# Self-organizing systems across scales

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In a self-organizing (or self-reinforcing) system, structure and processes mutually reinforce one another. The system may have a random seed, but, once initiated, pulls itself up by its own bootstraps and (within bounds) maintains order through internal interactions. Kauffman[1] describes self-organizing systems as 'anti-chaotic', because unlike chaotic systems (which are highly sensitive to initial conditions), they channel different initial conditions into the same final state[1,2]. Organisms are clearly self-organizing, as are many physico-chemical systems. Chen and Bak[3] suggest that the universe might be a self-organizing system, and the bootstrap theory of physics holds that all nature exists '...by virtue of mutually consistent relationships'[4]. Self-organization in ecological systems is suggested by the increasing recognition of ecosystems as thermodynamically open and far from equilibrium, with positive feedback as an important organizing force[5-11]. These are common ingredients of self-organization, though by themselves do not guarantee it.

Though the phenomenon of self-organization has been recognized for decades, within the past few years, various researchers have argued that self-organizing systems evolve to a critical state that Kauffman describes as balancing on the edge of chaos[1,2,6]. In the words of Bak et al.[2] '...ecological systems are organized such that the different species "support" each other in a way which cannot be understood by studying the individual constituents in isolation. The same interdependence of species also makes the ecosystem very susceptible to small changes or "noise". However, the system cannot be too sensitive since then it cannot have evolved into its present state in the first place. Owing to this balance we may say that such a system is "critical"'. Perry et al.[6] and Kauffman[1] refer to such systems as poised: robust against perturbations to which system components are adapted, but subject to threshold changes when the bounds of adaptability are exceeded. O'Neill et al.[12] call this 'metastability', and argue that it is a general property of ecological systems. Threshold transitions are increasingly reported in a variety of natural systems and are reproduced in models[5,6,12-20], though they might be produced by various mechanisms and are not in themselves proof of self-organization. These thresholds differ from normal successional changes in that they are irreversible (at least within human timescales) without external intervention, and sometimes not even then. As Knowlton[16] puts it, once the straw has broken the camel's back, simply removing the straw does not allow the camel to rise again.

There are many questions regarding self-organization in nature. How prevalent is it in ecological systems, and over what scales? How do self-organizing dynamics evolve? What

**Over the past few years, ecologists have increasingly recognized the existence of strong self-reinforcing (or self-organizing) interactions within systems at a variety of scales. Positive feedback within food chains has been reported from terrestrial and aquatic ecosystems. Accumulating evidence supports the existence within communities of cooperative guilds – tit-for-tat relationships based on diffuse mutualisms and favored by environmental unpredictability. At the landscape level, both real world experience and models indicate that processes such as hydrology and the propagation of disturbance can be strongly self-reinforcing (i.e. the landscape structure supports the process, and vice versa). Hence the picture emerges of a hierarchy of self-organizing systems that span food chains, communities and landscapes/regions.**

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does self-organization imply for ecological dynamics, particularly the existence of 'critical' states, the avoidance of thresholds and the sustainability of human interactions with our life support systems? Most research on self-organization has been via simulation modeling or analytical mathematics (Kauffman[1] and Murray[21] review various aspects of the formal theory). However, my focus here is field ecology, particularly the degree to which natural patterns and processes might signal self-organized behavior, and what that implies for ecosystem stability and the evolution of cooperation. Self-organizing (or self-reinforcing) behavior as used here refers to the creation of meta-stable dynamics through internal interactions, including, but not necessarily restricted to, positive feedback.

Since all subglobal ecological systems are open to transfers of energy and matter, self-organization in nature must be understood in relative terms – that is, system dynamics must involve not only internal interactions, but modification of external forces such that they reinforce, or at least do not overwhelm, internally generated order. It follows that interactions among scales and, in particular, boundary phenomena are central to understanding self-organization in ecology. A basic premise of this article is that natural systems comprise a hierarchy of self-organizing (self-reinforcing) systems embedded within one another and stabilized by cooperative (tit-for-tat) relationships, the latter focused particularly at spatial and temporal boundaries.

