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Review

Belowground feedbacks as drivers of spatial self-organization and community assembly

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Abstract

Vegetation patterning in water-limited and other resource-limited ecosystems highlights spatial self-organization processes as potentially key drivers of community assembly. These processes provide insight into predictable landscape-level relationships between organisms and their abiotic environment in the form of regular and irregular patterns of biota and resources. However, two aspects have largely been overlooked; the roles played by plant – soil-biota feedbacks and allelopathy in spatial self-organization, and their potential contribution, along with plant-resource feedbacks, to community assembly through spatial self-organization. Here, we expand the drivers of spatial self-organization from a focus on plant-resource feedbacks to include plant – soil-biota feedbacks and allelopathy, and integrate concepts of nonlinear physics and community ecology to generate a new hypothesis. According to this hypothesis, below-ground processes can affect community assemblages through two types of spatial self-organization, global and local. The former occurs simultaneously across whole ecosystems, leading to self-organized patterns of biota, allelochemicals and resources, and niche partitioning. The latter occurs locally in ecotones, and determines ecotone structure and motion, invasion dynamics, and species coexistence. Studies of the two forms of spatial self-organization are important for understanding the organization of plant communities in drier climates which are likely to involve spatial patterning or re-patterning. Such studies are also important for developing new practices of ecosystem management, based on local manipulations at ecotones, to slow invasion dynamics or induce transitions from transitive to intransitive networks of interspecific interactions which increase species diversity.

Keywords: Allelopathy; Plant-soil feedbacks; Scale-dependent feedbacks; Vegetation pattern formation; Ecotones; Invasion fronts

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Abbreviations: BGFs, Belowground feedbacks; PSFs, Plant-soil feedbacks; SDFs, Scale-dependent feedbacks; VPD, Vapor pressure deficit.

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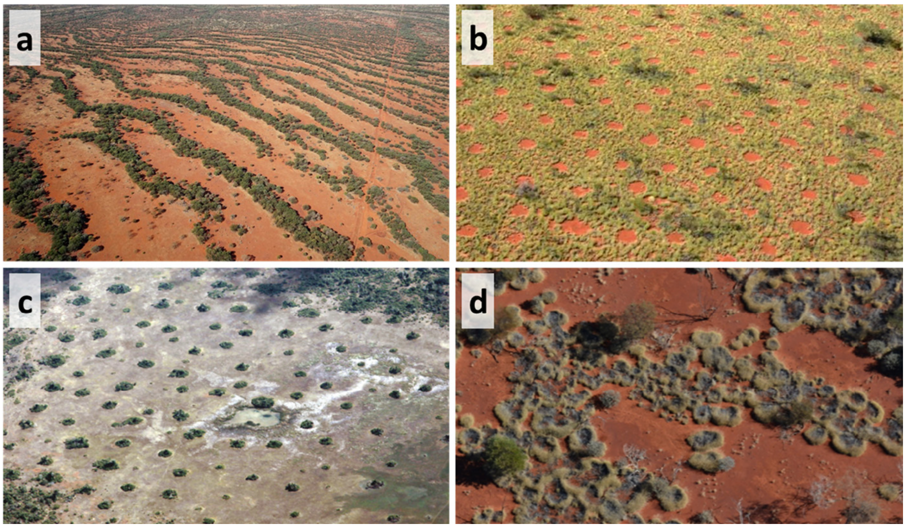


Fig. 1. Examples of vegetation patterns. (a) Banded (stripe) pattern of Mulga trees (*Acacia aneura*) on a sloped terrain in Western Australia. Mean inter-band distance is about 50 m. (b) Hexagonal pattern of bare-soil gaps in a flat terrain of Spinifex grass (*Triodia basedowii*) in Western Australia (often called "fairy circles"). Mean gap diameter is about 4 m. (c) A spot pattern of *Macrotermes* sp. termite mounds with associated woody-vegetation thickets in eastern Mozambique. (d) Pattern of Spinifex-grass rings in Western Australia. Ring diameters vary mostly in the range 1-2 m. (a) Courtesy of Stephan Getzin (see also Getzin et al. [195], Supporting Information), (b) adapted from Meron [13], (c) adapted from Pringle and Tarnita [24], (d) courtesy of Kevin Sanders. Reproduced after permission.

1. Introduction

The assembly of plant species into communities has been of fundamental interest to ecologists for decades [1–3]. The assembly of species-rich communities has been viewed by some as having a degree of self-organizing processes [4–8]. However, a potentially important element of this perspective on community development has been missing in most theory to date – the rich literature related to spatial self-organization derived from nonlinear physics, and more specifically pattern formation (Appendix A) [9]. Spatial self-organization draws on an extensive history of studies of how repeated, yet complex patterns form in nature, mostly from research fields outside ecology [10], but not exclusively [11–13]. Spatial self-organization provides insight into predictable landscape-level linkages between organisms and their abiotic environment in the form of regular and irregular patterns of biota and resources [14,15]. Here, we integrate the disciplines of pattern formation (Appendix A) [10,16] and community ecology to connect spatial self-organization of species on landscapes to community assemblage, and expand the potential drivers of spatial self-organization from a focus on plant-resource feedbacks to include plant – soil-biota feedbacks (hereafter "plant-soil feedbacks" or PSFs) and allelopathy. These drivers have largely been overlooked as mechanisms for community self-assembly [17–22], despite their possible effects on competitive and facilitative interactions and their potential to drive back and forth transitions between transitive and intransitive interactions in complex communities.

Many proposed mechanisms for the spatial self-organization of plant populations fall into the broad class of "scale-dependent feedbacks" (SDFs) between organisms and limiting resources (primarily water), where positive feedbacks act to enhance local vegetation growth concurrently with negative feedbacks that inhibit growth in the more distant neighborhood (Appendix A) [14,15,23]. Other mechanisms of current interest associate patterns of plant populations with pre-existing self-organized patterns of social insects, such as ants and termites, that compete for space and engineer their environments in ways that affect plant growth [24]. A recently proposed class of mechanisms for spatial self-organization targets microbially driven plant-soil feedbacks (PSFs) and allelopathy (Fig. 1) (Appendix A) [25,26]. Plant-soil feedbacks are plant-induced changes in soil biota that in turn feedback to affect plant performance [27–29]. Allelopathy is usually defined as a broad suite of chemically based negative effects of plants on each other [30,31].

Spatial self-organization stands out in the formation of periodic patterns of vegetation on landscapes, and in particular in arid and semi-arid regions. There are a wide variety of observed patterns and a fairly well-developed theory of the mechanisms and possible morphologies of these patterns. Two striking examples of vegetation patterns (Fig. 1a, b) are banded vegetation (“tiger bush”) on hill slopes [32,33] and patterns of bare-soil gaps (“fairy circles”) in grasslands [34–39]. These and additional examples, such as labyrinth-like vegetation stripes, vegetation spots and vegetation rings, are highly repeatable patterns of plant biomass, soil-water, soil-biota, organic matter, nutrients and plant chemicals that are found in many dryland regions across the world [40].

Although highly configured vegetation patterns have been observed most often in drylands, similar patterns have also been observed in wetlands and the arctic and shallow continental shelves under the sea [41–43], suggesting mechanisms other than the redistribution of water. Borum et al. [44] found that “fairy rings” forming in undersea eelgrass stands (*Zostera marina*) were likely to be due to substrate feedback processes allowing toxic sulfide to accumulate in sediment. Other studies indicate that seagrass stands (*Amphibolis antarctica* and *Halodule uninervis*) promote specific microorganisms in their sediment [45] and other seagrass species (*Zostera capricorni*) drive species-specific plant-soil feedbacks [46]. In hydric boreal peat bogs, Eppinga et al. [47] found regular spatial patterns of ridges and hollows induced by an SDFs between ridge vegetation and water-dissolved nutrients flowing towards the ridges.

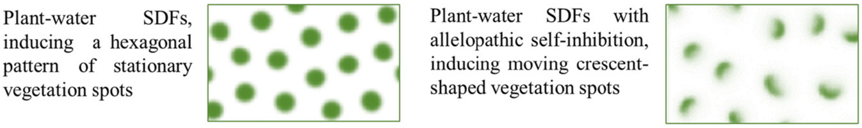
Pattern formation theory maintains that the emergence of periodic patterns from uniform states, such as vegetation patterning in drylands, is a global, landscape-scale self-organization process whereby small spatially periodic perturbations are amplified simultaneously across landscapes. Such processes are manifestations of non-uniform stationary instabilities, of which Turing instability is an example (Appendix A) [14,15,48,49]. However, spatial self-organization can also occur locally at ecotones, or fronts, that separate domains of different ecosystem states [50–53]. The spatial distributions of plant species, soil-biota, plant-released chemicals (allelochemicals) and resources that develop across ecotones (hereafter “front structure”) are likely to determine whether these fronts are stationary, mobile, and the direction and speed at which they move. Much like vegetation patterns can change their configuration, e.g., from gap patterns to labyrinth-like stripe patterns, also, fronts can change their structures and thus their directions and speed of propagation [54,55]. Ecotone structure and motion have been studied in various ecological contexts, including exotic invasion [56,57], shrub encroachment in arid grasslands [58], coastal vegetation on a salinity gradient [59] and consumer fronts [60], but transitions between different front structures have rarely been studied. However, such transitions have tremendous potential to slowing down or reversing desertification and invasion [53,61,62].

