Short Note

Ecosystem spatial self-organization: Free order for nothing?☆

Dong Xiaoliab, Fisher Stuart G.a

a School of Life Sciences, Arizona State University, Tempe, 85287 AZ, USA
b Department of Environmental Science and Policy, University of California, Davis, 95616 CA, USA

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ABSTRACT

Ecosystems are complex adaptive systems (CAS) by nature, which means that macroscopic patterns and properties emerge from, and feed back to affect, the interactions among adaptive individual ecological agents. These agents then further adapt (genetically) to the outcomes of those interactions. The concept of self-organization has become increasingly important for understanding ecosystem spatial heterogeneity and its consequences. It is well accepted that ecosystems can self-organize, and that resulting spatial structures carry functional consequences. Feedbacks from the outcome of spatial pattern to the individual agents from which patterns emerge, are an essential component of the definition of CAS but have been rarely examined for ecosystems. We explore whether spatial self-organization provides a mechanism for such feedback for ecosystems as CAS, that is, whether ecosystem-level outcomes of self-organized patterning could feed back to affect or even reinforce local pattern-forming processes at the agent level. Diffuse feedbacks of ecological and evolutionary significance ensue as a result of spatial heterogeneity and regular patterning, whether this spatial heterogeneity results from an underlying template effect or from self-organization. However, feedbacks directed specifically at pattern-forming agents to enhance pattern formation—reinforcing feedback—depend upon the level of organization of agents. Reinforcing evolutionary feedbacks occur at the individual level or below. At the ecosystem level, evidence for mechanisms of feedback from outcomes to patterning to agents forming the patterning remain tenuous. Spatial self-organization is a powerful dynamic in ecosystem and landscape science but feedbacks have been only loosely integrated so far. Self-organized patterns influencing dynamics at the ecosystem level represent “order for free”. Whether or not this free order generated at the ecosystem level carries evolutionary function or is merely epiphenomenal is a fundamental question that we address here.

1. Introduction

The idea of long term holistic ecosystem control and directional change has a long history in ecology (e.g., ‘community of interest’ by Forbes (1925); ‘ecosystems as superorganisms’ by Clements (1936)). It has been hypothesized that there are directional and predictable changes in many ecosystem properties over successional time (Odum 1969). Some of the specific predictions of Odum (1969) were later modified in light of empirical studies (e.g., Vitousek and Reiners, 1975; Fisher et al., 1982), but others remain untested. Similarly, the strong Gaia hypothesis (Lovelock and Margulis, 1974) largely fails as a model for understanding nature, as it treats the biosphere as if biologically mediated feedbacks necessarily enhance the environment to make it more suitable for life, although certain forms of weaker Gaia are accepted (Kirchner, 2002). These views of ecosystem change often invoke unspecified or controversial mechanisms (e.g., group selection, ecosystem selection) and are rooted in a tradition of wishful thinking derived from systems theory and cybernetics.

For many years, the ecosystem was studied as a “black box,” wherein ecosystem ecologists measured inputs and outputs of material and energy without explicit reference to spatial pattern (e.g., Odum, 1957; Bormann and Likens, 1967; Fisher and Likens, 1972; Bormann et al., 1977). In contrast, ecology has a long tradition of understanding the spatial pattern of organisms at a variety of scales (e.g., Watt, 1947; Whittaker, 1956; Curtis, 1959). In fact, ecology has been defined as the study of the distribution and abundance of living organisms (Andrewartha and Birch, 1986). Consideration of spatial dynamics received increased attention in the late 1970s and early 1980s with the ascendance of landscape ecology (White, 1979; Paine and Levin, 1981; Pickett and White, 1985). Landscape ecology brought a particular focus to spatial heterogeneity with attempts to link it with its functional consequences (Turner, 2005). Two ecosystems with identical

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Corresponding author at: Department of Environmental Science and Policy, University of California, 1 Shields Ave, Davis, 95616 CA, USA.

E-mail addresses: xldong@ucdavis.edu (X. Dong), s.fisher@asu.edu (S.G. Fisher).

