PNAS COMMENTARY

Fairy circle tales

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Spatial self-organization is a process by which intricate spatial patterns arise from originally disordered configurations (1). This occurs solely as a result of local interactions. Self-organized spatial patterns are widespread in ecological systems (1, 2). Diverse nonlinear interactions among organisms and between organisms and their environment can give rise to these regular patterns and can lead to an emergence of ecosystem-level properties unique to self-organized systems (3–5). Much research has been devoted to revealing the self-organizing processes that form patterning and their resulting ecosystem consequences. Most of this work, however, remains theoretical (6–8). Empirical validations of pattern-forming mechanisms and their ecological consequences are both rare and challenging. In this issue of PNAS, Guirado et al. (9) provide a set of multifaceted empirical observations of fairy circles (FCs), a well-known self-organizing system and thereby provide new opportunities to advance the theory of ecosystem spatial self-organization.

FCs are bare soil discs of 2- to 35-m diameter surrounded by rings of tall perennial grasses embedded in a grass matrix (Fig. 1). FCs have been reported heretofore only in drylands of Namibia and Australia (10, 11). Using remote sensing and deep learning, Guirado et al. conducted a scan around the globe and detected FC-like vegetation patterns at 263 locations in 15 countries, ranging from the Sahel, Western Sahara, Horn of Africa, Madagascar, and into Southwest Asia, in addition to already known sites in Namibia and Australia. Next, they quantified the effect of an array of environmental variables on the occurrence of FC-like patterns and their pattern characteristics (i.e., size, shape, and density of circles). Last, Guirado et al. assessed the consequences of vegetation pattern formation, by comparing ecosystem stability, indicated by interannual variability of primary productivity, between sites with FC-like patterns and nearby sites without this patterning. This large-scale, systematic analysis generates interesting insights into the origin of FCs.

The origin of FCs remains disputed, but two major competing hypotheses are predominant (Fig. 1 *A* and *B*). On one hand, many overdispersed vegetation patterns have been attributed to subterranean ecosystem engineering by the likes of termites and ants. The regular spacing of FCs is interpreted to be caused by intercolony territorial competition (12) (Fig. 1*B*). On the other hand, models of Turing scale-dependent feedback (TSDF; plants facilitate their own growth locally while competing with distant individuals; Fig. 1*A*) can reproduce various regular patterns formed in drylands, without involving animal activities (8, 11) (Fig. 1*C*). To conclusively distinguish between these two competing mechanisms requires direct manipulation of the hypothesized pattern-forming processes. This is challenging and is rarely attempted. However, we can evaluate the relationship between pattern occurrence and the environmental factors implied to be important by models that depict the different hypotheses.

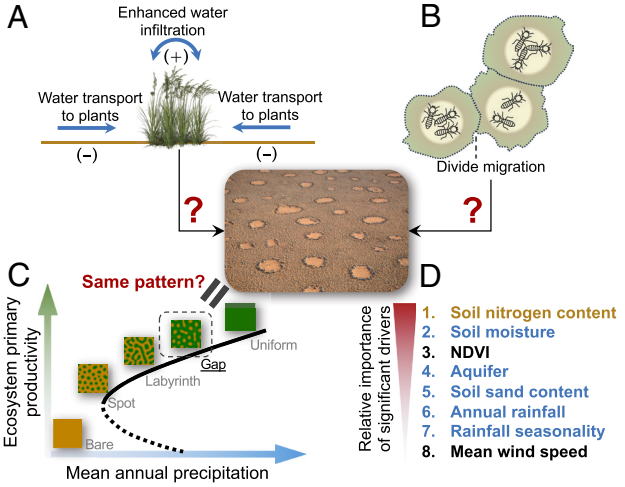

Fig. 1. Two major competing mechanisms for the origin of FCs. (*A*) Mechanism of scale-dependent feedback mediated by water-biomass feedback, i.e., plant growth enhances water infiltration, forming a short-range positive feedback, and the growth of plants reduces water availability nearby, forming a long-range negative feedback. (*B*) Mechanism of territorial competition among ant/termite colonies. (*C*) Transition of vegetation spatial patterns along the aridity gradient, predicted by models with the mechanism depicted in (*A*). (*D*) Statistically significant variables predicting the occurrence of FCs, ranked in order of their relative importance, derived from empirical environment-pattern correlations, according to Guirado et al. in this PNAS issue.

Empirical correlations are hints to causation and can help us gain some insights into the nature of the pattern-forming mechanism. This is what Guirado et al. cleverly did.

With the global atlas of FC-like vegetation patterns in hand along with the wide range of environmental conditions they encompass, Guirado et al. found that soil (its nitrogen, moisture, and sand content) and climatic variables (mean annual precipitation and wind speed) ranked as top factors predicting the presence of FC-like vegetation patterns (Fig. 1*D*). FCs are more likely to occur in drier conditions. This is supported by results from Guirado et al. on the association of FCs with lower soil moisture, terrain slope, and annual precipitation and higher soil sand content. Furthermore, they found that FC-like patterns are more likely to occur in places with lower soil nitrogen. In fact, soil nitrogen was the most important variable in predicting the occurrence of FC-like patterns. The effect of variables related to water availability seems to favor

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the mechanism of TSDF involving water and biomass (Fig. 1*A*); however, the paramount effect of nutrients might imply the role of termites, as termites can redistribute nutrients (13), and alter the efficiency with which plants convert water into biomass. This then affects the formation of patterned vegetation (6). However, Guirado et al. found that termites and ants were not important in predicting the presence of FC-like patterns globally, except at Namibian sites.