Vegetation patterns and self-organized ecotones are highly likely to affect community assembly, and the progress that has been made in understanding their formation and dynamics provides good starting points for exploring various mechanisms of community assembly. Communities may self-organize in space in response to spatially organized populations of keystone species, which as described above, often form distinct spatial patterns, or as a direct result of interspecific interactions, where each species independently may not form spatial patterns. Examples of the former can be found in woody-herbaceous systems, where shrubs or trees self-organize into spatial patterns and thereby modify the spatial distributions of soil water and nutrients, seed dispersal, light, and belowground biota [9,63–65]. In turn, these modifications can shape the assembly of understory species [6,66,67]. Other examples of the former are clonal plants that self-organize in space to form vegetation rings as a result of autotoxicity or negative PSFs in the inner zone of the clone [25,68]. Such patterns affect subsequent community assembly as they often enhance the recruitment and development of other plant species [25]. Examples of the latter case – spatial self-organization as a direct result of interspecific interactions – are intransitive (non-hierarchical) networks of interspecific interactions that result in traveling-wave patterns (Appendix A), where single-species domains cyclically exchange their resident species through species invasion and succession from adjacent domains [17,21,69,70].

Motivated by these studies we propose that spatial self-organization is an inherent aspect of many ecosystems, including drylands, wetlands, the arctic, and in undersea shallow continental shelves, that is driven by a broad suite of belowground feedbacks (BGFs), including PSFs, allelopathy and plant-resource interactions. We further propose that integrating spatial self-organization into studies of these ecosystems will increase our understanding of community assembly in general, and that a most appropriate approach to this integration is via pattern-formation theory [10,16]. Specifically, we propose the following hypothesis, which we term “the spatial self-organization hypothesis” illustrated in Fig. 2:

“BGFs can affect community assemblages through spatial self-organization of two main types. (*A*) *global self-organization by small-scale processes occurring in parallel across whole ecosystems, leading to large-scale self-organized patterns of biota, allelochemicals and resources, and thereby niche partitioning*, (*B*) *local self-organization by small-scale processes occurring locally in ecotones, determining ecotone structure and motion, invasion dynamics and species coexistence by multiple ecotone dynamics*.”

(a) Global self-organization: Large-scale self-organized vegetation patterns


Plant-water SDFs, inducing a hexagonal pattern of stationary vegetation spots

Plant-water SDFs with allelopathic self-inhibition, inducing moving crescent-shaped vegetation spots

(b) Local self-organization: Small-scale self-organized ecotones

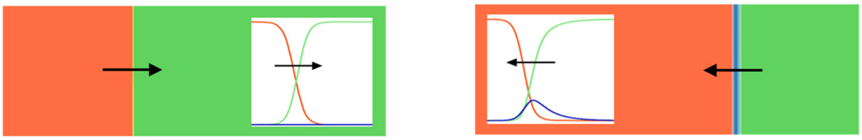


Fig. 2. The spatial self-organization hypothesis. Below-ground feedbacks (BGFs) can affect community assemblage through spatial self-organization processes of two types, illustrated here with model simulations: (a) processes occurring simultaneously across the whole ecosystem, such as self-organization in stationary spot patterns induced by plant-water scale-dependent feedbacks (SDF), or self-organization in patterns of moving crescent-shaped vegetation patches when allelopathic self-inhibitory effects are present, (b) processes occurring locally in ecotones, resulting in self-organized structures of different species distributions, and different directions of ecotone movement as the black arrows indicate (colors denote different species). The insets show the spatial biomass distributions across the ecotones. Adapted in part from Marasco et al. [26] and Contento and Mimura [163]. Reproduced after permission.

The first type of spatial self-organization typically occurs in ecosystems where a uniform vegetation state becomes unstable (Appendix A) and a patterned state develops. The second type is typical of ecosystems with multiple alternative stable states where front structures separating domains of different stable states can form. The hypothesis does not refer to patterns of community assembly that are dictated by geomorphological templates, such as in fractal river-basin networks [71,72]. We discuss the two types of processes outlined in our hypothesis and their implications for community assembly, focusing on homogeneous ecosystems where spatial variability is associated with spatial self-organization. Limited by the scope of available empirical studies, our discussion relies to a large extent on insights obtained from model studies and pattern-formation theory.

2. Self-organized patterns of biota, allelochemicals and resources

Global self-organization is generally associated with instabilities of spatially uniform states that drive the emergence of periodic stationary patterns or periodic traveling waves [14,48,49]. We focus here on community-assembly associated with pattern-forming keystone species that act as ecosystem engineers by modifying the distributions of soil water, nutrients, soil biota and chemicals [73]. These self-organized distributions can affect the establishment of other species and thereby community assembly. We discuss first the well-modeled patterns produced by plant-water feedbacks and the niches they form, and then proceed to patterns driven by the relatively new mechanisms of PSFs and allelopathy, alone and in combination with plant-water feedbacks.

2.1. Patterns driven by plant-water scale-dependent feedbacks

A common mechanism by which spatial patterns spontaneously emerge from spatially uniform states is a non-uniform stationary instability, often called a “Turing instability” (Appendix A). This mechanism involves the amplification of small spatially periodic perturbations and their monotonic growth to form stationary periodic patterns [16]. In the context of dryland ecosystems, the uniform state represents a landscape of constant vegetation-biomass and soil-moisture distributions. The amplification of small periodic perturbations occurs under conditions of water stress as a result of a positive feedback loop between local accelerated vegetation growth and water transport toward the site of accelerated growth [15]. Several forms of water transport have been distinguished in model studies, including overland water flow, water uptake by laterally spread roots, and soil-water diffusion.

The amplification of small non-uniform perturbations on uniform vegetation is understood as follows: an area with incidentally denser vegetation draws more water from its surrounding area (as compared with the water drawn by the surrounding sparser vegetation) by several possible mechanisms, associated with the various forms of water transport. These include (i) increasing the infiltration contrast (higher in denser vegetation), which speeds up overland water flow,

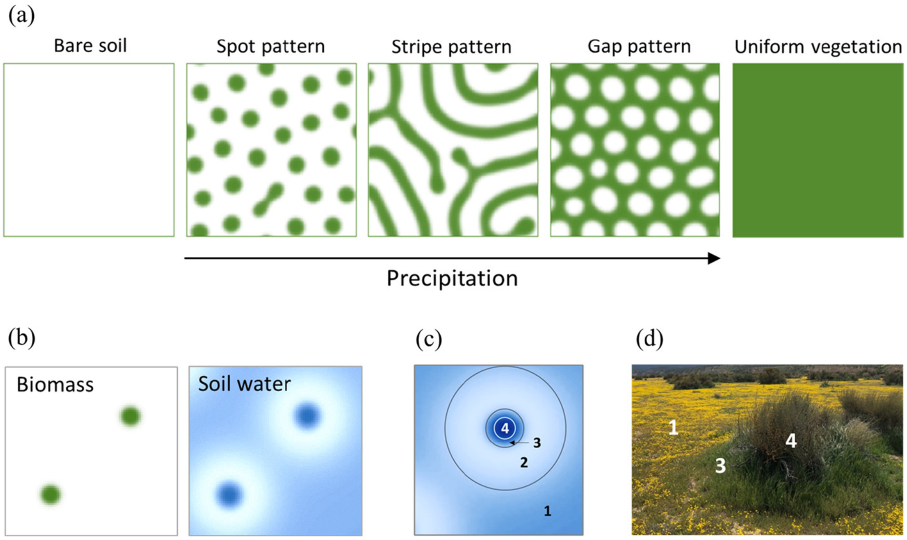


Fig. 3. Spatial self-organization and niche partitioning. (a) Biomass distributions of five basic vegetation states along the rainfall gradient, predicted by model studies (from Meron [13]). (b) Soil-water distributions associated with sparse spot patterns (adapted from Meron et al. [90]). (c) Illustration of different niches formed by the biomass and soil-water distributions associated with a single vegetation patch, as discussed in the text. Darker shades indicate higher soil-water densities. (d) Annual species in Niches 1 (*Lasthenia californica*) and 3 (*Bromus rubens*) associated with a woody ecosystem engineer (*Ephedra californica*) in the semi-arid San Joaquin Desert (see Lucero et al. [196] (photo credit Jacob Lucero). Reproduced after permission.

