narrow band approximately 100 km inland of the southwest African coast spanning the Namib Desert (van Rooyen et al., 2004) and also in Western Australia (Getzin et al., 2016, 2019). In Namibia, these FCs generally have conspicuously taller peripheral grasses in a shorter grass matrix. The strongest environmental association of the Namib FCs is with mean annual precipitation, which ranges between approximately 50 and 150 mm (Cramer & Barger, 2013) and occurs where sparse grassland is dominated by *Stipagrostis* species on soils that are predominantly coarse-textured, aeolian-derived sands that have a high capacity for water and nutrient movement (Cramer et al., 2017; Ravi et al., 2017). The origin of these FCs in water-limited drylands has puzzled scientists for decades (Sahagian, 2017; van Rooyen et al., 2004). The hypotheses include (a) allelopathic influences of a plant that no longer occurs in FCs (Meyer et al., 2015; Theron, 1979); (b) seepage of carbon monoxide, hydrocarbons, or other volatiles from below ground that kills grass in regular patterns (Albrecht et al., 2001; Jankowitz et al., 2008; Naude et al., 2011); (c) an unspecified microbial effect (Eicker et al., 1982; Ramond et al., 2014; van der Walt et al., 2016); (d) faunal removal of grasses by termites (Becker & Getzin, 2000; Juergens, 2013; Moll, 1994; Tarnita et al., 2017; Vlieghe et al., 2015) or detrimental influence on grasses by ants (Picker et al., 2012); and (e) self-organized emergent vegetation patterning arising from competitive and facilitative interactions between grasses (Cramer et al., 2017; Cramer & Barger, 2013; Getzin et al., 2015a, 2015b, 2016, 2019; Ravi et al., 2017; Tschinkel, 2012; van Rooyen et al., 2004).

The spatial pattern g function of FCs indicates that they not only exhibit a regular pattern, as do some insect nest patterns, but that the FCs are extremely regularly and periodically ordered, and that this order prevails equally over the landscape (Getzin et al., 2015a). In particular, the strongly periodic fluctuation of the g function above and below the simulation envelopes of the random null model (Figure 1c) indicates a grid-like hexagonal spatial arrangement where each FC has not only on average six nearest neighbors but, importantly, the six neighbors are located at approximately the same distance from the focal circle (Getzin et al., 2015b). Hence, it is primarily the low variation of the nearest-neighbor distances plus the large-scale homogeneity that results in a spatially periodic ordering of FCs. In contrast, social insect distributions have been interpreted to show "hexagonal patterns" when they merely have six nearest neighbors on average as an index value, without regard to their nearest-neighbor distances (Tarnita et al., 2017). This index is a strong
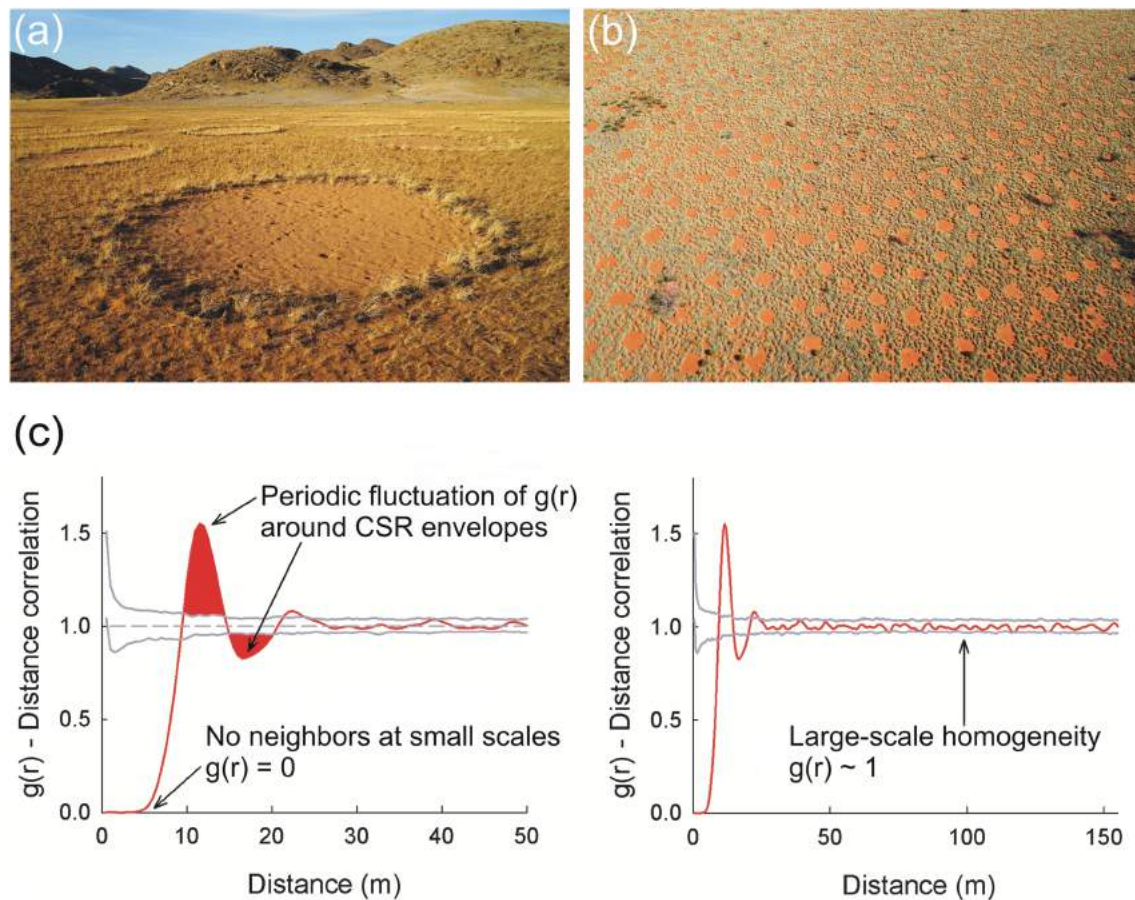
Figure 1. A large fairy circle (FC) near the Giribes Plains in northwest Namibia (a). Similarly, FCs near Newman in Western Australia are characterized by their large size and a spatially periodic pattern (b). Using the neighborhood-density function $g(r)$, the spatially periodic ordering of typical FCs is shown for a pattern of Australian FCs (c). The g function (red line) detects no neighbors for very small radii and fluctuates significantly thereafter around the null model of complete spatial randomness (CSR; red color filling above and below the grey simulation envelopes). These significant positive and negative deviations from the null model at the small scales and the sinusoidal shape of the g function indicate a spatially periodic pattern. The first pronounced peak with a strong amplitude at around 10 m distance indicates the mean nearest-neighbor distance of the FCs. The strong negative amplitude below the simulation envelope at around 16 m radius indicates the empty space between the first and second row of nearest neighbors, which is only possible because the FCs are periodically ordered as a hexagonal grid. At large scales, $g(r)$ approaches values of 1, indicating large-scale homogeneity.

simplification in describing regularity because patterns with low spatial regularity but also a random pattern, used for null model testing, can both have a mean number of six nearest neighbors (e.g., Tarnita et al., 2017, their Figure 1g). Since such random or slightly regular patterns are far from having a hexagonal lattice structure, we use here the detailed explanation provided in Getzin et al. (2015b, p. 670) to contrast between the *spatially periodic* benchmark patterns of FCs and those merely regular distributions that do not show the significant fluctuation of the g function around the null model.