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components could have very different ecological functioning if the components were arranged differently in space (e.g., Irlandi et al., 1995; van Nes and Scheffer, 2005; Virah-Sawmy et al., 2009). For example, the spatial arrangement of grassy and bare soil areas influences patterns of sediment losses from a semiarid savanna landscape (Ludwig et al., 2007). The classic perspective on formation of spatial heterogeneity emphasizes physical conditions set by the landscape as the main determining factor, i.e. the template effect (Buxbaum and Vanderbilt, 2007; Manolaki and Papastephanou, 2012; Ropars and Boudreau, 2012). But heterogeneity can also emerge from completely homogeneous conditions through interactions among ecosystem components, i.e., by the process of self-organization.

Ecosystems are considered complex adaptive systems, which means that “spatial patterns emerge from, and feed back to affect, the actions of adaptive individual agents” (Levin, 1998, 2005). Although this definition has been widely used, the essence of it, i.e., feedback that crosses levels of organization (e.g. between the level of ecosystem and the level of individual agent), has not been scrutinized. What is the mechanism for such feedback? Is the feedback directional—that is, is there feedback from the consequences of an ecosystem spatial property to the actions of individual agents that generated the spatial pattern. And does this intensify patterning or reinforce ecosystem functioning and thus render the system ‘adaptive’? If so, what are the mechanisms of this? Lastly, if ecosystems are complex adaptive systems, does such feedback provide a source of system-level adaptation? In this paper, we examine the mechanisms of feedback from the consequences of self-organized patterns to agents of pattern formation and assess whether self-organization, through these feedbacks, could contribute to a mechanism for directional ecosystem change akin to cybernetic control or to Gaia or to some other mechanisms of ecosystem control or directionality.

2. Origin of spatial heterogeneity

Other than the commonly studied template effects, where the existing geomorphic, hydrologic, or climatic variables determine biological patchiness, spatial heterogeneity can arise in other ways, with some degree of randomness or stochasticity. Spatial heterogeneity can also arise from a homogeneous template by spatial self-organization. For example, in many arid ecosystems, vegetation forms regular stripes (‘tiger bush’), labyrinths, spots (‘leopard bush’), and gaps (Rietkerk and van de Koppel, 2008). In the Florida Everglades, ridges and sloughs are self-organized into a regularly interspersed pattern, parallel to the direction of flow (Larsen et al., 2007). In the Namib Desert of southwestern Africa, fairy circles—nearly circular barren patches within a sparse matrix of small short-lived grass species surrounded by a halo of taller grass, are regularly spaced, and extend for kilometers across the landscape (Tschinkel, 2012). In mussel beds on intertidal flats, regular patterns develop at two scales, banded patterns occurring at the ecosystem level, and net-shaped patterns at the smaller scale of mussel assemblages (Liu et al., 2014). In all these cases, self-organized spatial patterns arise by the mechanism of scale-dependent feedbacks (SDF; Fig. 1). Scale-dependent feedbacks couple short-range positive feedbacks with long-range negative feedbacks (Rietkerk and van de Koppel, 2008). Depending on the sources for “activation” and “inhibition”, there are two basic mechanisms for scale-dependent feedback; one is through resource distribution and the other through amelioration of physical stress.

In resource-limited environments, positive feedback results from the local interaction between the resource-consumer agent (e.g., individual plants) and its limiting resource, resulting in long-distance depletion of the resource. This is the negative feedback. In arid systems, for example, vertical infiltration of water is locally enhanced by plants, which improves local conditions for plant growth. At a longer distance along the hydrologic flow path, this local depletion of water and gradual drying limits growth (Couteron and Lejeune, 2001; Rietkerk et al., 2002). Depending on the network of flowpaths generating SDF responses, spatial patterns emerge. When the resource is no longer limiting, self-organized patterns (resource islands) resulting from this mechanism disappear. Regular patterning is also found in environments with physical stress, such as in freshwater macrophyte patches in lowland streams and rivers exposed to shear stress (Schoelynck et al., 2012). At short range, amelioration of physical stress by plants enhances sediment accretion, insulating plants. At longer-range, stress forms erosion troughs around the plant tussock restricting its lateral expansion. Erosion decreases as sediment accumulates in the plant tussock, which in turn improves local habitat (short-range positive feedback). Meanwhile, in the area beyond vegetation patches, sheer stress and erosion greatly increase, preventing plant establishment (long-range negative feedback). Whereas scale-dependent feedbacks are often considered a general mechanism for pattern formation, Tarnita et al. (2017) and Pringle and Tarnita (2017) recently argue that other mechanisms (such as territorial interference competition between colonies of social-insect ecosystem engineers) could interplay with SDF in a dynamic way to contribute to landscape pattern formation under certain conditions. There is also a relatively rich body of literature on noise-induced pattern formation (that is, regular patterns emerge from stochastic noise), but it has had limited applications to the environmental sciences (Borgogno et al., 2009).