(ii) extending the root zone in the lateral dimensions, which allows uptake from a larger soil volume, and (iii) creating and steepening soil-water gradients by stronger local water uptake, which induces and enhances soil-water diffusion. The increased amount of water drawn from surrounding areas of denser vegetation increases water-dependent vegetation-growth rates, and thus accelerates growth in the denser-vegetation areas, while growth deaccelerates in the surrounding areas where water is depleted. Thus, incidental areas of slightly denser vegetation become yet denser and the surrounding vegetation yet sparser, a process that amplifies the initial incidental non-uniformity and leads to an instability of the original uniform vegetation state. This instability results in the development of stationary periodic patterns similar to the fairy-circle gap pattern shown in Fig. 1B [14,15]. The positive feedback loop described above involves short-range activation, or facilitation, due to accelerated growth of denser vegetation, and long-range inhibition, or competition, due to depletion of water in the areas of sparser vegetation around [23]. For this reason, the positive feedback loop is also termed a “scale-dependent feedback” or SDF [14]. The positive feedback loop represents the processes that amplify small perturbations and induce the instability of uniform vegetation, and the scale dependence entailed in these processes represents the nature of the perturbations that grow beyond the instability – spatially periodic.

Self-organized vegetation patterns that arise under conditions of water stress can undergo transitions to sparser patterns with reduced vegetation coverage as the stress increases [40,74]. Model studies have elucidated various mechanisms by which this reduction in vegetation coverage may occur: reduction in the size of vegetation patches, reduction in their number, and morphological changes leading to different vegetation patterns [15,75]. The latter mechanism results in five basic vegetation states along rainfall gradients: (1) uniform vegetation at relatively high precipitation, (2) hexagonal gap patterns, (3) stripe patterns and (4) hexagonal spot patterns as precipitation decreases, and (5) bare soil at very low precipitation (Fig. 3a) [13]. Hexagonal gap patterns are periodic arrays of circular bare-soil gaps in otherwise uniform vegetation, where any gap is surrounded by six other equidistant gaps. Hexagonal spot patterns are periodic arrays of circular vegetation spots in otherwise bare soil, where any spot is surrounded by six other equidistant spots.

On hillsides with soil properties that allow for sufficiently high infiltration contrasts (low in bare soil, high in a vegetation patch) stripe patterns oriented perpendicular to the slope direction become favorable and occupy wider precipitation ranges [32,76]. These stripes often migrate uphill forming a traveling-wave pattern [33,77–79]. The migration uphill can be understood as a gravity effect. Plants at the top part of a vegetation stripe intercept runoff from the bare soil uphill, whereas plants at the bottom part of the stripe cannot benefit from runoff; there is no runoff from the bare soil downhill, and runoff from the bare soil uphill infiltrates mostly in the upper part of the stripe and does not reach the bottom part. Vegetation growth at the water-rich top part along with vegetation death in the water-poor bottom part result in vegetation stripes migrating uphill.

Importantly, self-organized vegetation patterns along precipitation gradients may not be regular, lacking clear periodicity. For example, there are wide precipitation ranges where two or more basic states are stable, and under these multi-stability conditions a plethora of irregular self-organized vegetation patterns – hybrids of the basic states – are possible [49,80,81]. It is important to stress that these irregular vegetation patterns can arise even in completely homogeneous ecosystems. However, spatial heterogeneities, such as soil-rock mosaics, contribute to irregularities in vegetation patchiness and, when strong enough, even dictate them [82] (see also [83]).

Pattern formation phenomena are to a large extent universal; the same type of patterns, e.g., gaps, stripes and spots, are observed with different driving SDFs. However, there are also system-specific characteristics that depend on the particular SDFs at work. A good example are fairy-circle patterns observed in Namibia vs. those observed in Australia [36]; they look alike in terms of biomass distributions, but differ in their soil-water distributions because of the different soil types and the corresponding infiltration rates of surface water into the soil. In the following section system-specific aspects will be discussed in the context of plants that act as ecosystem engineers. The reader is referred to Appendix B for a detailed discussion of universal vs. system specific aspects of spatial self-organization.

2.2. Ecosystem engineering and self-organized niche partitioning

Spatially organized vegetation patterns in drylands are characterized not only by distributions of biomass, but also by the distributions of belowground water. According to model studies, the latter can be in-phase with biomass distributions (peaks of biomass and water coincide) or anti-phase (peaks of biomass and troughs of water coincide), depending on the dominant SDFs [84], or assume more complicated forms when two or more SDFs act in concert. Fig. 3b shows an example of soil-water distribution resulting from an interplay between SDFs associated with different water-transport mechanisms: overland water flow and water conduction by roots that extend well beyond the canopy area [64,85].

The capacity of pattern-forming plant species to modify the distributions of soil water, and thereby the colonization of other species, is a form of ecosystem engineering [73]. That capacity depends on various factors, including plant traits, soil properties, mean annual precipitation and spatial self-organization in dense or sparse patterns. These factors may change the relative strength of in-phase vs. anti-phase SDFs and thereby the engineering effects on other species [64]. Models of woody-herbaceous systems predict, in particular, a transition from competitive to facilitative interspecific interactions along rainfall gradients [63] and empirical studies support this prediction [66,86,87]. The models further predict corresponding transitions from mosaics of woody-only and herbaceous-only patches at high precipitation to mixed woody-herbaceous patches in otherwise bare soil areas at low precipitation. A similar transition is predicted to occur in a bi-stability range of woody spot patterns and uniform herbaceous-only vegetation, as the woody spot density decreases; sparse woody patches exclude herbs from their location while dense woody patches facilitate herb growth [63].

These transitions can be attributed to the relative strength of the SDF associated with water conduction by laterally spread roots that extend their range as the shoot grows (the “root-augmentation feedback”), and the SDF associated with overland water flow induced by the development of higher infiltration rates in denser vegetation patches (the “infiltration feedback”). The former SDF acts to deplete the soil-water content in a vegetation patch and its close surroundings by water uptake, whereas the latter SDF acts to increase the soil-water content by overland water flow towards the vegetation patch. The relative strength of these two SDFs depend not only on the parameters that control them, but also on factors such as precipitation rate and patch density. These factors affect the size of vegetation patches and surrounding bare-soil areas, and thus the water balance, that is, the amount of water per unit vegetation-patch area taken up by the roots relative to the amount of overland water infiltrating into that unit area. A decrease in precipitation, for example, results in smaller vegetation-patch sizes, and a shift from dominance of the root-augmentation feedback and anti-phase biomass-water relations to dominance of the infiltration feedback and in-phase biomass-water relations [63,64].

These model predictions, which are consistent with the stress-gradient hypothesis [66,88,89], can provide conceptual frameworks for addressing additional soil factors, besides plant-water interactions, and broader BGFs and their possible effects on community assembly. We illustrate this with model results for sparse patches of a woody ecosystem engineer in a xeric environment, shown in Fig. 3b [90]. The woody species creates four different niches that have the potential to drive self-organization of populations and communities (Fig. 3c). These niches include (1) open habitats beyond the canopies and root zones, with moderately moist soil, (2) open habitats beyond the canopies but within the root zones, with relatively dry soil due to transpiration, (3) the edge of plant canopies with moist soil, roots and litter, and importantly, high light, and (4) below-canopy habitat with moist soil, high concentration of woody roots, high deposition of canopy litter and low air vapor pressure deficit (VPD) and light. In systems with dense-vegetation, Niche 1 may be absent because of overlap among root zones, as in Mediterranean oak woodlands where very extensive lateral root spread may occupy most open space between canopies [91]. Depending on the traits of specific ecosystem engineer species, Niche 2 may or may not exist, but roots of woody species commonly extend beyond canopy edges, especially in arid and semi-arid climates [91,92]. In fact, lateral root extension far beyond canopy edges may be essential for woody plant survival in these climates [93].

These specific niche conditions can promote the survival and growth of particular groups of species, when considering other BGFs, in addition to those associated with plant-water interactions [6,94]. In Niche 2, other species must cope with the competitive or allelopathic effects of roots in the absence of any positive or negative effects of canopies. Niches 3 and 4 often provide higher nutrients, water and shade, and cooler microenvironments. Niche 3 – the canopy edge – is environmentally unique because of the higher light and soil fertility it provides in comparison to Niche 2 (lower fertility) and Niche 4 (less light). Contributing to the higher soil fertility are airborne nutrients trapped at the woody-patch edges that increase throughfall fluxes of dissolved inorganic nitrogen and calcium. These conditions can promote species that do not colonize Niches 2 or 4 [95]. Niche 4 – the canopies of woody species – generally enrich soil fertility, provide shade that favors some species over others, decrease VPD, and provide physical protection [96]. Fig. 3d shows an example of a woody-herbaceous landscape where Niches 1, 3 and 4 are realized, but not Niche 2. These effects can alter the presence and abundance of herbivores, detritivores and microbial communities. Canopies can also compete for light and leach potent allelochemicals [97,98], processes that can contribute to either suppression or facilitation of conspecifics or other species [6,99]. The roots of woody ecosystem engineers can also have profound effects on conspecifics and other species [100–102].