Pringle and Tarnita (2017) recently reviewed the role of territorial interference competition between colonies of social insects compared to scale-dependent vegetation feedbacks but did not analyze the spatial ordering of these patterns. This leaves the question as to whether sessile plants are more or less regularly spaced than motile insect nests. An answer to this question requires consideration of the relative strength of spatial regularity and the fraction of total cases typically showing such regularity. This can be achieved with modern pattern analysis because it has the methodological potential to accurately describe the inherent structure of spatial distributions and to link pattern to process (McIntire & Fajardo, 2009; Velázquez et al., 2016).

While there are multiple hypotheses for FCs origins, the two that enjoy current support are that dependent on faunal termite causation and on emergent vegetation patterning (Sahagian, 2017). Several studies have demonstrated that there are no direct observational data of past or present termite activities that support

their potential role in the genesis of FCs in the central or southern Namib (Ravi et al., 2017; Tschinkel, 2010, 2012) or in Australia (Getzin et al., 2019). There has also been no empirical verification of the role of either termites or vegetation patterning in the formation of FCs. Although various termite species do occur in areas where FCs occur, their activities such as nests do not appear to correspond with regularity and spatial extent of FCs (Ravi et al., 2017). As a consequence, spatial pattern analysis of faunal features from other landscapes has been associated with the FC pattern (e.g., Tarnita et al., 2017). Therefore, pattern-process inference based on the fundamental scales of spatial FC organization is needed to find a more generalizable and perhaps unifying answer to the mystery (Box 1).

Box 1. Pattern-process inference in a nutshell

Since the early 1990s, spatial patterns, their multiscale characteristics, and their causes and consequences have been highlighted as "a final frontier for ecological theory" (Kareiva, 1994; Levin, 1992). Space was increasingly recognized as source of ecological information, rather than as noise, because spatial patterns should conserve a signature of the underlying processes. Pattern-process inference uses "space as a surrogate" for unmeasured processes in order to maximize inference about ecological processes through the analysis of spatial patterns (McIntire & Fajardo, 2009).

A prerequisite in this endeavor is a thorough application of scale-dependent spatial point pattern methods to enable the identification of specific key structures in patterns that may characterize a specific causal agent or process (Velázquez et al., 2016). For example, patterns may commonly be clustered due to habitat heterogeneity or dispersal limitation, but identification of specific characteristics such as nested cluster properties within the overall aggregated pattern may help to establish links between pattern and process (Wiegand, Gunatilleke, Gunatilleke, & Okuda, 2007). Likewise, many patterns are regular, which can be caused by multiple processes. Thus, a more insightful question is to ask if specific patterns show a spatial periodicity as a special case of a regular distribution.

Generally, in pattern-process inference "the focus should be on identifying unlikely processes rather than on 'verifying' others, and the most parsimonious explanation for the observed pattern should be kept as working hypothesis" (Schurr et al., 2004). Consequently, patterns and potential causal agents should be compared within similar systems such as within dryland ecosystems or within wetlands so that the hypothesis under investigation can be formulated as specific as possible. In a pattern-oriented context, this is what has been called "strong inference by contrasting alternative theories of the agents' behavior" (Grimm et al., 2005). This inference approach allows selection of the processes that best explain the observed pattern signatures (Vinatier et al., 2011).

To resolve these different interpretations of spatial patterns and variation in the degree of ordering, we studied a diversity of spatial patterns ($n = 25$) from around the globe. These patterns include four Namibian and four Australian FC sites, as well as simulated FCs from a process-based vegetation self-organization mathematical model. As examples of social insect nests, we analyze 16 termite and ant nest patterns from Australia, the United States, Namibia, South Africa, Kenya, Brazil, and Mozambique. These analyses are discussed as examples of emergent spatial pattern but also in the context of the debate about whether FC patterns more likely originate from termite activity or from the plant self-organization, which are currently the most controversially discussed theories explaining FC formation.

2. Materials and Methods

2.1. Data Sources

Spatial data were retrieved from aerial or satellite images in observation windows typically >500 m × 500 m (Tables 1 and S1 in the supporting information). The observation windows were selected to minimize obvious abiotic landscape heterogeneities such as rivers, rocky outcrops, or slopes. One random null model pattern was generated (cf. Table 1: CSR) with a Poisson point process representing CSR. It was based on 630 simulated points in an area of 25 ha, equivalent to the FC site at Marienfluss (Getzin et al., 2015a).

From Namibia, we analyzed three FC patterns from the Marienfluss Valley and the Giribes Plains (Getzin et al., 2015a) using orthorectified aerial images and a Google, DigitalGlobe satellite image from

Table 1
Landscape Features and Summary of Their Spatial Characteristics From This Study

Data category	Data name	Mean NN distance (m)	1 - CV of NN distance	Clark-Evans index R	Small-scale pattern (g function)	Large-scale pattern (L function)
Random null model	CSR	10.1	0.45	$1.01^{n.s.}$	Random	Homogeneous
FC	FC Namibia M	16.3	0.83	1.65^{***}	Spatially periodic	Homogeneous
FC	FC Namibia G1	12.4	0.81	1.63^{***}	Spatially periodic	Homogeneous
FC	FC Namibia G2	11.6	0.82	1.62^{***}	Spatially periodic	Homogeneous
FC	FC Namibia W	14.4	0.86	1.68^{***}	Spatially periodic	Homogeneous
FC	FC Australia C1	10.0	0.84	1.60^{***}	Spatially periodic	Homogeneous
FC	FC Australia C2	9.8	0.85	1.66^{***}	Spatially periodic	Homogeneous
FC	FC Australia L2	9.6	0.85	1.64^{***}	Spatially periodic	Homogeneous
FC	FC Australia 1	9.9	0.85	1.65^{***}	Spatially periodic	Homogeneous
FC Model	FC Australia Mod	11.0	0.91	1.75^{***}	Spatially periodic	Homogeneous
Social insect nest	T Australia C2	14.0	0.26	$1.02^{n.s.}$	Random/aggregated	Heterogeneous
Social insect nest	A Australia C2	7.9	0.49	$0.98^{n.s.}$	Random/aggregated	Heterogeneous
Social insect nest	T Australia Jiga	13.4	0.68	1.34^{***}	Regular	Heterogeneous
Social insect nest	T Australia Kiwi	11.5	0.63	1.16^{***}	Regular	Heterogeneous
Social insect nest	T Australia Pilb	21.1	0.28	$0.92^{n.s.}$	Aggregated	Heterogeneous
Social insect nest	A Arizona 1	16.8	0.72	1.38^{***}	Regular	Heterogeneous
Social insect nest	A Arizona 2	18.9	0.73	1.35^{***}	Regular	Heterogeneous
Social insect nest	T Namibia 1	46.5	0.68	1.35^{***}	Regular	Homogeneous
Social insect nest	T Namibia 2	46.0	0.77	1.47^{***}	Regular	Homogeneous
Social insect nest	T South Africa	32.7	0.66	1.35^{***}	Regular	Homogeneous
Social insect nest	T Kenya 1	51.8	0.77	1.52^{***}	Regular	Homogeneous
Social insect nest	T Kenya 2	52.7	0.78	1.54^{***}	Regular	Homogeneous
Social insect nest	T Kenya 3	78.2	0.68	1.47^{***}	Regular	Homogeneous
Social insect nest	T Brazil 1	16.2	0.79	1.51^{***}	Regular	Homogeneous
Social insect nest	T Brazil 2	17.6	0.79	1.51^{***}	Regular	Homogeneous
Social insect nest	T Mozambique	43.9	0.60	1.37^{***}	Regular	Homogeneous