### Positive feedback and metastability within food chains

The importance of mycorrhizal fungi to most of the world's plants has long been known and thoroughly discussed. More recently, research has expanded to include self-reinforcing dynamics and metastability in systems comprising primary producers, their symbionts and hetero-trophs that cycle nutrients and perform other services facilitating energy capture[5,6,8-11]. The globally widespread inability to reforest following clearing in certain environments (montane, boreal, moist and dry tropics) suggests that there are threshold transitions from one steady state to another, and complex transitions in belowground food chains and processes have been implicated.

Intensive research at Cedar Camp, one of many un-reforested clearcuts at high elevations in western USA, reveals a number of differences relative to adjacent forest soils, including spread of actinomycetes of the genus *Streptomyces* (which allelopathically inhibit both plants and mycorrhizal fungi), sharp drops in ethylene (a microbially

on various historical and environmental factors. However, two requirements would seem central[33]: (1) positive feedback in key processes; and (2) hiatus in the presence (or participation) of one or more partners in the feedback. Hiatus may take quite different forms in different kinds of guilds. To give a well-known example, few tree species in moist tropical forests flower year round: those that do (e.g. figs) form close pairwise mutualisms with pollinators; those that don't participate in diffuse mutualisms that assure pollinators year-round food[38]. The rain forest tree *Bertholletia excelsa* (Brazil nut) illustrates how species can come to rely on guild structure; planted in monocultures, the tree is not pollinated and does not set seed[39]. Disturbance, generally an important factor in community assembly, has been hypothesized to favor the formation of cooperative guilds because it frequently leads to hiatus in one or more plant species[33].

### Interactions across scales: does unpredictability catalyze cooperation?

Much has been written over the past few years about the dynamical implications of interactions among hierarchical levels[40,41]. While a given hierarchical level may constrain and canalize the dynamics of its parts, the complex of positive and negative feedbacks across scales up to the global also creates disequilibrium that propagates uncertainty from higher to lower levels. Anecdotal evidence and modeling (not to mention common sense) suggest that varying and unpredictable environments are a powerful incentive for species that depend on common resources to cooperate[33,42]. For example, stochastic wildfire patterns in forests of southwestern Oregon and northern California, USA, create unpredictability regarding which plant species survive a given event. Most woody plants in these systems are ectomycorrhizal, with some plant–mycorrhizal fungi specificity but also a great deal of generality. Once diffuse mutualisms develop between plants and mycorrhizal·fungi, the stage is set for interplant linkages, movement of nutrients among plants, alleviation of competition, and facilitation during succession[33]. In contrast, old-growth ponderosa pine (*Pinus ponderosa*) forests of interior North America experienced a relatively predictable disturbance regime of frequent, gentle ground fires that killed only occasional small patches of overstory trees. Trees and understory plants in these forests do not readily form the same types of mycorrhizal fungi.

Quite another kind of unpredictability exists in moist tropical forests (MTF) characterized by small-scale gap disturbances[33]. There, uncertainty resides in timing of gap creation, gap size, and which trees actually colonize, among the many potential species. It is perhaps no coincidence that most trees in MTF form mycorrhizae with the highly general vesicular–arbuscular (VAM) fungi. These examples do not imply that shared mycorrhizal fungi (or other mutualists) offer the only basis for risk-spreading. Any ecological commons maintained in nonequilibrium by flows of metabolic energy are subject to threshold degradation when energy flow is reduced (e.g. nutrient capital, food webs that cycle nutrients, soil physical structure, triggering factors for mycorrhiza formation). All species that depend on a commons benefit when any one stabilizes it. Diffuse mutualisms may be viewed in this light as mechanisms for smoothing environmental variability[43].