2.3. Patterns driven by PSFs and allelopathy

2.3.1. Plant-soil feedbacks

Soil biota comprise a multifaceted collection of consumers and mutualists that have strong direct and indirect negative and beneficial effects on plants, and regulate the nutrient cycles that sustain plants [103,104]. In turn, plants shape the microbiome around their roots, likely via root exudates, such that bacteria appear to have adapted in specific ways to "the rhizospheric niche" [104]. These reciprocal effects of plants on soil biota and soil biota on plants contribute to a wide range of complex and dynamic feedback interactions between plants and the microbial communities that develop around their roots as predicted by PSFs [27,28]. Positive PSFs are thought to occur when plant species disproportionately accumulate biota around and in their roots that have beneficial effects on the plants that cultivate them, such as mycorrhizal fungi and nitrogen fixers [105–107]. Positive PSFs are thought to decrease plant community diversity because they confer strong advantages to a few species [108]. This appears to occur in some exotic invasions, where exotic plant species escape biota with negative effects and are enhanced by soil biota in their new ranges, while natives in these new ranges are suppressed by the same biota [109,110]. In general, negative PSFs occur when plant species disproportionately accumulate pathogenic biota in their rhizospheres, which can create conditions that are increasingly hostile to the plants that cultivate the pathogens [27,28,111]. Negative PSFs are thought to enhance diversity by increasing species turnover rates and reducing mono-dominance [112].

2.3.2. Allelopathy

Currently, allelopathy describes chemically based negative interactions among plants [30], although it is not restricted to plants [113], and is common among microbes [114]. As a case study, the fine roots of *Sorghum bicolor* store and release large amounts of the chemical sorgoleone, which can be taken up by other species in which it interferes with photosynthesis [115]. Sorgoleone is also produced by the invasive *Sorghum halepense* [116]. Rout et al. [117] found that leachate from shoots and roots of *S. halepense* strongly suppressed the native grass, *Schyzachyrium scoparium*. Correspondingly, *S. halepense* expanded rapidly into native grassland and dramatically decreased native

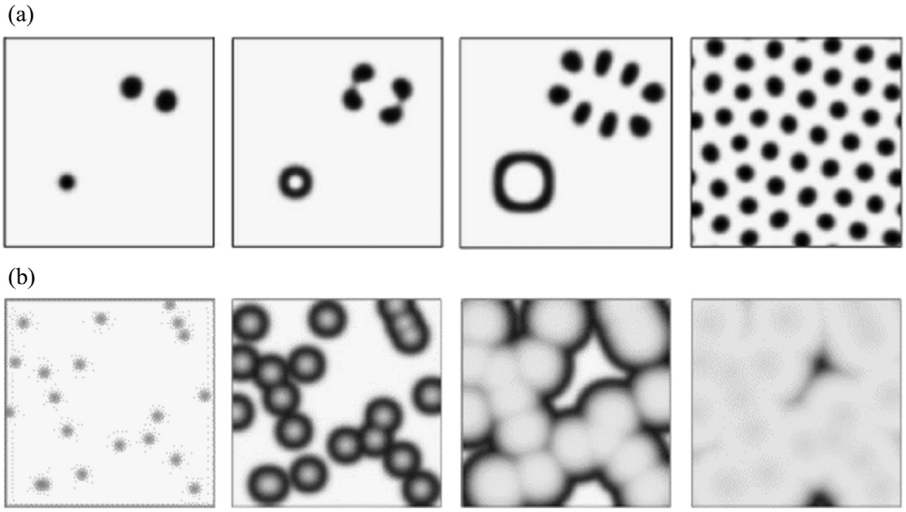


Fig. 4. Snapshots of model simulations showing the development of rings from initial spots and their long-time dynamics (a) in a model that captures plant-water SDF, and (b) in a model that captures auto-toxicity. Time proceeds from left to right. Adapted with permission from (a) Meron et al. [137], (b) Cartenì et al. [68]. Reproduced after permission.

diversity and virtually eliminated *S. scoparium*. Many other studies have shown that either through direct effects on plants, or indirect effects on plants through soil biota, allelopathy can affect communities and alter networks of interspecific interactions [103,118,119]. Allelopathy is not mediated by resource uptake, nor even necessarily coupled with resource uptake. However, soil water content can influence allelochemicals in ways that affect ecosystem processes and plant growth [120]. Also, abiotic stress, such as drought, can increase the production of secondary compounds and modify allelopathic effects [121]. Importantly, for spatial self-organization, allelopathy can operate on conspecifics, referred to as autotoxicity [101,122,123].

Allelopathy can interact with PSFs because soil microbes can utilize allelochemicals as carbon sources and break them into more or less toxic by-products [124–126]. Thus, either through their direct effects on plants or indirect effects on plants through soil biota, allelochemicals can change interspecific interaction networks and shape communities [103,118,127].

2.3.3. PSFs, allelopathy and pattern formation

Because both PSFs and allelopathy can exert negative effects on plant growth, they can induce or change spatial patterning independently of resource-based feedbacks. An example that has attracted considerable attention is ring formation by perennial clonal species [25] from pre-existing spot patches (Fig. 1d). Ring formation can be explained by plant-water interactions alone [128–130], but other factors have also been suggested as major drivers of this robust phenomenon. These include morpho-phenological processes [131,132], aeolian processes [133,134], negative PSFs, and allelopathy [135,136].

Model studies suggest that vegetation ring formation is a transient traveling-wave behavior. In models that capture plant-water SDFs, vegetation rings develop by central dieback as spots grow in size and the competition for water at the spot centers increases. As the rings increase in diameter and approach other vegetation patches they break into spots, forming eventually a spot pattern (Fig. 4a) [137]. In models that capture autotoxicity, the central dieback is caused by the release of an allelochemical [68]. Model studies suggest that in the absence of SDFs and allelochemical dispersal, expanding rings collide and annihilate one another to form a state devoid of live vegetation (Fig. 4b) [68]. The common appearance of vegetation rings in nature suggests that these transient behaviors can be quite long in time, possibly because of plant-water interactions or fast allelochemical dispersal, relative to seed dispersal or clonal growth, e.g., through overland water flow in rain episodes.

A model that includes both plant-water SDFs and allelopathic autotoxicity [26] indicates the possible appearance of persistent traveling-wave behaviors under relatively mesic conditions where water limitation is less important. Stationary periodic patterns (Fig. 2a left) still prevail when toxicity fades away fast enough, but persistence of toxicity for longer times can result in traveling crescent-like vegetation spots (Fig. 2a right). The inclusion of autotoxicity in models of water-limited vegetation can also create more complex traveling-wave behaviors, including bouncing spots upon head-on collisions, spot splitting and others [26]. Similar behaviors have been analyzed in models of activator-inhibitor systems consisting of a single activator and two inhibitors [138], analogous in our case to vegetation biomass (activator), lack of soil water (first inhibitor) and toxicity (second inhibitor). Candidate systems for such spatiotemporal behaviors include species for which there is evidence for both allelopathy and competition for water, such as *Larrea tridentata* [139], *Encelia farinosa* [140], and *Artemisia tridentata* [141].

Whether autotoxicity alone can induce an SDF leading to stationary periodic patterns is an open question. Such an SDF may possibly result from fast allelochemical dispersal relative to seed dispersal, which would stabilize a vegetation patch locally, by reducing the allelochemical concentration, and prevent plant growth in the patch neighborhood due to the accumulation of the allelochemical there. Fast allelochemical dispersal may be achieved when the allelochemical is advected by water flow. A model consisting of two state variables, plant biomass and allelochemical concentration with fast diffusion, or more realistically, a model that includes in addition a water variable, is likely to capture a Turing instability that leads to stationary periodic patterns.

Vegetation rings may have unusually important secondary effects on community assembly because of their strong facilitative effects on other species [25]. Plants that form rings often act as ecosystem engineers in that they modify the microenvironment within the ring and ameliorate the effects of harsh environments on other plant species. This can increase overall diversity. However, the facilitative effects of these species are not restricted to harsh environments [25]; facilitative nurse effects by ring-forming species were common in a wide range of environments, including the complex effects of *Ampelodesmos mauritanicus*, a ring-forming Mediterranean shrub, for which 23 species were preferentially or exclusively associated with the interior of the rings.