Note. Assessment of the small-scale pattern was based on the scale-dependent pair-correlation or g function (Figure 3). Assessment of the large-scale pattern was based on its cumulative counterpart, the L function (Figure 4). Highly significant Clark-Evans indices are indicated with *** ($p < 0.001$) and nonsignificant values with n.s. ($p > 0.05$). NN = nearest neighbor, 1 - CV = 1 - coefficient of variation, CSR = complete spatial randomness, FC = fairy circle, T = termite, A = ant.

Wolwedans/NamibRand Nature Reserve (cf. Table 1: FC Namibia M, G1, G2, W). From Australia, we analyzed four FC plots in aerial images (FC Australia C1, C2, L2, 1) and a process-based model output (FC Australia Mod) in which the pattern-forming process was solely based on biomass-water feedbacks and resultant vegetation self-organization (Getzin et al., 2016). The three plots "FC Australia C2, L2, 1" were mapped with a quadcopter Microdrone md4-1000 (www.microdrones.com) and a 24-megapixel photo camera Sony

NEX-7 in July 2017 (Getzin et al., 2019) and subsequently orthorectified and georeferenced with OneButton software (www.icaros.us). To make these high-resolution aerial images (3 cm/pixel) directly comparable with published image analyses of FC patterns (Getzin et al., 2015a, 2015b, 2016), we used a threshold value of 2 m for the smallest identified gap diameters. Together, these nine patterns serve as a benchmark pattern for the spatially periodic FCs.

To compare the Australian FC patterns directly with local termite and ant activity in Western Australia, we provide two types of spatial data. The first data sets are ground-mapped harvester termite (T Australia C2) and ant (A Australia C2) nest locations that have been recorded with a handheld GPS within the same plot (FC Australia C2) for which FCs have been digitized. Due to the effort associated with ground mapping, only these two plots are smaller in size (210 m × 210 m; Getzin et al., 2016). The other data sets based on orthorectified aerial images are grassland gap patterns created by harvester termites (T Australia Jiga, Kiwi) and spinifex termites (T Australia Pilb) within Western Australia (Getzin et al., 2019).

In order to infer potential causality, Namibian FCs are sometimes directly compared with grassland gaps created by North American harvester ants (e.g., Picker et al., 2012) or with *Macrotermes* termite mounds in Namibia (e.g., Juergens et al., 2015). For this reason, we reanalyzed the original data for harvester ants from Arizona (A Arizona 1, 2) of Tarnita et al. (2017). We then digitized three large plots with *Macrotermes* termite mounds in Namibia and South Africa. The data set "T Namibia 1" is a digitized image published in Grohmann et al. (2010, their Figure 9), where the large inhabited mounds on 1 km × 1 km had heights between 0.8 and 4.4 m. The *Macrotermes* plot "T Namibia 2" is a mound location near Outjo/Namibia, cited in Juergens et al. (2015), where we used a large plot size of around 1 km × 1 km and carefully digitized all termite mounds visible in this DigitalGlobe satellite image. The *Macrotermes* plot "T South Africa" is from Kruger National Park. With around 1 km × 0.5 km, it has smaller plot dimensions, which was necessary to avoid large-scale topographical heterogeneity as reported by Davies et al. (2014) for this area. Six further insect nest patterns that can be directly interpreted as true positions of individual termite mounds were analyzed. Two data sets (T Kenya 1, 2) from Kenya were the original data files from Tarnita et al. (2017), but these spatial data contained duplicate coordinates (sites "Kenya_1" and "Kenya_2" had 69 and 17 duplicate points, respectively), and we therefore removed the duplicate points. A third Kenyan termite mound pattern (T Kenya 3) was digitized on a plot size of approximately 2 km × 2 km. The two Brazilian (T Brazil 1, 2) and the Mozambican (T Mozambique) termite mound patterns were again from Tarnita et al. (2017). We avoided using ungeoreferenced oblique aerial imagery with a low viewing angle (i.e., sites "Australia_1" and "Australia_2" in Tarnita et al., 2017) because these are unsuitable for precise spatial pattern analysis.

As in Tarnita et al. (2017), the features of social insect nests were clearly distinguishable in the georeferenced aerial and satellite imagery. We digitized the point locations with their *x,y* coordinates using QGIS-2.18 software (https://qgis.org/en/site/). For the digitized satellite images, we used DigitalGlobe images and verified the correct identification of features with additional information from Bing aerial image service in QGIS-2.18. Consequently, our digitized features include all those termite mounds that are large enough to be identified with publicly available, rather coarse-grained remote-sensing images. An example of the importance of correctly identifying all termite mounds in a plot is demonstrated for the data set "T Kenya 3" in Figure S1 and is discussed below.

2.2. Data Analysis

We used four spatial statistics to analyze the patterns. These included (a) the Clark-Evans *R* index of dispersion, (b) the coefficient of variation (CV) of the nearest-neighbor distances (expressed as 1 - CV), (c) the *g* function, and (d) the *L* function.

The *R* index (Clark & Evans, 1954) is defined as $R = \bar{r}_A / \bar{r}_E$ where $\bar{r}_A$ is the average distance from randomly selected points to their nearest neighbors and $\bar{r}_E$ is the theoretically expected average distance between nearest neighbors based on the Poisson distribution of CSR. $R = 1$ for random patterns, whereas aggregated (clumped) patterns have values approaching $R = 0$, and perfect hexagonal patterns have a maximum value of $R = 2.1491$ (not achieved in ecological systems). For comparative reasons, the *R* index is presented without edge correction because those have been primarily published in the past. As our analysis confirms, for large data sets with >100 points, the importance of edge correction is diminished (Velázquez et al., 2016), although it is important for smaller data sets, especially with <50 points (Schuurman & Dangerfield, 1997).