### Self-reinforcing dynamics at the landscape scale

To recapitulate, evidence from a variety of ecosystem types indicates strong positive feedback among plants, plant mutualists and heterotrophs responsible for cycling nutrients. Environmental uncertainty, spinning out of complex interactions at landscape, regional and global scales, coupled with vulnerability of self-reinforcing food chains to threshold degradation, is hypothesized to favor the evolution of cooperative guilds that spread risk and lower the probability of threshold food chain collapse[33]. These self-reinforcing community-level networks can be embedded within landscapes whose dynamics are themselves self-reinforcing.

A burst of spatially explicit modeling in recent years shows numerous links between landscape patterns and ecological processes, with self-organizing dynamics in at least some cases. Model host–parasitoid systems generate complex self-organized spatial patterns that permit species to coexist in uniform environments[44,45]. At another scale, recent models predict that deforestation or desertification reduces precipitation in South America and Africa[46–48], a self-reinforcing dynamic that implies some threshold of regional collapse. The so-called 'forest-fire' cellular automata[49] (which are probably better models of pathogen spread than of forest fires) exhibit self-organizing criticality providing that the timescales are sufficiently different between the periodicity of the external forcing (lightning strikes in the model) and system response to the forcing. Timescales of disturbance frequency and system recovery are also important determinants of landscape pattern in the models of Turner *et al.*[50], which link the size of a disturbance in a heterogenous landscape to its ability to cross boundaries; an ability that is, in turn, related through a positive feedback loop to the overall size and intensity of the disturbance.

Some landscapes tend to absorb and damp the spread of disturbances, while other landscapes magnify them, with the process reinforcing the structure in both cases. Large intact blocks of healthy mature or nondecadent old-growth forests are less susceptible to catastrophic fires than young or fragmented forests, and landscapes dominated by these types buffer and damp the spread of crown fires, hence acting to preserve the forest structure[30,51]. Once some threshold proportion of the landscape becomes fragmented and permeated by flammable young forests or grasses, the potential exists for a self-reinforcing cycle of catastrophic fires. Invasion of ecosystems by alien grasses, a growing problem throughout the world, is greatly facilitated by positive feedbacks between grass cover and flammability of landscapes[52,53]. Vulnerability to fire is clearly linked to the hydrologic cycle: the more forests that burn, the lower the precipitation, the greater the vulnerability of remaining forests to fire – a dynamic that literally feeds on itself. Kauffman and Uhl[51] suggest that even small changes in regional climate would greatly increase the probability of fire in the primary forests of Amazonia.

### Do 'critical' states exist in nature?

Are self-organizing ecological systems 'critical', balancing on an edge as predicted by Bak *et al.*[2] and Kauffman[1]? If so, is it possible to generalize about the system characteristics that maintain stability at the edge? In the model critical systems of Bak *et al.*[1,2], energy is dissipated following a power-law distribution with many small and a few large events, producing a fractal spatial structure that is effectively a snapshot of the temporal dynamic. Bak and colleagues consider these spatial and temporal patterns to be signatures of self-organized criticality. Fractal-like patterns (structures that are not space-filling and may or may not be self-similar) are common in nature. Temporally, the size distribution of forest fires approximates a power law in some areas[54], though that is not always the case.

produced plant hormone that stimulates root production) and lower rates of nitrogen (N) mineralization[22-24]. Seedlings planted at Cedar Camp become nutrient-stressed and also form fewer mycorrhizae than seedlings grown in forest soils – not because of reduced mycorrhizal inocula, but because mycorrhiza formation is inhibited (perhaps by *Streptomyces*) or some triggering factor has been lost (or both). Enhanced growth and survival of seedlings given small amounts of soil transferred from nearby forests were related to at least two factors: (1) increased rate of root tip production, possibly because of the higher ethylene content of forest soils; and (2) reintroduction of microinvertebrates and protists that compose the higher trophic levels in soil food webs[24,25]. We hypothesize that the higher trophic levels were impacted by reduced energy flow to belowground food webs accompanying the transition from trees to annual grass, leading to a breakdown in the nutrient cycle and perhaps other regulatory mechanisms. *Streptomyces*, one of the relatively few microbes able to decompose lignin, may have been favored by the shift of primary carbon source from root exudates and fine litter to woody residues.