As pointed out earlier, positive PSFs can provide competitive advantages to invasive species, which may result in species exclusion and decreased species diversity [142]. Spatial patterning may have positive effects on species coexistence and diversity in this case as well. Species capable of forming patterns may exclude other species locally, in the patches they form, but allow the establishment of other, less competitive species in the open areas and thus maintain higher species diversity. Such effects have been found in several model studies in flat terrain [63] and in sloped terrain [143,144]. A possible context where such behaviors may arise is when exotic species invade under conditions of water stress. Invasive species often have high water uptake rates relative to associated natives, which not only contributes to the success of the invasion process [145], but can also play a role in spatial patterning [64,84]. Possible candidates for pattern-forming invasive species include *Cecropia obtusifolia*, *Macaranga mappa* and *Melastoma septemnervium* in the lowland wet tropical forest on the Island of Hawaii [146] or *Pinus halepensis* in southern Australia [147]. Other possible candidates are species in the *Acacia* genus [148,149]. *Acacia mearnsii*, is an invasive tree species reported to have high transpiration rates compared to native species [150], and the resulting competition for water suppresses the natives [151]. *Acacia dealbata* is a highly invasive species that benefits from positive PSFs, exerts allelopathic effects on other species, and has high water uptake [152,153]. We are not aware of studies reporting spatial patterning by these species, but another species in the *Acacia* genus – *Acacia aneura* (mulga) – does form spatial patterns [154] (Fig. 1a), and forms mosaic patterns with the grass *Trioda spp. Poaceae* (spinifex) [155]. However, more empirical studies are needed in order to examine and substantiate possible relations between invasive species, spatial patterning and species coexistence.

The possible emergence of persistent traveling waves when autotoxicity fades away slowly enough, such as the traveling crescent-like vegetation spots in Fig. 2a, may have an additional positive effect on species coexistence and diversity. In this case, local exclusion of species by a highly competitive autotoxic species may be a transient behavior that is followed by recolonization of the excluded species once the autotoxic species locally decays and re-establishes in the toxic-free neighborhood. However, further model studies are needed to test these ideas, e.g., by extending Marasco et al. [26] model to include a second less competitive species.

3. Self-organized ecotones

The second form of spatial self-organization we consider is related to processes occurring locally in ecotones that separate spatial domains of alternative stable states [51]. This form of self-organization is associated with the development of particular spatial distributions of plant biomass, resources, soil biota and allelochemicals across narrow ecotones, which define front structures (Fig. 5). We first consider community-assembly aspects associated with the dynamics of single ecotones in bi-stable ecosystems (Appendix A) [156], examples of which are desertification and

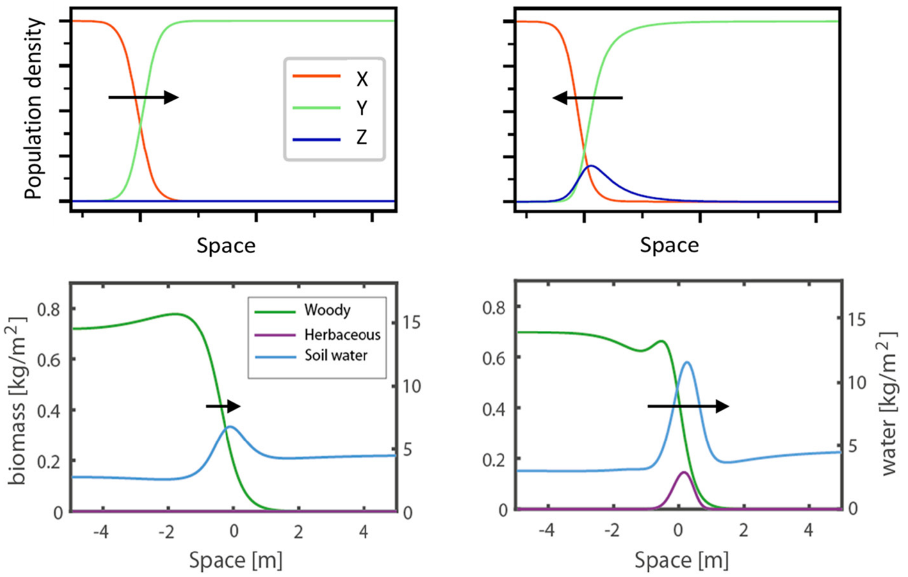


Fig. 5. Model predictions of possible self-organized front structures. Shown are snapshots of spatial distributions of relevant state variables. Arrows indicate the directions of front propagation. (A) Fronts in a three-species Lotka-Volterra model, for two strongly competing species, X and Y, and a third species Z that is strongly competing with X and weakly competing with Y. In the absence of Z the X species invades the Y species. That invasion process is reversed when Z colonizes the front zone (right panel). Adapted from Contento and Mimura [163]. Reproduced after permission. (B) Fronts in a woody-herbaceous vegetation model that captures plant-water feedbacks. Shown are spatial profiles of two alternative stable fronts, describing slow woody-vegetation expansion into bare soil (green curve in left panel), and fast woody-vegetation expansion (green curve in right panel). The increased expansion rate of the latter is due to the colonization of herbaceous vegetation in the front zone (magenta curve) and the consequent increase in infiltration rate and, thus, soil-water content (blue curves). Adapted from Zelnik and Meron [53]. Reproduced after permission.

invasion fronts. We will then consider community assembly associated with multiple ecotones located at different positions and the spatial patterns they form. There are two cases of multiple ecotones: (1) those in which all ecotones separate the same pair of alternative states, and 2) those in which ecotones separate different pairs of alternative states. The latter case applies to tri-stable and higher multi-stable systems (Appendix A). Because the particular microenvironments that ecotones form depend on the pairs of states they separate, case 2 should provide a wider variety of microenvironments and lead to differences in alpha diversity between individual ecotones, and greater beta diversity across the whole multiple-ecotone system. Thus, we would expect case 2 to drive different trajectories of community assembly than case 1. Multi-stability can arise due to additional feedbacks that stabilize alternative states, such as Allee effects [157], due to entrainment of ecosystem states to seasonal periodicity at different phases of oscillations (Appendix C) [16], or due to more diverse communities with strongly competing species [158]. We discuss the dynamics of single and multiple ecotones and their impact on community assembly in light of the theory of front dynamics in multi-stable systems [16].

3.1. Dynamics of single ecotones: desertification and invasion fronts

Two significant manifestations of single-ecotone dynamics are desertification and invasion fronts (Fig. 6, Appendix A). Desertification fronts are moving ecotones that separate spatial domains of functional and dysfunctional (or less functional) ecosystem states. A positive front speed represents a desertification process where the functional state locally transforms into the dysfunctional state at the front zone, while a negative front speed represents the inverse process of recovery of the functional state. The dysfunctional state represents a state of reduced productivity and related ecosystem services, such as bare soil devoid of live vegetation, or shrubland in grassland to shrubland transitions that involve loss of palatable grass and soil fertility (Fig. 6a) [159,160]. Invasion fronts are moving ecotones that separate domains of native species and exotic species, where the latter may displace the former in the narrow front zone by releasing allelochemicals directly or indirectly through microbial activities (Fig. 6b). Since the focus here is on fronts in multi-stable systems, we do not refer here to fronts propagating into unstable states [56,161].

Fig. 6. Self-organized ecotones. (a) A desertification front that shifts a shrubland (left) into a grassland (right) in the Chihuahuan Desert of New Mexico. Courtesy of Curtis Monger, New Mexico State University. (b) An invasion front of *Sorghum halepense* (yellow ribbon) that shifts a species-rich native community (left) into a species-poor community dominated by invader (right). See Rout et al. [117]. Photo by Ragan Callaway.

Both desertification fronts and invasion fronts have negative effects on biodiversity and ecosystem function [160,162]. Understanding what factors control the direction and speed of front propagation is crucial, as they exert fundamental controls on these self-organized ecotones, and may delineate ways for slowing down or even reversing undesired desertification and invasion processes. Importantly, consideration of combined effects of PSFs, allelopathy and plant-resource feedbacks may uncover new controls on ecotone dynamics with knock on effects for community assembly and ecosystem management. The key to understanding the factors that control front dynamics lies in the different structures that self-organized fronts can assume. Empirical evidence for the existence of alternative front structures is not yet available, but model studies predict their feasibility. Studies of desertification and invasion phenomena indicate that fronts with particular self-organized structures may go through instabilities to different front structures (Appendices A and C). This may result in the slowing down or reversal of front propagation, or in undulated fronts that propagate non-uniformly along the front line. Furthermore, parameter ranges may exist where two stable alternative front structures exist [53,62,163].

As an illustrating example of the factors that control front propagation, we consider here a study of a three-species Lotka-Volterra model [163] where front solutions separating domains occupied by strongly competing species, denoted as X (orange) and Y (green) in Fig. 5a, have been studied. The third species, denoted Z (blue), is a strong competitor with X, but a weak competitor with Y. Consequently, the uniform single-species Z state is unstable. While species Z cannot colonize large domains of either X or Y, it can colonize the front zone where the densities of X or Y are lower. We adopt here a different interpretation of the three species than that of Contento & Mimura [163], and regard X and Y as strongly competing invasive and native species, respectively, and of Z as a control species that can be introduced into the system as part of a management practice. The colonization of Z in the front zone has a dramatic effect, as it changes the direction of front propagation; in the absence of Z, the species X invades Y, while in the presence of Z the species Y invades X, as the arrows in Fig. 5a indicate. This behavior reflects the existence of two stable self-organized front structures, and possible shifts between the two fronts by controlling the local density of the third species Z in the front zone.