We present the R index together with 1 - CV of the nearest-neighbor distances on a two-axis classification scheme because both measures are nonredundant but highlight different aspects of nearest-neighbor based pattern structures (Wiegand & Moloney, 2014). While 1 - CV plotted on the x-axis is straight forward with regard to the distances of nearest neighbors, the R index on the y-axis assesses the distance to the nearest neighbor and its deviation from the theoretical expectation under the null model distribution CSR. For example, a point pattern that consists of only four separated clusters where the points within each cluster have all the same distances to their nearest neighbors will have an R index of approximately 0.3 (clustering) but a CV of the nearest-neighbor distances of 0 (hence, 1 - CV = 1), indicating a perfectly ordered grid within the clusters. In contrast, if all points would be spread homogeneously across the plot and each point would have six equidistant nearest neighbors, the CV of the nearest neighbor distances would also be 0 but the R value will be 2.1491. These two-axis classification schemes are currently commonly used in spatial ecology (Wiegand, Gunatilleke, & Gunatilleke, 2007) and can be used to quantitatively separate point clouds, similar to classic ordination techniques (Pielou, 1984).

To assess the multiscale spatial ordering of all patterns in more detail, we applied the g function and thereafter the L function. The pair-correlation function or g function $g(r)$ is the expected density of points at a given distance r from an arbitrary point, divided by the intensity (λ) of the pattern (Stoyan & Stoyan, 1994). This scale-dependent neighborhood-density function is highly effective for analyzing critical scales and the strength of ordering in a pattern (Perry et al., 2006), and it is "the most powerful summary characteristic when used in isolation" (Wiegand et al., 2013). It can reveal if a pattern is merely regularly distributed or, in contrast, spatially periodic. The latter is a special form of a regular distribution that is typical only for grid-like hexagonal patterns (Figure 1c). Typically, the CSR null model generated by a Poisson point process, where $g(r) = 1$, is used to construct simulation envelopes to indicate whether deviations from $g(r) = 1$ are statistically significant (Baddeley et al., 2014). Values of $g(r) = 0$ commonly occur at small spatial scales and indicate that there are no points within the immediate neighborhood. Significant $g(r)$ values outside the simulation envelopes with $g(r) < 1$ indicate regularity, while $g(r) > 1$ indicates aggregation (Illian et al., 2008). If the g function strongly fluctuates at small scales around the simulation envelopes of the null model, this indicates a spatially periodic pattern with a distinct density peak at the radius where the first six, approximately equally spaced, nearest neighbors occur (Figure 1c). Such patterns are thus arranged on a hexagonal grid and can therefore be called to be "hexagonal," albeit still deviating from a truly hexagonal pattern where the Clark-Evans index $R = 2.1491$. Periodicity of a pattern is indicated by $g(r) = 0$ at shortest scales, then a steep high amplitude of $g(r)$ above the upper simulation envelope, followed by a steep significant negative amplitude that is clearly below the lower simulation envelope of the null model (Getzin et al., 2015b). In contrast, if patterns show only significant negative deviations from the null model at smaller scales but no periodic fluctuation above and below the CSR null model envelopes, such less ordered patterns are merely regular.

The L transformation (L function) of Ripley's cumulative K function, $L(r) = (K(r)/\pi)^{0.5} - r$, is used to more accurately assess departures from CSR at larger scales (i.e., 50–250 m) than the noncumulative g function (Wiegand & Moloney, 2014). For a random pattern, $L(r) = 0$ and values of $L(r) < 0$ indicate regularity, while values of $L(r) > 0$ indicate aggregation. Hence, if the L function, after the first small-scale deviations from CSR, moves consistently into the null-model envelopes of the simulated random distribution, this indicates a pattern that is homogeneous at a large scale. In contrast, significant departures from the CSR null model at these large scales indicate that a pattern is heterogeneously distributed on the landscape (Getzin et al., 2008; Wiegand & Moloney, 2004). The spatial correlation functions $g(r)$ and $L(r)$ of the 25 patterns were tested against CSR using the 5th-lowest and 5th-highest values of 199 Monte Carlo simulations for getting approximately 95% simulation envelopes of the null model (Baddeley et al., 2014; Wiegand & Moloney, 2014). All analyses were carried out using R software (package Spatstat, http://www.R-project.org/).

3. Results

No matter the method of analysis, the spatial distributions of FCs were more ordered than any of the other insect distributions (Figure 2). The Clark-Evans indices (R) for the random null model distribution (CSR) and the Australian termite and ant data (T Australia C2, A Australia C2, T Australia Pilb) were not significantly different from a random pattern (Table 1). All other patterns had highly significant R values ($p < 0.001$), and these results were unaltered when edge corrections, such as "cdf" or "Donelly," were applied (data not shown). The strongest regularity ($R = 1.75$) was for the vegetation self-organization model output of
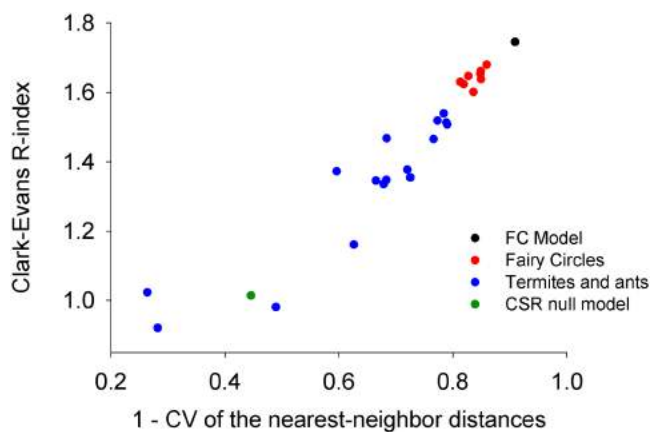
Figure 2. Two-axis classification scheme. The degree of regularity based on the Clark-Evans index *R* of dispersion and 1 - CV of the nearest-neighbor distances. $R \approx 1$ indicates randomly distributed patterns like the CSR (complete spatial randomness) null model. Higher *R* values indicate increasingly ordered patterns. The modeled FCs based on biomass-water feedbacks show the strongest regularity, followed by a group of eight FC patterns from Namibia and Australia that are separated from all less ordered patterns of social insect nests.

simulated FCs, followed by all eight measured FC patterns (*R* values ranging between 1.60 and 1.68; mean = 1.64; SD = 0.02). These *R* indices are similar to previously reported values (Albrecht et al., 2001). All 16 *R* indices of insect nest distributions were lower (range = 0.92-1.54; mean = 1.33; SD = 0.20), and the means between FC and insect patterns were highly significantly different based on a two-tailed *t* test ($p < 0.001$).