3. Ecosystem consequences of self-organized patterns

Spatial heterogeneity has been shown to influence a range of ecosystem properties regardless of whether spatial variety is generated by an underlying template or is self-organized. In resource-limited environments (e.g., deserts), self-organized heterogeneous patterning relies on movement of a limiting resource (e.g., water, nutrient) along flow paths, and is realized as organisms themselves affect the availability and spatial distribution of the resources upon which they depend. With the emergence of patterns, the structure of flow paths is also altered, as well as consequent ecosystem nutrient retention. This altered ecosystem nutrient retention is caused by the modified pathway of flows among patches, evolving patch geometry, nonlinear biogeochemical processing rates with distance along a flow path, and their collective consequences at the ecosystem level. When several patch types are present, the results can be a complex function of the spatial arrangement of patch types transected by operant flowpaths that integrate patch variety (Reiners and Driese, 2001; Fisher et al., 2004; Fisher and Welter, 2005). As a consequence, banded vegetation in arid and semiarid ecosystems can retain more runoff and sediments than non-patterned ecosystems (Ludwig et al., 1999; Ludwig et al., 2005). Patterned landscapes also have implications for trophic structure in communities. Pringle et al. (2010) suggested that evenly spaced termite mounds produced dramatically greater abundance, biomass, and reproductive output of consumers across trophic levels than would be obtained in landscapes with randomly distributed mounds.

Regular patterns also can alter ecosystem stability and resilience, which are among the most holistic of ecosystem properties. Self-organized landscapes exhibit catastrophic shifts from self-organized patchiness to a homogeneous state in response to altered levels of stress (e.g., amount of precipitation; Rietkerk et al., 2004). Patterned mussels in intertidal flats are more resilient to wave action and have higher productivity at landscape scales than non-patterned mussels (van de Koppel et al., 2008). Whether self-organization leads to increased resilience and stability or to increased vulnerability may depend on the ecosystem involved. Mathematical models predict that the emergent self-organization of mussel beds affects the functioning of mussel bed ecosystems by enhancing productivity and resilience against wave disturbance (van de Koppel et al., 2005a). Van de Koppel et al. (2005b) found that self-organization induced by local positive feedbacks between clay accumulation and plant growth enhanced the resilience of salt marsh ecosystems on short time scales. On longer time scales,
however, self-organization led to the destruction of salt marsh vegetation. Using an evolutionary host-pathogen model, Jackson et al. (2014) showed that patterned landscapes have higher resistance to the spread of pathogens. These and other examples illustrate that self-organized spatial patterns have a significant effect on several ecosystem properties (e.g., nutrient retention, stability) considered to be essential ecosystem attributes (Odum, 1969). But the question remains, are individual agents of patterning themselves influenced or even rewarded for pattern generation? If so, how?

4. Taxonomy of pattern-forming agents

Spatial self-organization is driven by a system of agents. This system initiates change that is distributed across a relatively homogeneous platform interacting with a propagating vector (wind, flow of water, resource movement along a concentration gradient) to set up the spatially distributed feedback network upon which spatial patterns emerge (symmetry-breaking instability). The agent itself is a component of patches in the self-organized landscape. Patterns do not instantly emerge, but develop at a rate commensurate with agent and patch growth and/or movement constants (e.g., fast with sand ripples on a stream bed; slower with banded forest vegetation). Once formed, the patterned landscape may eventually disappear, for example when nutrient or water limitation is relaxed, and re-form when it reoccurs (Meron, 2017). Such self-organized dynamics in time is similar to the dynamics described by the theory of the adaptive cycle (Gunderson and Holling, 2002).