For ecosystem management, the existence of two alternative stable fronts propagating in opposite directions hold promise for reversing invasion, because minimal intervention is needed to reverse the direction of front propagation. The intervention is only needed in the narrow front zone, and it is limited to the time required to shift one front structure to the other. Once this shift is established a self-recovery process begins with minimal further intervention [53,62]. In the Lotka-Volterra model discussed above, the intervention needed to reverse the invasion of X is limited to the time required to introduce the Z species in the narrow front that separates the domains occupied by X and Y.

Although population densities in the Lotka-Volterra model can represent plant species, the model does not capture BGFs and, thus, does not contain information about soil factors that might be manipulated in efforts to reverse invasion. Invasion models that do capture PSFs have not been studied yet for the possible existence of alternative stable front solutions propagating at different velocities, but desertification and recovery fronts have been explored by Zelnik & Meron [53]. They reported fronts separating domains of woody vegetation from domains of bare soil using a model of water-limited woody-herbaceous ecosystems, and identified a precipitation range where two stable fronts exist, describing slow and fast recovery of woody vegetation (Fig. 5b). What makes this essential difference between the two fronts is a positive feedback associated with herbaceous vegetation colonizing the front zone; that colonization increases the infiltration rate of surface-water into the soil and thereby the soil-water content, which, in turn, accelerates woody-vegetation growth and thus speeds up the front. Here, a front shift to the faster front implies accelerated recovery of degraded landscapes, and a local one-time intervention in the form of judicious introduction of herbaceous vegetation at the front zone might induce that shift.

Several models of plant invasion that do consider BGFs, specifically allelopathy, have been proposed [52,164–166], employing different hypotheses for the invasion mechanism. Eppinga et al. [166] used a model for two plant species, native and invasive, and two soil-communities amplified by the two plant species, to study exotic plant invasion, where the mechanism at work is invader-assisted accumulation of local pathogens that harm the native species. They found that initially small patches of the invasive species expand uniformly to form circular patches with radii that increase linearly in time, implying constant-speed invasion fronts, and no indications of a transverse front instabilities (Appendices A and C). In the course of time, growing circular patches merge to form bigger patches, indicating weak or no repulsive front interactions (see Section 3.2), until a uniform invasive species state (full coverage) is achieved. Fassoni & Martins [52] studied a model of a native species and an invasive species that exerts a negative effect on the native species by producing a phytotoxin. They identified several cases of bi-stability of uniform states, including bi-stability of native-only states and invasive-only states obtained from strong interspecific competition, and bi-stability of a native-only state and a mixed native-invasive state that were derived from weak interspecific competition. The latter bi-stability state allows for invasion fronts that leave behind a mixed community of native and invasive plants. In Fassoni & Martins too, fronts propagate at constant speed and form growing circular patches of the invaded state, indicating no transverse front instability. A more complicated case has been considered by Souza et al. [165] who included in their model also phytotoxin-resistant native species. In the absence of resistant species, patches of the invasive species grow uniformly in a circular manner, displacing the native species at a nearly constant speed. The presence of an additional, resistant species results in persistent patches of that species and slower, nonuniform growth of invasive-species patches.

3.2. Dynamics of multiple ecotones: species coexistence by spatial patterning

Multiple ecotones can result from strong disturbances, such as overgrazing, clearcutting, fires, pest outbreaks and others, which form domains of alternative stable states (Fig. C.1a). Multiple ecotones can also arise from a single initial ecotone that goes through a front instability and develops into a patterned state (Fig. C.1b-d) [62]. We consider first the case of multiple ecotones or fronts that separate the same pair of alternative stable states and have the same structure (e.g., fronts in Fig. C.1a). The eventual state that develops from arbitrary initial conditions of multiple moving fronts strongly depends on the interactions between fronts as they approach one another (Appendix C). When these interactions are repulsive and sufficiently strong, persistent vegetation patterns can develop, such as the Giraffe-like pattern shown in Fig. C.1a. The ecological origin of repulsive interactions and the patterns they induce can be understood by considering, for example, a precipitation range where bare soil and uniform vegetation are alternative stable states. At relatively high precipitation in that range, where vegetation patches expand into bare soil, repulsive front interactions can result from water depletion in the retreating bare-soil areas between growing vegetation patches, which slows down or halts further patch growth [53,167]. At relatively low precipitation, where bare soil expands into vegetation patches, strong repulsive interactions can result when vegetation patches become narrow and plants draw water from larger surrounding areas of bare soil (Fig. C.1a) [53]. The precipitation downshift needed to change a scenario of expanding vegetation patches into a scenario of retreating vegetation patches can be quite small if it involves precipitation values near the Maxwell point, that is, the particular precipitation value where a single non-interacting front is stationary (Appendix C).

These two pattern-formation scenarios have interesting implications for species coexistence and community assembly when the pattern-forming species is dominant and excludes other species. In the first scenario, with high precipitation, other species may not be able to colonize the small bare-soil areas because of low soil-water content. However, such species may colonize large bare-soil areas in the second low-precipitation scenario (Fig. C.1a), despite the lower precipitation rate, which need not be much lower, but only on the low-precipitation side of the Maxwell point. Such spatial patterning leading to species coexistence may possibly result also from repulsive interactions associated with dispersal of allelochemicals, where water is not a limiting factor. In the case of autotoxicity, accumulation of allelochemicals in retreating bare-soil areas, as vegetation patches expand and approach one another, may halt the expansion and result in patterns consisting of small bare-soil gaps. Other species that are excluded from the vegetation

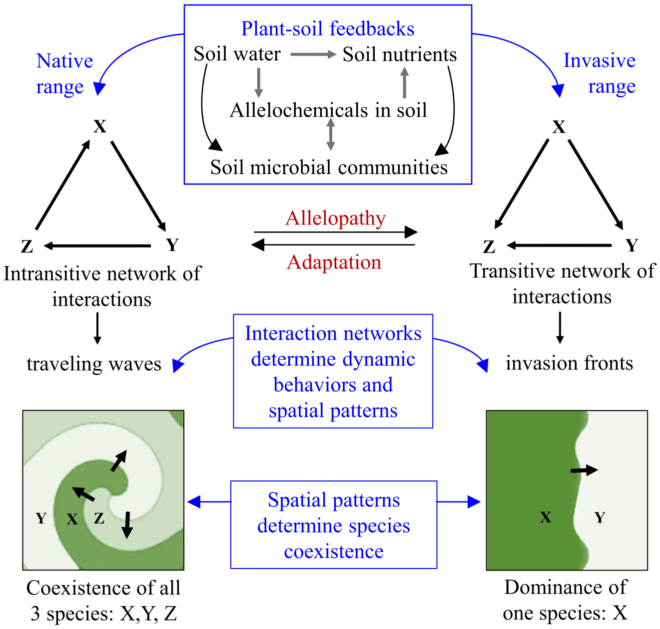


Fig. 7. Schematic illustration of invasion and species coexistence as spatial self-organization processes involving multiple ecotones, driven by allelopathy and adaptation to allelopathy. Plant-soil feedbacks determine interspecific interaction networks through the mediating effects of soil moisture, nutrients, allelochemicals and microbial communities. In native ranges these networks are generally intransitive, reflecting a lack of competitive hierarchy. Intransitive networks can result in traveling waves, and spatial coexistence of all species, X, Y, Z. In invasive ranges these networks are transitive, or hierarchically competitive, and can result in invasion fronts that lead to communities dominated by a single species, X. Allelopathy can induce a change from intransitive to transitive networks, and thereby reduce species diversity, but adaptation can induce the opposite change and increase species diversity. Other dynamics behaviors are discussed in the text.

patches, e.g., species intolerant to shade and that are resistant to the particular allelochemicals in question may then colonize the gaps.

In tri-stable and higher multi-stable systems, fronts separating different pairs of stable states may appear. These states may represent 1) different single-species states in a community of strong interspecific competition [158,168], resulting, for example, from allelochemical warfare [21], 2) states of seasonally forced ecosystems oscillating at different phases (Fig. C.2) [16,169], 3) combinations of different uniform and patterned states (Zelnik et al. [53]), or various mixtures of these three cases. We focus here mostly on the first case – communities of strongly competing species – and consider for simplicity a community consisting of three species, X, Y, Z, where all single-species population states (also denoted by X, Y, Z) are stable, i.e., forming a tri-stable system [158]. Such a system has three front (ecotone) types, separating the three different pairs of stable states, X and Y, Y and Z and Z and X. The system represents a transitive interaction network if one species invades (by means of front propagation) the other two species (Fig. 7 right), and an intransitive network when cyclic relations hold: X invades Y, Y invades Z, and Z invades X (Fig. 7 left) [163,170].