Spatial variability estimated as the coefficient of variation of the nearest-neighbor distances was consistently lowest for the FC model and all eight FC patterns and higher for all insect nest patterns. Thus, expressed as 1 - CV of the nearest-neighbor distances (Table 1, Figure 2), all eight measured FC patterns showed higher values (range = 0.83-0.86; mean = 0.84; SD = 0.02) than the 16 insect patterns (range = 0.26-0.79; mean = 0.64; SD = 0.17), and the means between FC and insect patterns were significantly different ($p < 0.001$). Thus, the simple nearest-neighbor measures provide a first indication that the patterns of FCs form a distinct separate group relative to the insect patterns (Figure 2).

Pattern differences, however, need to be more accurately related to scale dependency. The *g* function for all eight FC sites had $g(r) = 0$ at smallest distances because no FCs are detected in the immediate neighborhood of another FC (Figure 3). For all FC sites, the curve rises steeply to a peak value of $g(r)$ at the scale where all six nearest neighbors are detected. This is because all six nearest neighbors (across the landscape) have approximately the same distance to the focal FC. This first strong positive crest is immediately followed by a steeply declining *g* function where the negative trough is below the lower simulation envelope of the null model (cf. Figure 1c). This trough indicates the empty space between the first and the second row of nearest neighbors and thus an "echo effect" of the process that separates the FCs. This spatial periodicity, which indicates a grid-like hexagonal array, is only matched by the deterministic FC model output based on simulated plant self-organization, which is even more ordered because of the lack of natural noise. In contrast, none of the 16 insect mound or nest distributions show the first high-amplitude peak of $g(r)$ above the null model, immediately followed by a significant negative trough. For example, all *Macrotermes* mound patterns from Namibia and South Africa (T Namibia 1, 2, T South Africa) show a negative distance correlation up to about 40–50 m and then the *g* function remains within the null model envelopes or has just a marginally significant positive deviation from it at about 50 m (Figure 3). This absence of a sinusoidal fluctuation of the *g* function above and below the null model envelopes indicates a regular pattern for the termites but not the spatially periodic pattern typical of FCs. All analyzed termite and ant patterns, some of which have been used previously to argue for a correspondence between FC and faunal patterning, are thus less ordered than FC patterns because the null model envelopes are the reference for the comparison of patterns. In contrast to FCs, seven of the termite and ant examples are also not homogeneous but heterogeneous at larger scales with significant variation in local density across the landscape (Table 1, Figures 4 and S2).

4. Discussion

4.1. Assessing Spatial Regularity From Satellite and Aerial Images

Our analysis of global dryland examples of FCs and social insect patterns provides quantitative and qualitative insights into the inherent strength and resultant gradient of pattern ordering of these regular features. While plants or animals may commonly exhibit nonrandom patterns such as clustered or regular distributions, within these basic categories, they may show typical spatial signatures that reflect dispersal modes, behavioral constraints, or life-history strategies (Wiegand et al., 2013; Wiegand, Gunatilleke, Gunatilleke, & Okuda, 2007). Generally, a single process can create a single precise pattern, and the more unique a pattern is, the fewer candidate mechanisms are able to create such precise patterning (McIntire & Fajardo, 2009).

Despite many of the analyzed patterns having high nearest-neighbor Clark-Evans *R* values, the spatial regularity detected by the more sensitive scale-dependent density functions varied significantly. Only the *g* functions of the Namibian and Australian FC patterns, as well as the modeled FCs, showed a spatially periodic
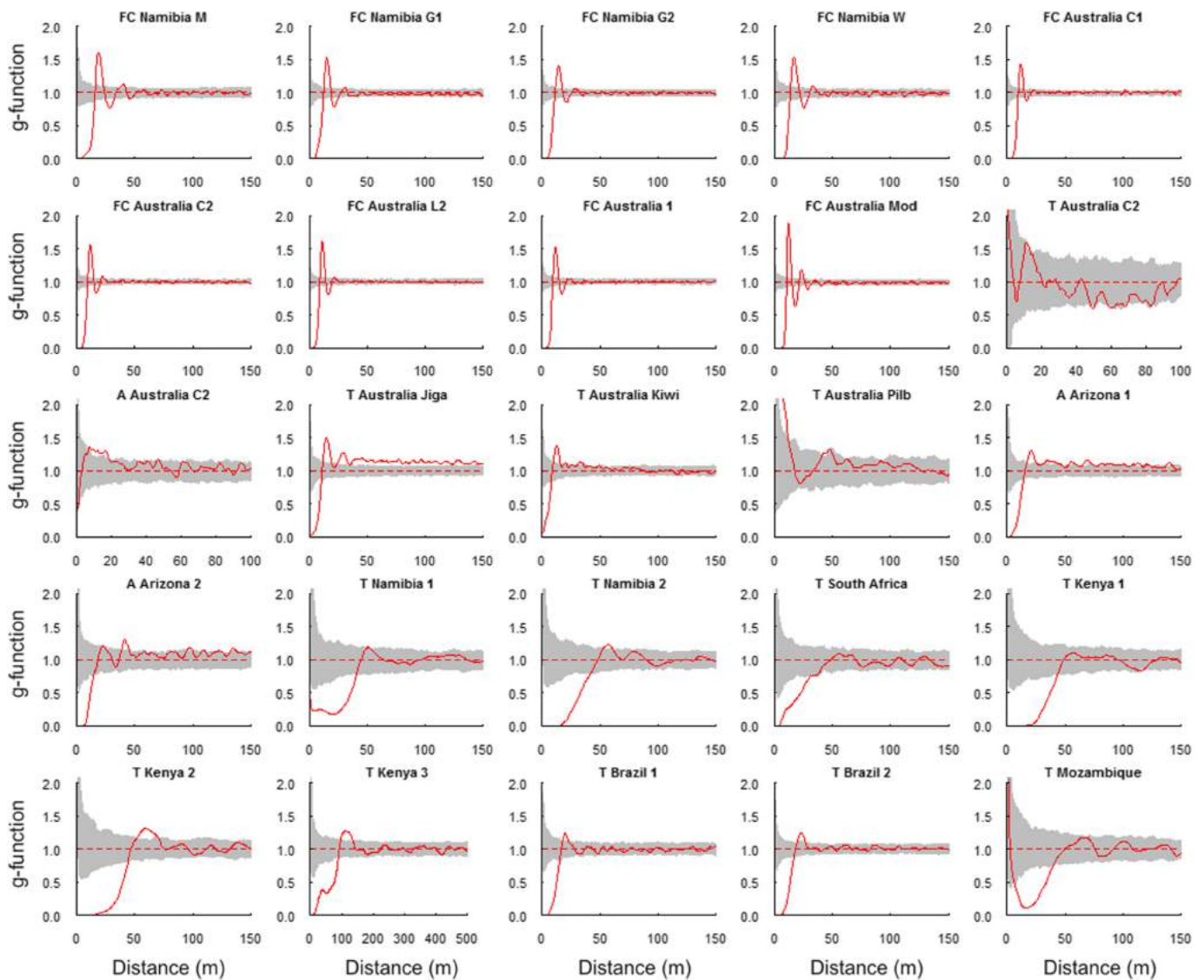
Figure 3. The degree of ordering based on scale-dependent analysis with the pair-correlation or *g* function shown for the 25 geographically distinct fairy circle and social insect patterns. The pattern is regular or aggregated at circular neighborhood distances if the red line of the *g* function is either below the lower or above the upper grey lines of the simulation envelopes, respectively. Null model envelopes were constructed using the 5th-lowest and 5th-highest value of 199 Monte Carlo simulations of the randomly distributed Poisson point process. For a detailed interpretation, see Figure 1.