Self-organized patterning can occur by a variety of agents, some simple and purely physical and others biological and more complex (Table 1). For example, sand grains form regularly spaced dunes and ripples driven by wave or wind action. These undulating patterned systems may affect organisms, but are not themselves biological—and they have also been observed on the presumably lifeless Mars and Venus (Hanes et al., 2001). Clouds display regular patterns by self-organization (Garay et al., 2004). Dye added to water in a shallow pan, instead of mixing, forms intricate patterns such as labyrinthine stripes (Strombom et al., 2012). Clearly, lifeless systems can self-organize to form order.

Self-organization can involve sub-organismal biological levels of organization. Cells, organelles, and organs can act as agents of self-organization and patterns can appear in these same subsystems (Table 1). At the subcellular level, the Min protein forms regular wave patterns on the cell membrane of Escherichia coli (Loose et al., 2008). Cells form regular stripes at the growth zone of the mammalian palate (Economou et al., 2012). At the organismal level, pigment cells form Turing patterns on the skin of Zebrafish (Nakamasu et al., 2009), and presumably other vertebrates. These examples involve biological agents forming regular patterns at the sub-organismal and organismal level. As we shall see, these examples involve investment on the part of agents and are subject to natural selection at the level of the individual.

In the realm of ecology, self-organization can form spatial patterns at a range of organizational levels. Populations can act as pattern-forming agents. For example, ant and termite colonies form regular spaced nests on the landscapes (Ryti and Case, 1986; Tarnita et al., 2017). Communities of mixed species can also act as agents. For example, banded vegetation in deserts (often characterized by a mix of species, e.g., tarbush, sod grasses, mesquite, juniper brush etc.; Penny et al., 2013), ribbon forests in subalpine environments (Bekker and Malanson, 2009), and coral reefs (Mistr and Bercovici, 2003)—all exhibit patterns generated by communities. In some cases, an agent can be considered an ecosystem itself, with both biotic and abiotic components, such as regular patterned cypress depressions embedded in Big Cypress National Preserve in South Florida (Watts et al., 2014) or ridge and slough configurations in the nearby Everglades (Larsen et al., 2007) (Table 1).

As we discussed earlier, all of the changes resulting from patterning can have substantial ecological consequences (e.g., resource retention, productivity, resilience, and stability). These changes alter the “ecological theater” (sensu Hutchinson, 1965) and change the evolutionary adaptive landscape, thereby potentially affecting all species of the ecosystem—some positively, and others negatively—to varying degrees. In this diffuse manner, self-organization alters the “evolutionary play” for all organisms, pattern-forming agents included. This feedback is what we call diffuse feedback II (Fig. 2). Our focal question, however, concerns feedback I (Fig. 2), a reinforcing feedback between the consequences of spatial patterns and the evolution of traits contributing to self-organization (pattern forming traits). Can consequences of self-organized patterns feedback specifically to reinforce the activities of pattern-generating agents? And in cases where pattern formation is self-limiting, might pattern formation represent a control system, defining a set point and holding fluctuation within certain limits? For example, when patterns emerge in a nutrient-limited landscape such that nutrient uptake is enhanced as pattern develops, the agent benefits from increased nutrients. When nutrients surpass limiting levels, the pattern breaks down and nutrient retention declines, only to resume when limiting levels are again reached. In this hypothetical example, the patterning agent regulates ecosystem nutrients by turning patterning on and off. Will it work? The answer to this question depends on the properties of agent-pattern-feedback system.

5. Evaluating feedbacks

5.1. Agents at different organizational levels

Below we consider agents of different categories and at different organizational levels (abiotic agents, biotic agents at the sub-organismal/organismal level, biotic agents above the organismal level including populations, communities, and ecosystems, and also the case of

Fig. 1. (A) Schematic of scale-dependent feedback (SDF) giving rise to regular patterning, and (B) self-organized patterns: (B1) ribbon forests; (B2) sand ripples; (B3) evenly spaced termite mounds; (B4) regularly-spaced stripes on zebra fish; (B5) banded mussel bed; (B6) spiral waves formed by the Min protein in E. coli.