In intransitive networks, initial conditions containing all three front types can converge to persistent traveling waves containing three-state spiral waves, which imply coexistence of all three species (Fig. 7 left) [17,168]. However, when one species, say X, releases allelochemicals that negatively affect species Z, the interaction network may change to transitive: X displaces Y and Y displaces Z, as before, but now X also displaces Z (Fig. 7 right). As a consequence, domains occupied by Z will diminish relatively fast because of the invasions of both X and Y, and ultimately Z will disappear leaving fronts of X expanding into Y, until species X dominates the system. Thus, an allelopathy-induced change in the direction of front propagation, e.g., as a result of changes in abiotic stress such as temperature [125,171,172], can result in a transition from an intransitive network to a transitive network that reduces species diversity (Fig. 7).

On the other hand, native plant and microbial species may adapt to allelochemicals released by an invasive species [127,173,174]. The resulting decline in allelopathic effects on communities may drive a transition from a transitive to an intransitive network (Fig. 7). Such adaptations might modify the competitive effects of otherwise dominant species [118] or generate "competitive loops" in which otherwise dominant competitors are suppressed by inferiors [175].

The transitive and intransitive networks of interactions considered above are relatively simple in that all three species X, Y and Z are strongly competing with each other and all single-species states are stable, forming a tri-stable system. More complex interaction networks, however, may exist [163,170]. In fact, we have discussed an example for such a network in the context of single-front dynamics in a three-species Lotka-Volterra model. In this case the single-species state of Z is unstable, but Z still plays a crucial role in the dynamics of fronts that separate domains occupied by species X and Y. As Fig. 5a shows, the presence of Z in the front zone between X and Y domains can change the direction of front propagation from X invading Y (Fig. 5a left) to Y invading X (Fig. 5a right). As discussed in Appendix C and demonstrated in Fig. C.1b, when two alternative stable fronts propagating in opposite directions exist, persistent traveling waves can appear [176,177]. These waves can take the form of rotating spiral waves involving all three species, as well as more complex traveling-wave patterns [163]. This peculiar effect of species Z colonizing a front between X and Y and thereby changing its direction of propagation, has another interesting implication – in larger networks involving more than three species it can result in transitions between transitive and intransitive networks.

4. Conclusion

We present a new hypothesis that links spatial self-organization of biota and resources, driven by BGFs, to community assembly. Two forms of spatial self-organization are distinguished: 1) global, involving spatial patterning across whole systems (Fig. 2a), and 2) local, involving ecotone (front) structuring and restructuring (Fig. 2b).

Spatial patterning across whole systems (form 1) may occur via plant-resource SDF, and lead to regular and irregular stationary vegetation patterns of various morphologies (Figs. 1a, b, 3a). Spatial self-organization may also occur because of negative PSFs and allelopathy, alone or in conjunction with plant-resource SDF, but then allelopathy leads to traveling-wave behaviors, such as expanding vegetation rings, traveling crescent-like patches and complex spatio-temporal patterns (Fig. 1d, Fig. 2a right, Fig. 4b). As vegetation patterning involves changes in the spatial distributions of soil water, nutrients, soil biota and allelochemicals, it affects community disassembly and reassembly in ways that differ from the independent responses of individual species to the abiotic environment (Fig. 3). This is particularly relevant to the response of plant communities to climate extremes, such as prolonged droughts, often compounded by heat waves, which are likely to result in spatial patterning or re-patterning.

Ecotone structuring and restructuring (form 2) occur via BGF that act locally at the narrow ecotone zone and dictate particular distributions of biota, resources and allelochemicals across it – the ecotone structure. This structure determines, in turn, the ecotone motion, which can be manifest in desertification and exotic invasion fronts (Fig. 6). Ecotones may possibly go through instabilities that restructure them, and may result in alternative stable front structures moving at different speeds or even directions (Fig. 5). Such dynamic behaviors, predicted by pattern formation theory, can provide important clues for how to reverse or mitigate desertification and invasion processes. They have been found in models of desertification fronts [53,62], and in a three-species Lotka-Volterra model [163], but have not been reported yet in model studies of invasion. This may simply be due to limited awareness of front instabilities occurring as generic dynamical behaviors, or due to oversimplified modeling of PSFs and allelopathy.

Ecosystem states involving multiple ecotones, induced by front instabilities or strong disturbances, may show a variety of spatial patterns that may affect community assembly in various intricate ways. For example, multiple ecotones in multi-stable systems may increase species diversity as different front types, associated with different pairs of states, can form different microenvironments and a variety of niches for other species. These species, in turn, may change the direction of front motion (Fig. 5a), and thereby induce transitions between transitive and intransitive networks. Network transitions can also be induced by allelopathy and the subsequent adaptation of other species to allelochemicals (Fig. 7).

So far, most model studies of spatial self-organization have been restricted to small communities consisting of a few species, the large majority of which address just two species [see for example [178] and references therein]. However, in order to relate model predictions to empirical observations, model studies of spatial self-organization in large communities are needed. A first step towards that goal has been made by integrating a trait-based approach to community assembly into models of spatial self-organization [9,179]. In this approach the species pool is divided into functional groups of species that share the same values of a few selected functional traits. Further simplification is made by taking into account possible tradeoffs between different functional traits, such as a tradeoff between investment in growth vs. investment in tolerance to an environmental stress. The plant community is then described by a biomass variable that depends not only on space and time, but also on trait coordinates. The latter dependence provides information about community level properties [9], such as composition and various components of functional diversity (functional richness, evenness, functional divergence) [180]. Using this approach, relations between community-level properties and spatial self-organization of the two types might be uncovered. These relations can then serve as informed hypotheses for long-term empirical studies.

Because empirical studies of spatial patterning induced by BGFs and associated community dynamics are generally limited in duration and spatial extent, advances in understanding these processes have depended to a large extent on modeling and model analyses, but stronger empirical links to ecology and evolution are crucial. This calls for close collaborations between ecologists, ecohydrologists, physicists and mathematicians, and for the development of a common language that promotes interdisciplinary research.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Glossary

Some of the terms appearing below are mathematical concepts. In describing them we favored intuitive clarity over mathematical rigor, given the broad background of the journal's readership.

Allelopathy The phenomenon by which chemicals released by plants exert negative effects on other plants.

Belowground feedbacks (*BGFs*) A suite of processes, including allelopathy, plant – soil-biota interactions, and plant-water interactions that operate belowground and influence plant growth and spatial patterning.

Bi-stable ecosystem A multi-stable ecosystem (see below) with two alternative stable states.

Desertification front A moving front that separates domains of functional and dysfunctional ecosystem states, in which the latter displace the former by local feedbacks involving various biotic and abiotic factors.

Fronts in multi-stable ecosystems Transition zones across which system states change from one stable state to another. Fronts self-organize in particular spatial distributions of biotic and abiotic state variables across the front, which define their structure and determine their motion. Fronts can be regarded as *self-organized* ecotones in that they are shaped by local feedbacks rather than dictated by external abiotic patterns.

Front instability An instability that involves a local change in the structure of a front. The change can be limited to variations across the front that are uniform along the front line (longitudinal instability) or involving periodic undulations of the front line (transverse instability). Although front instabilities begin locally at the front zone, their effects often propagate to entire systems (Fig. C.1b-d).

Instability A threshold phenomenon in which a combination of feedback processes acts in concert to amplify small perturbations about system states and lead to state changes. The particular form of the perturbation that grows, spatially uniform or periodic, and the manner of growth - monotonic vs. oscillatory - generally determine the new state that the system evolves to.

Instability types of spatially uniform stationary states Several instability types can be distinguished, all involving the simultaneous growth of small perturbations across whole systems:

1. *Uniform stationary instability*. Involves the monotonic growth of spatially uniform perturbations. Such instabilities generally result in different stationary uniform states.
2. *Uniform oscillatory instability*. Involves the oscillatory growth of spatially uniform perturbations. Such instabilities lead to spatially uniform time-periodic oscillations, or to long-wavelength traveling waves.
3. *Non-uniform stationary instability*. Involves the monotonic growth of spatially periodic perturbations. Such instabilities lead to stationary periodic patterns, such as Turing patterns.
4. *Non-uniform oscillatory instability*. Instabilities that are driven by the oscillatory growth of spatially periodic perturbations. Such instabilities lead to short-wavelength traveling waves.

Invasion fronts Moving fronts that separate domains of native species and exotic species, where the latter displace the former by releasing allelochemicals, directly or indirectly by microbial activities.

Multi-stable systems Dynamical systems that possess two or more alternative stable states in some range of relevant parameters. Different kinds of multistability can be distinguished by the combinations of the alternative stable states - uniform or patterned, stationary or oscillatory.

Pattern formation An interdisciplinary research field that centers on spatial self-organization and the emergence and dynamics of regular and irregular spatial patterns in various fields of science. Studies in pattern formation involve field and laboratory experiments, modeling, and mathematical model analysis.