distribution, homogeneously across the landscape. In contrast, all pattern examples from social insects did not show such a sinusoidal fluctuation of the *g* function with significant positive and negative deviations from the CSR null model (Figures 1c and 3). Additionally, all eight empirical FC patterns constitute a distinct highly ordered group separated from all insect patterns (Figure 2), consistent with scale-dependent *g*- and *L*-function analyses (Figures 3 and 4). Despite continental and density differences (densities vary approximately threefold), the inherent spatial signatures of pattern regularities of Namibian and Australian FCs are nearly identical. Furthermore, from north to south across Namibia (up to 1,000 km apart), the spatial pattern characteristics are remarkably similar, which may indicate that FCs are an emergent pattern that is critical to the capture, storage, and recycling of limited resources by the grassland system (van Rooyen et al., 2004). Such emergent phenomena are the products of causal mechanisms at lower levels of organization, but they are expressed primarily in behavior of higher-order components (Newman et al., 2019).

The *L* function of the FCs demonstrates homogeneous patterns at large scales. Hence, these patterns do not show significant variation in local density even at large landscape scales. This is also demonstrated by
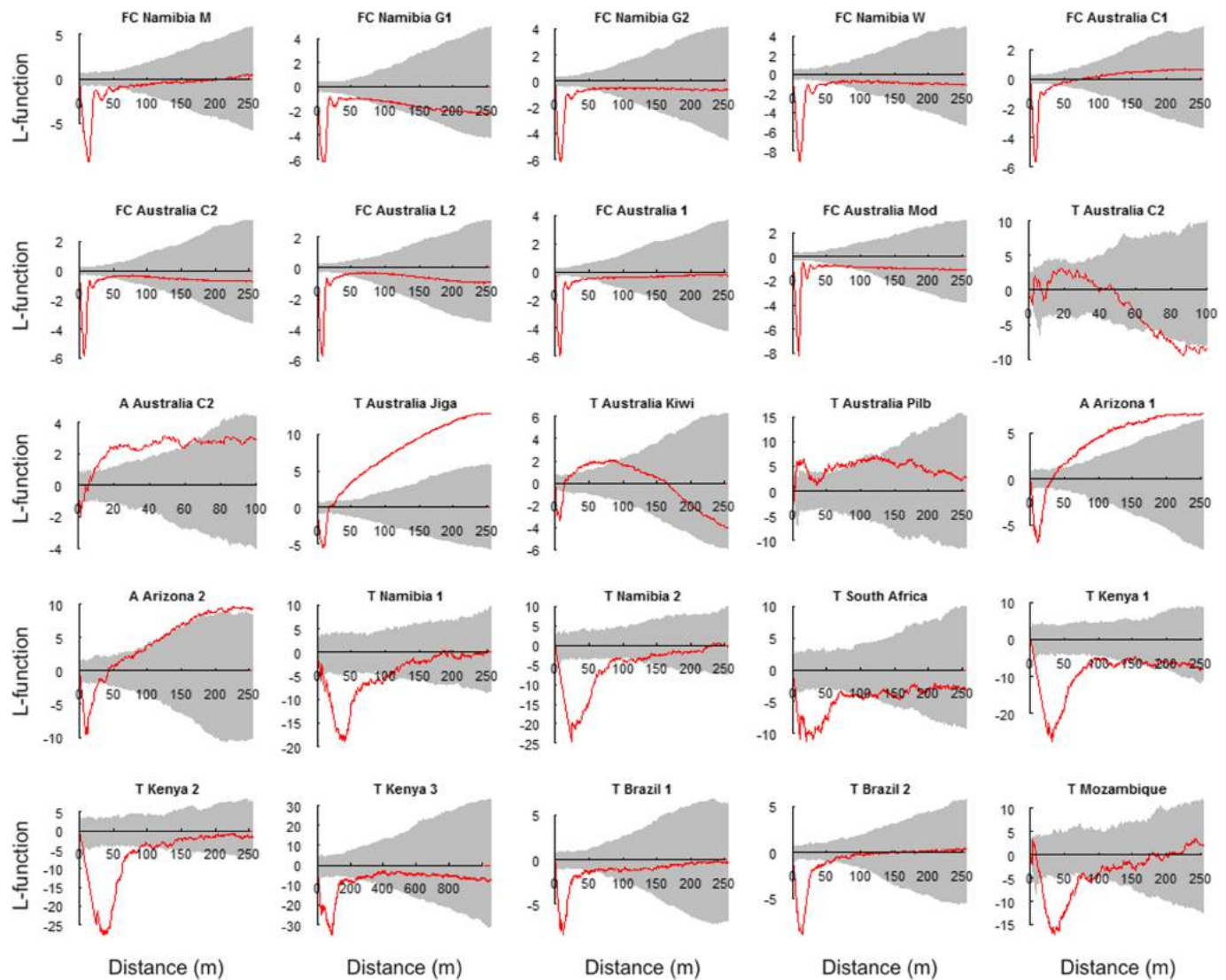
Figure 4. The spatial ordering based on scale-dependent analysis with the L transformation of Ripley's K function shown for the 25 fairy circle and social insect patterns. The pattern is either regular or aggregated at circular neighborhood distances if the red line of the L function is below the lower or above the upper grey lines of the simulation envelopes, respectively. Null model envelopes were constructed as for Figure 3. Large-scale homogeneous patterns are indicated by an L function that, after small-scale deviation from randomness, moves into the null model at large scales and stays within the simulation envelopes.

Fourier analyses of four 2 km × 2 km plots in the Giribes Plains of Namibia where all plots have the same spectral peak at around 14 m, which indicates the critical wavelength of FC distribution (Getzin et al., 2015b). The FCs thus constitute a unique benchmark pattern against which other patterns and potential causal agents can be compared. Only our process-based FC model of vegetation self-organization showed a higher degree of regularity than the observed FCs. Clearly, any model is a simplification of the real world (Grimm et al., 2005), and the model is deterministic and perfectly uniform, explaining the stronger ordering than observed in the ecosystem. Nevertheless, the vegetation model indicates that plant competition for water alone can replicate and explain FC patterning.