[Table 1]
bacteria colony of the same genotype) to evaluate whether reinforcing feedback (feedback I in Fig. 2) and diffuse feedback (feedback II) are possible.

5.1.1. Abiotic agents

For a feedback to reinforce the ability of an agent to form patterns, there must be (i) a signal detectable by agents from outcomes of the spatial patterning that returns to the agent, and (ii) a capacity for the agent to change its patterning capacity in response to the detected signal and to store information specifying that capacity. Apparently, abiotic agents such as sand grains forming sand dunes and ripples do not possess any of these capabilities. While regular patterns can emerge spontaneously in the inanimate world, they only involve simple physical forces and properties of the agent system, with no purpose (evolutionary benefit or drive)—they are mere epiphenomena.

5.1.2. Biotic agents at the organismal level

At the organismal level (e.g., Turing patterns on animal coat and protein patterns on cell membranes), feedback reinforcement of self-organized patterns does occur by evolution and natural selection. Pattern formation of individual agents (e.g., protein or pigment cells) at this level is fundamentally controlled by genes. The agents form patterns that are functional traits of adaptive significance. Natural selection occurs at the level of the individual, operating on the variation of these functional traits, resulting in differential survival and reproduction, enhanced fitness, and ultimately a change in the frequency of genes controlling such patterning. In these cases, the pattern formed is an adaptation (sensu Williams, 1966) and feedback can select among these pattern-forming adaptations and intensify the self-organized pattern. For example, a zebra with self-organized stripes may enjoy higher survival, reproductive output, and thus fitness than its non-

Table 1

<table>
<thead>
<tr>
<th>Pattern-Forming Agent Involved</th>
<th>Pattern/Pattern Involved</th>
<th>Category of agents</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Self-organized patterns</strong></td>
<td>Patches in pattern</td>
<td></td>
</tr>
<tr>
<td>Sand grains</td>
<td>Sand grain aggregation</td>
<td>Abiotic particles</td>
</tr>
<tr>
<td>Trees</td>
<td>Tree aggregation</td>
<td>Plants</td>
</tr>
<tr>
<td>Overdispersed systems</td>
<td>Tree aggregation, including crypts and other wetland species</td>
<td></td>
</tr>
<tr>
<td><strong>Patchy patterns</strong></td>
<td>Patchy patterns in various environments</td>
<td>Mobile objects</td>
</tr>
<tr>
<td>Sand dunes</td>
<td>Tree, crypt, other wetland species</td>
<td>Plants</td>
</tr>
<tr>
<td><strong>Overdispersed patterns</strong></td>
<td>Overdispersed patches on a landscape</td>
<td>Community</td>
</tr>
<tr>
<td><strong>Ripple patterns</strong></td>
<td>Ripples, including crypts and other wetland species</td>
<td>Ecosystem</td>
</tr>
<tr>
<td><strong>Turbulent patterns</strong></td>
<td>Turbulence, including crypts and other wetland species</td>
<td>Population</td>
</tr>
<tr>
<td><strong>Overdispersed termite mounds</strong></td>
<td>Overdispersed patterns on a termite mound</td>
<td>Colony</td>
</tr>
<tr>
<td><strong>Mussel population banding</strong></td>
<td>Mussel clumps</td>
<td>Mobile animals</td>
</tr>
<tr>
<td><strong>Microorganism colony</strong></td>
<td>Microorganism aggregations</td>
<td>Bacteria</td>
</tr>
<tr>
<td><strong>Patterns on zebra</strong></td>
<td>Pigment aggregation, including pigment cells</td>
<td>Cells</td>
</tr>
<tr>
<td><strong>Spiral waves</strong></td>
<td>Protein aggregations</td>
<td>Protein</td>
</tr>
</tbody>
</table>