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If FCs are formed solely by TSDF (11), then the FC pattern is merely a stage in the sequence of vegetation pattern transition along the aridity gradient predicted by TSDF models (Fig. 1*B*)—from uniform vegetation cover, to bare gaps in a vegetation matrix (gapped pattern), to labyrinthine or striped vegetation cover, and then to spotty vegetation in a bare soil matrix (8). FCs represent the "gapped pattern" in the broad theory of spatial self-organization of dryland vegetation. Is this true? We can gain some hints by comparing the results from Guirado et al. with those from an earlier study by Deblauwe et al. (14), who detected the global distribution of various regular vegetation patterns (i.e., stripe, spotted, gapped, and labyrinthine patterns predicted by TSDF models) using remote sensing and analyzed the conditions requisite for patterns to occur. Deblauwe et al. (14) also found significant effects of climatic and soil variables, but no effect of soil nitrogen, counter to Guirado et al. (Fig. 1*D*). FCs detected by Guirado et al. largely fall within the geographic areas for vegetation patterning predicted by Deblauwe et al. (14). Furthermore, Guirado et al. quantified the annual precipitation envelope to be 100 to 300 mm when FC-like patterns are mostly likely to occur, while the range of 450 to 550 mm y^{-1} was identified for "gapped pattern" in the Sudano-Sahelian area by Deblauwe et al. (15). These similarities and differences suggest that mechanisms forming FCs and gapped patterns are related, but not identical. It is very likely that both TSDF and territorial competitions by ant/termite colonies operate simultaneously to form FCs (7, 16), and the relative importance of each mechanism may vary from region to region and over time. A new question thus arises: What determines the relative importance of each FC self-organizing mechanism?

Areas of regular vegetation patterns, including FC-like patterns, make up only a small fraction of drylands worldwide (14). Guirado et al. delineated regions that meet the required conditions, but where FC-like vegetation patterns are not present. They attributed this absence to human activities. It might also have to do with species present—given requisite environments, are all plant species equally likely to form regular patterns? The broad-scale occurrence of regular vegetation patterns across continents suggests that pattern formation is not limited to one plant species (14). Rather, dominant pattern-forming species across regions display common functional traits (17). Biodiversity and species interactions might also matter (16, 17). Although species richness is relatively low in drylands, strong species interactions do indeed occur. For instance, biological soil crust communities in drylands (e.g., cyanobacteria, mosses) alter major hydrological and biogeochemical processes and can form competitive or facilitative interactions with vascular plants (18). Guirado et al. found that the degree of regularity of FC spatial distribution diminishes as grass species richness increases in the ecosystem. This supports the contention that species diversity and interactions affect FC pattern formation.

Theoretical models predict that spatial self-organization can mediate ecosystem functions, such as biodiversity and stability (3, 4). Results by Guirado et al. suggest that ecosystems with FC-like patterns have higher stability (as indicated by lower interannual variability in productivity) than do nearby sites without patterning. This is consistent with theoretical predictions (19). Faced with environmental changes, a pattern adaptation can occur, causing the system to shift from one patterned state to another—meanwhile limiting the effect on the ecosystem's productivity during the state shift (5, 19). Related results are reported by Guirado et al. showing pattern adjustment with environmental change—density of FCs declines and circles become rounder with intensifying aridity across sites. The 18-y dataset assembled by Guirado et al. could be used to evaluate, for a given site, how pattern characteristics and ecosystem productivity change as a function of aridity over time.

While the evidence presented in Guirado et al. remains correlative in nature, their analysis provides several aspects of patterns that could be used to compare with predictions by alternative model formulations representing competing hypotheses: for example, i) changes of the FC density and size and the degree of pattern regularity along the aridity gradient; ii) trajectory of ecosystem primary productivity under drying conditions in areas with and without FCs; iii) the paramount effect of nutrients on the occurrence of FCs, currently only considered by a few models to account for the role of termites (6); and iv) the life cycle of FCs that can be derived from the 2000 to 2017 time series dataset assembled by Guirado et al. These diverse independent aspects of patterns enhance our capacity to distinguish among competing hypotheses, as exemplified in ref. 7.

Some ecosystem properties (e.g., productivity and biodiversity) might be influenced solely by extant spatial patterns, without regard to the operant pattern-forming mechanism that generated the pattern (4). Other properties, e.g., ecosystem responses to perturbation, are sensitive to the specific mechanism that generated the patterns (20). Whether FCs are formed by vegetation scale-dependent feedback, territorial competition among colonies of ants/termites, or by a combination of mechanisms will shape how drylands respond to climate change (6, 7). A reliable prediction of dryland changes in the future will require a robust mechanistic understanding. The new global-scale FC-like patterns revealed by Guirado et al. present an exciting opportunity to elucidate mechanisms for dryland vegetation pattern formation, especially if empirical analyses are supplemented with theoretical modeling.

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