The sand termite (*Psammotermes allocerus*) has been suggested to cause Namibian FCs (Juergens, 2013), but there has been no spatial analysis of the nest pattern of this termite species because the nests are rare and cryptic and termite colonies possibly migrate between ephemeral nests (Vlieghe et al., 2015). As a consequence of this, the Namibian FCs have instead been compared to grassland gaps of harvester ants in North America (Juergens et al., 2015; Picker et al., 2012) and other remote termite patterns (Tarnita et al., 2017). While individual harvester ant grassland gaps look similar to individual FCs, the spatial patterns of gaps created by

harvester ants are not spatially periodic as FCs and are often heterogeneous at larger scales. For Namibia, an analogy is often made between FCs and mound patterns of *Macrotermes* sp. (e.g., Juergens et al., 2015), based on the geographic proximity. However, all *Macrotermes* mounds analyzed here are significantly less ordered than the FCs and lack the spatial periodicity typical of FCs. Nearest-neighbor distances from our digitization of all visible termite mounds 200 km southwest of Outjo in Namibia (T Namibia 2) were very similar to those ground-mapped large mounds, with heights between 0.8 and 4.4 m (T Namibia 1). The three termite mound patterns from Kenya also lacked spatial periodicity. Here we highlight the need for correctly digitizing all the visible mounds in a plot. In Kenya, for example, the large-scale gap pattern of this 2 km × 2 km plot seems highly regularly spaced, but closer inspection of the white vegetation-less patches shows that the spacing of the individual termite colonies is characterized by considerable nearest-neighbor variability and the large gaps are partly interconnected by nearby mound arenas (Figure S1). Finally, the three termite mound patterns of Brazil and Mozambique provided by Tarnita et al. (2017) are also regularly distributed but not spatially periodic. Notably, these Brazilian termite mound patterns were claimed to be "the greatest example of insect biopedoturbation and ecosystem engineering at a landscape scale yet recorded" and have been called "extremely regular" (Funch, 2015) but still do not show the spatial signature that characterizes FCs. Hence, within a pattern-process inference framework, these well-known agent behaviors are unlikely drivers of the typical Namibian and Australian FC patterns (Grimm et al., 2005; Schurr et al., 2004).

4.2. Factors That May Affect Variability in Patterns

The systematic differences between social insect patterns and FCs are not related to the sample size or size of the observation window (Table S1). For example, the "T Brazil 2" pattern with 693 mounds had more data points than the 630 FCs in Marienfluss, but nevertheless, the termite pattern did not show the strong degree of ordering (Figure 2) and lacked the spatial periodicity typical of FCs (Figure 3). Observation windows with a size of 500 m × 500 m or more are thus sufficient for comparison of these patterns.

Large-scale heterogeneity is another factor that may influence the spatial patterns and density of FCs (Getzin & Yizhaq, 2019), termite mounds (Muvengwi et al., 2016), or biotic populations in general (Getzin et al., 2008). Such effects have, however, been excluded by selecting topographically, edaphically, and floristically homogeneous rectangular areas. One could then hypothesize that the lower spatial regularity of insect nests than of FCs was still due to more variable microtopographic, edaphic, or floristic environments for insect patterns. However, this would imply that none of the 16 insect patterns would have been taken from a landscape that is as homogeneous as the Australian and Namibian FC landscapes. This can be falsified for all termite and ant patterns from Australia. Here, the ground-mapped nests of harvester termites and ants cooccurring with FCs within the identical study plot were distributed randomly or aggregated and did not match the FC pattern (Getzin et al., 2016). A similar lack of correspondence with FC patterns is also evident for harvester and spinifex termites in three *Triodia*-dominated grasslands of Western Australia. Ground visits of the plots "T Australia Jiga" and "T Australia Pilb" confirmed that the substrate is as flat and edaphically as homogeneous as for the typical FCs patterns 50 km further to the south (Getzin et al., 2019). A lack of an effect of topographic or floristic variation on spatial patterns of insect mounds has been also reported for North American harvester ants, which do sometimes inhabit very homogeneous grasslands (Dibner et al., 2015).

For the Namibian FCs, one could speculate that the "nest systems of *P. allocerus* might be the most regularly spaced of all social insects because of the unusually homogeneous environment" (Juergens et al., 2015). There are no data to support the assumption that *P. allocerus* nests are regular or were even periodically ordered. It would imply that there is a strong pattern-process link between the location of nests and the distribution of the mature FC centers, because it is the mature FCs that make up the spatially periodic pattern. However, field data do not support this, because if *P. allocerus* are present in a FC area, the nests can be found both along the edges of the mature FCs as well as in the matrix (Vlieghe et al., 2015). In many other areas, nests of *P. allocerus* are not found near FCs at all (Ravi et al., 2017; Tschinkel, 2010). It is also doubtful that the Namibian FC environment is homogeneous for sand termites that are just 5 mm long. The mean nearest-neighbor distance between FC centers is 10 to 15 m (10,000 to 15,000 mm), which is a distance being 2,000 to 3,000 times greater than the size of the sand termite. It is more likely that microtopographic variation, trampling routes of ungulates, or the undulating terrain in aeolian-derived sand are rather perceived as heterogeneous from the point of view of a 5-mm-long sand termite. In contrast, the roots of the *Stipagrostis* grasses surrounding the FCs are about 100 times larger and water moves horizontally between the FCs

over distances of more than 7 m (Cramer et al., 2017; Cramer & Barger, 2013). It will be a challenge for future research to assess the fine-scale variation in abiotic heterogeneity and how it affects the relative spatial variability of different biota such as grasses and insects.

4.3. Causes of the More Variable Insect Patterns in Drylands

Spatial pattern analysis of aerial or satellite images focuses on the larger objects that make up the final landscape-scale pattern. It is thus a method of *coarse graining*, by which finer-scale processes, structures, and states are aggregated and combined into useful metrics at the larger landscape scale (Newman et al., 2019). Thereby, our analysis highlights the final outcome of competition for resources because it is usually the large and mature termite colonies that require the largest space and that attain the highest degree of spatial regularity (Grohmann et al., 2010). Our data demonstrate that termite and ant patterns in drylands typically show a higher spatial variability at small and/or large neighborhood scales than the benchmark pattern of FCs in such comparable drylands. There are many well-documented processes that can explain the higher degree of spatial variability in insect nest distributions.