Fig. 2. Consequence of and feedbacks in self-organization by agents at the sub-organismal/organismal levels and at the ecosystem level (or levels above organismal level). Feedbacks I (reinforcing feedback): agents form regular patterns, and the outcome of the pattern formation feeds back to reinforce the traits governing pattern formation, which further alters the spatial patterns. Feedback II (diffuse feedback): agents form regular patterns, and the outcome of pattern formation feeds back to influence the pattern-forming agents. Such influence does not result in directional changes in the spatial patterns. At the sub-organismal or organismal level, feedback I is possible realized via natural selection on the formed patterning. At the above-organismal level (e.g., population, community, and ecosystem), regular patterns can have ecological and evolutionary consequences on pattern-forming agents, as well as on all other organisms in the ecosystem (feedback II). Reinforcing feedback by natural selection on individual pattern-forming agents (feedback I) requires further investigation.
striped conspecifics.

5.1.3. Microorganism at the colony level (same genetic information)

Self-organized pattern formation is observed in bacterial colonies of identical genotype (reviewed by Ben-Jacob et al., 2000). When nutrient levels are high, the bacteria behave as any independent unicellular organisms. Under hostile environmental conditions, self-organized patterns begin to form, as shown in *Bacillus subtilis*, *Escherichia*, and *Salmonella typhimurium* (Fujkawa and Matsushita, 1991). The pattern formation of the bacterial systems is a consequence of attractive chemotaxis (Gloag et al., 2013), which is heritable (Ben-Jacob et al., 1994). In this case, reinforcing feedbacks between pattern and pattern-forming agents occur, as a result of selection acting on a specialized signaling system to assist pattern formation by the bacteria colony of same genotype. When a foreign group of a different genotype is present, regular patterns disappear, and the non-patterned mixture of bacteria strains exhibit less efficient resource use and lower productivity (Xavier et al., 2009), akin to an evolutionary tragedy of the commons (Rankin et al., 2007).

5.1.4. Organisms at the population level

Genetically unrelated individuals of the same species may form regular patterns in ecosystems. For example, mussels (*Mytilus edulis*) on intertidal flats form patterns by two opposing mechanisms: cooperation and competition (van de Koppel et al., 2005a). Through movement into cooperative aggregations, mussels increase their local density, which decreases wave stress and predation risk. Conversely, competition for algal food places an upper limit on the size of clumps. Mussels actively self-organize into large-scale labyrinth-like patterns, aggregating into a group of conspecifics and employing byssal threads to attach to the shells of conspecifics within reach. Formation of local clustering relies on specific traits of agents: movement strategy and attachment by byssal threads, which requires investment. Both traits are robust against free-riders (cheaters). Here, the ‘resource’ generated by the group is ‘stability’ (resistance to wave disturbances), which is exclusive: mussels which do not get into the clump fast enough or those who do not develop enough byssal threads get ‘punished’ (high mortality, fewer offspring) immediately.

The number of byssal threads (hence the size and tightness of clusters) responds to the stress level of the environment until it reaches an evolutionarily stable state (De Jager et al., 2017). Order emerges at the landscape scale as a result of individuals sorting uniformly relative to resource availability, and the eco-evolutionary feedback occurs between the clustering and traits involved in forming clusters at the patch scale, instead of at the landscape scale—that is, the landscape-scale spatial order forms without cost and is not likely a function (sensu Williams, 1966). However, the study by De Jager et al. (2011) on the rise of Lévy walk in regular musselbeds implied the likelihood of direct feedback between individual search behaviors and order at the landscape scale (as opposed to the patch scale). Lévy walk improves the survival chances of individual mussels by allowing them to form a group faster, which in turn decreases predation risk (De Jager et al., 2011).

Theoretical models imply Lévy walk results from feedback between animal behavior and mussel-generated environmental complexity. The fitness of individual mussels is assumed to be the product of individual mussel survival, which is proportional to short-range mussel density and fecundity, which is inversely proportional to long-range mussel density and the energy invested in movement (De Jager et al., 2011). These studies indicate the possibility of the promotion of spatial patterning over time by natural selection at the level of individual constituent agents, similar to the selfish herd theory proposed by Hamilton (1971) that animal grouping behavior could evolve if individuals selfishly avoided predation. In the example of mussel aggregation here, it is to avoid being washed away by wave action.