It is now widely accepted that many rangelands throughout the world have converted from one steady state to another, and that changes in soils are probably involved[13,14], though little research has addressed the soils aspect. The annuals that frequently invade degraded grasslands and deserts are either nonmycorrhizal or facultatively mycorrhizal, and research suggests that loss of mycorrhizal fungi is a factor in degradation in some cases but not in others[26,27]. Similarly, degradation of pastures in the moist tropics is often accompanied by increasing cover of nonmycorrhizal weeds[28]. In Costa Rica, a pasture well-stocked with grasses contained abundant mycorrhizal inocula, but bare plots contained little[29], suggesting that stresses that are too frequent or severe (e.g. frequent fire, overgrazing) eventually deplete the soil of these keystone mutualists and favor the shift from mycorrhizal to nonmycorrhizal plants[28]. However, mycorrhizal fungi are unlikely to be the whole story. Disrupting energy flow may trigger reorganization of the belowground community from one metastable state to another, as happened at Cedar Camp. This is not to argue that biotic effects are the sole drivers of soil degradation; clearly, abiotic effects, such as nutrient loss and compaction, are important and may interact strongly with soil biota (see next section). In general, this whole area of research is rich in plausible hypotheses but poor in experiments and measurements.

## Biological legacies and cooperative guilds

Given the ubiquity of natural disturbances in virtually all ecosystems, why aren't threshold transitions from one community type to another more common? (In fact, are they more common than is suggested by the relatively brief time that scientists have been observing?) In the 1980s, ecologists began to focus on biological legacies, elements such as large dead wood, sprouting plants, mycorrhizal fungi and large soil aggregates that survive disturbance and facilitate reassembly of the parent system[6,28,30]. The concept of biological legacies is consistent with recent research showing the importance of history in community organization[31]; succession rarely occurs on a blank slate; rather, biotic imprints communicate through time to canalize and shape community dynamics. The next section explores some current thinking regarding the mechanisms by which this happens.

### Cooperative guilds

Mycorrhizal researchers applied the term 'cooperative guild' to species groups linked through diffuse mutualisms

with mycorrhizal fungi[6,32]. Here, I use guild more broadly to denote groups linked through any diffuse mutualism or through shared dependence on ecological commons (e.g. nutrient stores, food webs that cycle nutrients or control pests, and soil physical structure). The modifier 'cooperative' is to minimize confusion with more common ecological usage; guild members may compete as well as cooperate.

Diffuse mutualisms involving mycorrhizal fungi (and perhaps other belowground organisms) link different plant species, in time and in space[32-34]. In southwest Oregon, USA, soils beneath various species of ectomycorrhizal hardwoods significantly increase the growth of Douglas fir (*Pseudotsuga menziesii*) compared to soils beneath annual weeds in clearcuts or old-fields. This phenomenon has been associated in one or more studies with accelerated root-tip formation, greater numbers of total and mycorrhizal root tips, shifts in mycorrhizal type, increased associative N-fixation and increased ratios of iron to manganese in seedling foliage (reviewed by Perry *et al.*[33]). Soils beneath sprouting hardwoods have only 10% as many streptomycete colonies as open areas within a clearcut, a phenomenon that may relate to the fact that hardwoods accumulate manganese, a known inhibitor of streptomycin. The evidence points to a biological pattern imposed by hardwoods rather than inherent differences in soil fertility. The effect of transferred hardwood soils on recipient conifer seedlings is strongly influenced by the biological context, suggesting complex multiple species interactions. Unpasteurized soils transferred to Douglas fir seedlings from beneath an ectomycorrhizal hardwood, *Arbutus menziesii*, are found to increase N-fixation in Douglas fir rhizospheres more than fivefold when the conifer is growing amidst the ectomycorrhizal shrub *Arctostaphylous viscida*, but to decrease it by 80% when the conifer is growing amidst annual grasses[35]. Pasteurized soils have no effect in either case.