Under comparable habitat conditions, the variable spatial patterning of social insects is commonly not attributable to abiotic factors (e.g., altitude and soil type), but spatial trends in density or pattern are rather caused by biotic interactions and the mobility of the dispersing or competing insects (Blanco-Moreno et al., 2014). For example, founding queens choose preferential areas for colony establishment that might be influenced by vegetation, wind directions, or magnetometry, leading to large-scale heterogeneity in insect-induced grassland gaps (Nicolai et al., 2010; Wajnberg et al., 2010; Wiernasz & Cole, 1995). The number of dispersing queens may vary spatially across the landscape or variability in colony spacing is due to variability in colony age and size (Crist & Wiens, 1996) and daughter colonies typically aggregate around established parent colonies (Cole & Wiernasz, 2002; Grohmann et al., 2010; Tarnita et al., 2017), leading to less overall ordering and regularity. Most ecosystems are inhabited by several termite or ant species and thus interspecific competition may induce considerable spatial noise, such as in Namibian *Macrotermes* mounds (Grohmann et al., 2010). Such interspecific influences on the spatial activity of nest-building termites will likely also affect *P. allocerus* in the Namibian FC regions because termite and ant diversity within or nearby FCs includes diverse genera such as *Psammotermes*, *Hodotermes*, *Baucaliotermes*, *Tetramorium*, *Anoplolepis*, *Messor*, and *Pogonomyrmex* (Juergens, 2013). Furthermore, intraspecific interaction between colonies does not necessarily lead to differential survival (Adams & Tschinkel, 1995; McGlynn, 2012). Another reason for greater variability in termite nest spacing is the fact that neighboring nests are often polycalic and belong to the same colony (e.g., Australian harvester termites, Holt & Easey, 1985; *P. allocerus*, Vlieghe et al., 2015), resulting in a lack of aggressive territorial and competitive interactions between regularly spaced nests. Furthermore, the Brazilian mounds (T Brazil 1, 2) created by *Syntermes dirus* termites may even show small-scale positive associations because many mounds may belong to one and the same colony and intraspecific aggression is absent in the immediate mound neighborhood (Martin et al., 2018). Additionally, the nests of social insects are often not centered in their territories or home ranges and vary greatly in size, so that the size of their territories and intercolony spacing varies, dampening the regularity of the spatial distribution patterns (Crist & Wiens, 1996).

The high mobility of social insects (versus sessile plants), particularly in drylands where water is scarce, rainfall is spatially stochastic, and nomadism is erratic in terms of timing and direction, may be an important reason for their spatially more variable nest patterns in such water-limited environments (McGlynn, 2012; Teitelbaum & Mueller, 2019). Given that social insects are mobile in three-dimensional space (e.g., wing dispersed in air or deep burrowing in sand), the source of spatial variability is not only due to direct horizontal interaction. The location of termite nests may also be dependent on the water table in deeper soil layers (Davies et al., 2014). For example, termites of the genus *Psammotermes* have been reported to range as deep as 40 m to the water table in sandy deserts and bring up moist particles with which they humidify their nest (Howse, 1970).

4.4. Contrasting Alternative Hypotheses

Within a pattern-process framework, information from spatial patterns cannot verify a certain agent as being causal, but based on quantitative evidence on pattern signatures, unlikely hypotheses can be identified and more likely working hypotheses can be formulated (Box 1, Schurr et al., 2004). Our spatial analyses are not consistent with a termite origin for the spatially periodic FC patterns. Rather, we consider the vegetation self-organization hypothesis to be more likely for inducing the observed FC patterns, which look so striking from

a bird's-eye view. The grass vegetation where FCs typically occur in Australia or Namibia is dominated by only one or sometimes two grass species that compete directly with each other in horizontal space. The sessile plants in these almost monospecific grass communities along the desert margins are strongly dependent on limiting soil moisture and also nutrients (Cramer & Barger, 2013), which allows for the development of structurally simple and highly symmetric regular vegetation patterns (Meron, 2012).

In Australia, the driving mechanism is suggested to be positive biomass-water feedbacks associated with water runoff over clay-rich, compacted soil crusts that seal the soil surface and induce spatially periodic vegetation patterns such as banded *Acacia* trees on slopes (Figure S3) or FC gaps in flat *Triodia* grassland (Dunkerley, 2010; Getzin et al., 2019). Hence, the vegetation-dependent infiltration of water on the FC periphery likely causes the positive biomass-water feedback and induces the barren FC areas (Getzin et al., 2016). The Australian FCs are an important benchmark ecosystem with regard to this pattern study because recent systematic excavations of 154 holes revealed no termite causality of these FCs (Getzin et al., 2019).

For Namibian FCs, there is evidence for positive biomass-water feedbacks mediated by subsurface water flow through highly permeable sands (Cramer et al., 2017; Ravi et al., 2017). The size of mature FCs and number of newborn FCs increases after prolonged dry years while FCs tend to disappear and shrink in size after cumulative wetter years, which underlines the importance of water as a main driver of the pattern (Zelnik et al., 2015). Despite differences in the details of the biomass-water feedbacks, FCs in both these dryland systems function as an extra source of water for the matrix vegetation. They are thought to demonstrate a universal principle of pattern formation through a symmetry-breaking process (or instability) that is manifested in the highly periodic wavelength of the emerging vegetation gaps (Getzin et al., 2016; Meron, 2012; Meron, 2018). By forming symmetric patterns, the vegetation benefits from the additional water resource provided by the FCs and thereby keeps the arid ecosystem functional at lower precipitation values compared with uniform vegetation (Meron, 2018). We consider FCs to be a striking example of the concept of *emergence*, where new patterns, processes, or structures appear at higher levels of organization that are not present at lower levels of organization. Emergent patterns are best examined with methods of *coarse graining*, hence with methods for aggregating finer-scale processes or patterns to larger-scale summaries. Such coarse-graining summary statistics applied to any quantity in a complex system should be by default expected to be scale dependent (Newman et al., 2019), as demonstrated by the spatial statistics methods used in this analysis.

5. Conclusions

While many plant or animal patterns can have six nearest neighbors on average, it is the details of those pattern signatures that need to be described by using several summary statistics simultaneously. The scale-dependent neighborhood-density functions are more sensitive indicators of spatial regularity, and especially the sinusoidal-like significant fluctuation of the *g* function around the null model can be used to differentiate between spatially periodic FCs versus merely regular insect distributions. While some faunal patterns are very regular (e.g., Brazilian termite mounds; Funch, 2015), none of these known termite patterns in drylands approach FCs in spatial periodicity. We suggest that the reasons for this lie in the characteristic variability of the interactions between mobile faunal colonies versus the less complex interactions between sessile plants in monospecifically dominated communities of arid ecosystems where all plants commonly compete for the same resource: water. The more ordered self-organization mediated by symmetry-breaking short- and long-range biomass-water feedbacks likely drives the periodic emergent vegetation patterns in drylands.

Spatial statistics cannot rule out hypotheses, but it can provide critical information to evaluate competing explanations of causal mechanisms as unlikely for a specific ecosystem based on theory and comprehensive quantitative evidence (McIntire & Fajardo, 2009; Schurr et al., 2004). While our study uses state-of-the-art analyses of global regular ecological patterns to inform the debate, it is not a substitute for fieldwork in uncovering the ecophysiological mechanisms at play.

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Erratum

In the originally published version of this article, the Acknowledgments included a link only for data in the seven point patterns citing Tarnita et al. (2017) in Table S1. The authors have since uploaded data from the 19 patterns in Table S1 that do not cite Tarnita et al. (2017), and these data are now available at https://datadryad.org/stash/dataset/doi:10.5061/dryad.44j0zpcb9.

The acknowledgments are now corrected, and this version may be considered the authoritative version of record.