5.1.5. Organisms at the community level

Agents involved in pattern formation may belong to multiple species (a community) or may also include the physical environments in which biological agents reside (an ecosystem). In these cases, can the pattern-forming agents receive reinforcement via the favorable changes their formed patterns have wrought (feedback I in Fig. 2)? To form periodic patterns, long-distance negative feedback is essential. Short-distance positive feedback alone, unaccompanied by long-distance feedback, is not sufficient to form periodic patterns (Rietkerk and van de Koppel, 2008). For example, plants of arid ecosystems invest in a root system that takes up water and nutrients but also can prevent erosions and increase water infiltration. This extra investment in the root system acts to improve soil condition (that is, local facilitation). In terms of its effect on landscape patterning, the strength of local facilitation could affect the sharpness of the patch (Eppinga et al., 2009); however, it is not essential for forming the periodic patterning. A large body of literature has shown that local facilitation has important evolutionary implications both theoretically and empirically (Laland et al., 1999; van Nuland et al., 2017). Local facilitation is costly and is subject to cheaters (which do not invest to facilitate, but benefit from the facilitation of others; Kéfi et al., 2008). Unlike the example of pattern formation in mussel beds, where the resource ‘stability’ produced by the group is exclusive to cooperating members, many resources created by local facilitation—e.g., physical protection, improved soil texture, shade, and increased resource availability in harsh environments (e.g., arid ecosystems)—are available to all and are subject to exploitation by cheaters. Kéfi et al. (2008) examined such eco-evolutionary feedback in scale-free vegetation patterns of dryland ecosystems and suggested that the direction of this eco-evolutionary feedback does not necessarily enhance patterning at the local patch scale. Instead, it could lead to extinction of the local plant population as a result of cheaters taking advantage of local facilitation invested by facilitators in the population when dispersal is widespread. Regardless of the complex eco-evolutionary feedback between traits of pattern-forming agents and characteristics of patches at the local scale, at the landscape-scale, the emergence of periodic patterning occurs as individual agents assort uniformly relative to resource availability. The heterogeneity of resource availability is generated by long-distance negative feedback with no need to invoke eco-evolutionary feedback. Hence spatial patterning is an incidental consequence of ordinary biological processes (e.g., water uptake by roots), requires no additional investment.

Across a wide variety of agents from the sub-organismal to ecosystem levels as we examined above, spatial patterning resulting from local interactions of agents all suggests evolutionary consequences for the agents—that is, diffuse feedback is ubiquitous. Reinforcing feedbacks—patterning outcomes that would reinforce pattern formation—would occur at or below the organismal level by natural selection. This includes the bacterial colony of a single genotype, which can be viewed as one organism. For levels above the organismal level—population, community, and ecosystems—a few existing studies suggest a theoretical possibility for feedback I; however, definitive research is still limited and we remain skeptical.

5.2. Free order for nothing?

Kauffman (1993, 1996) coined the phrase “order for free” to describe self-organized patterning: meaning that order (regular spatial pattern) spontaneously forms through combined physical forces and properties of individual agents. Ecosystem spatial self-organization is different from pattern formation by non-living agents (e.g., sand grains), which are not subject to natural selection. It is also distinct from self-organization at the level of the individual organism, which relies on external molecules specialized in forming patterns. For example, assisted self-organization is involved in formation of stripes on the skin of zebra fish, a process that relies on investment in specialized melanophores and xanthophores that act as inhibitor and activator at local and distal
points; Nakamasu et al., 2009). Order formed by assisted self-organization apparently requires an investment, hence, is not free, and the formed pattern is of adaptive significance, through natural selection at the level where patterning occurs (i.e., the level of the individual organism).

Is the order formed in ecosystems free? More importantly, is Kauffman’s free order in ecosystems of adaptive significance, or is it order for nothing? Diffuse feedback (feedback II) occurs in patterned landscapes and influences evolutionary change (Fig. 2). There are significant pattern-related ecological and evolutionary dynamics at similar overlapping temporal scales that can profoundly influence ecosystems. However, reinforcing feedback (feedback I) realized through strong, direct selection operating on the entire ecosystem level to enhance spatial patterns or the processes that generated them to make ecosystems ‘‘adaptive’’ is unlikely, as it would require natural selection at the level of population, community, and ecosystems, which remains at least controversial and widely disputed (Williams, 1966; Wilson, 1983; Stevens et al., 1995; Johnson and Boerlijst, 2002; Price, 2012).