### Spatial links within guilds

Considerable evidence indicates that mycorrhizal fungi form linkage networks among plants within a community, mediating the distribution of nutrients and significantly influencing plant–plant interaction[32-34]. In some cases, mycorrhizal fungi exacerbate competition between plant species; however, in other instances the fungi promote coexistence among plant species (thereby increasing plant community diversity) and convert interspecies interactions from negative to neutral or synergistic – a phenomenon accompanied by greater nutrient uptake or more equitable distribution of nutrients among plants[28,36]. Various mechanisms might explain this effect. Sitka spruce (*Picea sitchensis*) grows better when mixed with Scots pine (*Pinus sylvestris*) on peats and heathlands, at least in part because pine mycorrhizas mineralize organic N, which spruce mycorrhizas apparently cannot do[37]. Nutrient movement through direct hyphal linkages is also possible. Numerous labeling studies have shown that carbon and nutrients move from one plant to another and that this occurs more readily among plants known to share common mycorrhizal fungi species[32-34]. Hyphal linkages have been demonstrated in the laboratory and are probably common in the field but very difficult to demonstrate. Read[32] attributes the high plant diversity of phosphorus-deficient grasslands to the generality of mycorrhizal fungi in these systems, which 'enables a large number of hosts to be incorporated into and supported by a common mycelium'.

The potential for cooperative guilds exists in any ecosystem where sets of species share an ecological commons. The degree to which that potential is fulfilled may depend

The question of whether fractal structure and power-law temporal fluctuations signal self-organized criticality (stability at an edge) in natural systems cannot be answered until more is known about the processes underlying these patterns, but interactions across scales have been found to be important in generating and stabilizing pattern at a variety of scales. For example, fractal-like patterns produced during growth of crystals, even-aged plant populations, and landscapes, result from interactions between boundary processes and macroscopic constraints or driving forces[50,55,56]. Self-organized criticality (i.e. power-law dissipation of energy) in Drossel and Schwabl's forest fire model emerges from separation of timescales associated with tree growth and fire, which guarantees that a large amount of energy accumulates between dissipation events[49]. In nature, separation of timescales of disturbance and recovery are controlled, in part at least, by processes operating at different spatial scales: energy dissipated through disturbances correlates with global, regional and landscape processes, while the rate of system recovery from disturbance is strongly influenced by community level interactions that stabilize food webs.

## Cascading thresholds

If a hierarchical level is self-organizing, thresholds can be crossed such that the signals transmitted to lower levels change abruptly[12,50]. If such a change exceeds the bounds of adaptability of lower levels, cascading effects can rapidly move the entire system to a new domain that may itself be self-reinforcing[50]. A growing number of ecologists believe this has happened in connection with the widespread replacement of native grasslands by fire-prone exotic grasses[14]. Overgrazing and/or drought weakens the natives and allows exotics to gain a foothold. A self-reinforcing dynamic sets in at the landscape level in which the spread of exotics alters the fire regime to favor the spread of exotics. Eventually, soils degrade to the point that native grasses cannot be re-established without massive rehabilitation efforts.

Gosz[57] points out that ecological systems have numerous boundaries in space and time, and argues that threshold dynamics are most likely at these boundaries. It follows that ecological systems are characterized not by stability at an edge, but by stability at a multiplicity of edges. The sum of edge dynamics creates, in turn, the macroscopic dynamics that condition edge stability. Seen in this light, it is not surprising that many relationships within communities function to focus adaptability at boundaries (e.g. those between plants and fungi and between animals and gut organisms) or to blur boundaries through spatial and temporal linkages (e.g. cooperative guilds, biological legacies). Thresholds result from 'foreign' disturbances that are capable of defeating edge-stabilizing mechanisms and that gain self-reinforcing momentum as they cascade through boundaries. Once started, such changes may be difficult or impossible to stop, which lends new urgency to understanding the ecology of self-organization in nature.

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