A few studies have proposed the possibility of such reinforcing feedbacks realized via natural selection at the level of individual agents (De Jager et al., 2011, 2017; Kéfi et al., 2008). Order emerges at the landscape scale as a result of individuals assorting uniformly relative to stress or resource availability (long-distance negative feedback). The eco-evolutionary feedback however occurs at the patch scale to reinforce the characteristics of individual patches/clusters. The direct interaction and feedback between the free order at the landscape scale and the clustering at the patch scale at which eco-evolutionary feedbacks occur remains to be demonstrated.

Ecosystems are often considered complex adaptive systems, suggesting that “spatial patterns emerge from, and feed back to, the actions of adaptive individual agents” (Levin, 1998, 2005). In view of the prediction of complexity theory that patterns emerge as epiphenomena in the inanimate world (e.g., strikingly regular patterning of sand dunes formed by sand grains), it is hard to argue that every self-organized spatial pattern involving biological agents has a functional purpose (in an evolutionary sense). Which patterns confer fitness and which are simply epiphenomena is a fundamental question. Further examples from a variety of ecosystems (other than mussel beds and dryland vegetation) displaying spatial self-organization—e.g., ridge-slough pattern in peatlands (Larsen et al., 2007), cypress dome pattern in South Florida (Watts et al., 2014), and fairy cycles (Tschinkel, 2012)—formed by very different biophysical processes have yet to be examined. A theoretical framework addressing the eco-evolutionary dynamics in spatially self-organized ecosystems and its relationship with ecosystems as complex adaptive systems is needed. Such framework will shed light on questions such as whether spatial self-organization contributes to ecosystems as complex adaptive systems, and if so, the conditions under which this occurs, by what mechanisms, and its overall importance in determining ecosystems’ responses to environmental change.

Effects of spatial structure on population dynamics has been a major theme in theoretical ecology and evolutionary biology in the past two decades. For example, it has been shown that spatial structure may be potent promoter of cooperation (Nowak and May, 1992; Pavlogiannis et al., 2018). Evolutionary graph theory stresses that graph structure can have an important consequence on the probability of fixation of advantageous mutants (Lieberman et al., 2005). These and other theoretical horizons are promising.

Understanding regular pattern formation and other more general self-organized patterns occurring in ecosystems, their consequences, and their relationships with biological evolution is not a trivial or esoteric challenge. Such phenomena occur at a wide range of spatial scales, in distinctly different systems worldwide and on other planets. While self-organization is not the Holy Grail of ecosystem cybernetic control (goal-directed feedback loops to enhance ecosystem functioning; Wiener, 1948; Patten and Odum, 1981), it can greatly alter ecosystem structure and thereby ecological functioning and has strong implications for enhanced understanding and effective management, relationships as yet largely unexplored.

Declarations of interest
None.

Ethical statement
We have followed all the required duties of authors, including:

1 Reporting standards: our article presents an accurate account of the work performed as well as an objective discussion of its significance.

2 Data access and retention: the article doesn’t include any data.

3 Originality and acknowledgement of sources: we ensured that the article is original, and in places where we used the work and/or words of others, they were appropriately cited or quoted.

4 Multiple, redundant or concurrent publication: this article was only submitted to Ecological Complexity.

5 Confidentiality: not applicable to our article.

6 Authorship of the paper: both authors contributed substantially to the paper.

7 Hazards and human or animal subjects: the research doesn’t involve any human or animal subjects in the study.

8 Declaration of competing interests: none.

9 Notification of fundamental errors: if we discover a significant error or inaccuracy in our work, we will notify the journal editor or publisher and cooperate with the editor to retract or correct the paper.

10 Image integrity: we didn’t enhance, obscure, move, remove, or introduce a specific feature within an image.

11 Clinical trial transparency: not applicable to our article.

Supplementary materials
Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecocom.2019.01.002.

References
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