Plant-soil feedbacks (*PSFs*) Plant-induced changes in soil biota that in turn feedback to affect the performance of conspecifics and other species.

Scale-dependent feedbacks (*SDFs*) Combinations of positive and negative feedbacks between organisms and resources that operate at different spatial scales and lead to spatial patterning. SDFs that form vegetation patterns in drylands involve fast water transport towards denser vegetation patches. That transport further enhances the growth in these patches, making them yet denser (short-scale positive feedback), while inhibiting the growth in the sparser patch surroundings, making them yet sparser (long-scale negative feedback).

Spatial self-organization The emergence of regular or irregular spatial patterns of organisms, resources and allelochemicals, as a result of disturbances that trigger endogenous feedbacks between these entities. Two major forms of spatial self-organization can be distinguished. The first is associated with weak disturbances of unstable uniform states that induce periodic patterns, such as Turing patterns. The second is associated with strong disturbances of stable uniform states of multi-stable systems that form domains of alternative stable states enclosed by fronts (ecotones). Periodic and non-periodic patterns may then form as a result of repulsive front interactions and front instabilities (Fig. C.1).

Stable and unstable states A system state is stable if any sufficiently small perturbation or disturbance of that state decays in the course of time. The state is unstable if there exists a perturbation that grows in time.

Traveling wave phenomena A general term describing moving spatial distributions of organisms, resources and allelochemicals, the simplest of which are traveling fronts (Fig. 5) and periodic traveling waves (Fig. C.2, Fig. 7 left). More complex forms are traveling patches, such as expanding rings or moving crescent-like patches that interact as they approach one another, slow down, change direction or even split (Fig. 2a, right).

Appendix B. Universal vs. system-specific aspects of pattern formation

A striking aspect of pattern formation phenomena in nature is their universal character; the same types of patterns – stripes, spots, spiral waves and others – are observed in completely different physical contexts. For example, stripe patterns appear in clouds, in animal coat patterns and in dryland vegetation, although the mechanisms responsible for these patterns are obviously specific to the system in question, and different. The universality of pattern formation phenomena is closely related to the instabilities that induce patterns.

Models of pattern forming systems are often described by a set of partial differential equations (PDEs), e.g., reaction-diffusion equations, for some characteristic state variables. Although these equations are specific to the system in question and vary from one system to another, they may capture the same type of instability. For example, both the fluid equations that describe thermal convection and account for stripe cloud patterns, and the reaction-diffusion equations that describe vegetation stripes, capture a non-uniform stationary instability of a uniform steady state (see Appendix A). An important result of pattern formation theory, which explains the origin of universality, is that systems that go through the same type of instability behave similarly sufficiently close to the instability threshold.

Mathematically, starting from the equations that describe each system, it is possible to derive new equations – the so called "normal-form equations" – that look alike for all systems that share that type of instability [16]. This is a very powerful result of pattern formation theory, because it means that once a specific instability is identified for a particular system (empirically or theoretically), a whole range of potential universal behaviors, predicted by the corresponding normal-form equations (most of which have thoroughly been studied) are readily known. This encouraging conclusion has one serious drawback – the limited ability to relate these universal behaviors to the particular system under consideration. Many questions of interest are left unanswered when a particular type of instability is identified, and the normal-form equations are known. Examples of such questions include: (i) Is a particular universal behavior likely to be observed in realistic ranges of biotic or abiotic parameters? (ii) What biotic and abiotic parameters control the instability threshold and the corresponding dynamical behaviors? (iii) How different state variables are correlated; do they show in-phase, anti-phase or other, more complex relations between spatial distributions of biomass, resources, or allelochemicals? Addressing these and additional questions call for (i) informed hypotheses about the basic feedbacks that drive instabilities in a particular system, (ii) the development and studies of models that capture these feedbacks, and, (iii) when possible, derivation of normal-form equations to uncover their dependence on system-specific parameters.

The distinction between universal and system-specific aspects of pattern formation is important in order to avoid mistakes, such as attempts to infer about system-specific mechanisms from universal behaviors, as different mechanisms can lead to the same universal behavior. On the other hand, familiarity with universal behaviors can assist in explorations of system-specific models by informing what types of dynamical behaviors can potentially be found in such explorations.

Appendix C. Front dynamics in multi-stable systems

The simplest realization of multi-stable systems is that of bi-stable systems that consist of two alternative spatially-uniform stationary stable states. Also, the simplest context of front dynamics in such systems is the dynamics of a single front. Fronts separating such states move in general in one direction or another, depending on the values of control parameters. The dynamics associated with front motion can be followed by observing the temporal changes that the various state variables go through at a fixed point in space through which the front is passing. A critical parameter value at which the front is stationary, the so-called Maxwell point, may exist, but this is not a generic case as any deviation from that value results in front motion [181,182]. In contrast, when one of the stable states is spatially patterned the front may be stationary (pinned) in a parameter *range* [182,183]. This type of bi-stability is significant because it generally implies a multitude of additional stable states, representing hybrids of the two basic states, a behavior known as "homoclinic snaking" [183].

Another aspect of single-front dynamics in bi-stable systems is the possible occurrence of front instabilities [10,16,181]. These can be classified into longitudinal instabilities, associated with changes in the spatial distributions of state variables across the front, and transverse instabilities, associated with periodic undulations along front lines (curvature variations) [184]. Longitudinal instabilities can result in additional stable front structures (separating the same alternative stable states) that move at different speeds and even in opposite directions. In the latter case, persistent traveling waves may develop, including rotating spiral waves (Fig. C.1b) [176,177,185]. Transverse instabilities may result in growing domains of labyrinthine patterns through fingering, tip splitting and repulsive front interactions (Fig. C.1c) [184,186]. Moreover, longitudinal and transverse instabilities may interact to form complex dynamics (Fig. C.1d), where front interactions and curvature variations drive spontaneous appearance and disappearance of pairs of counter-rotating spiral waves [184,187,188].

Single fronts can be viewed as building blocks of spatially extended patterns made of multiple fronts that delimit patches of different states to form patch-mosaic patterns (Fig. C.1a). In the course of their dynamics, fronts may

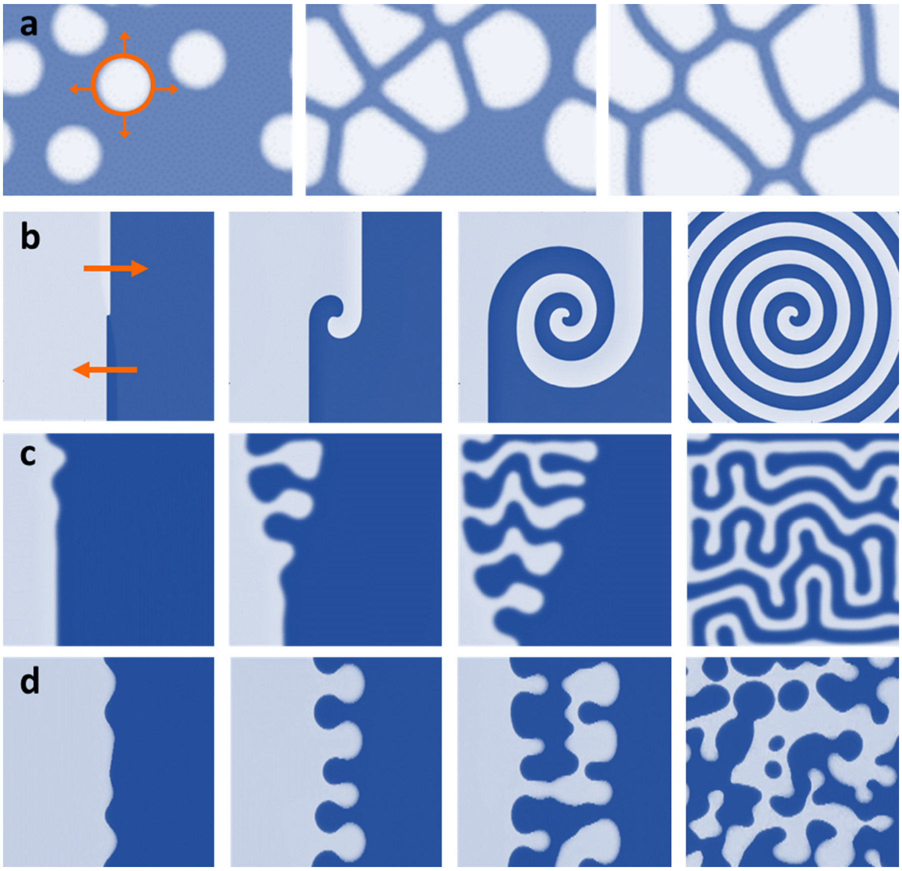

Fig. C.1. Illustrations of different forms of front dynamics in bi-stable systems and the asymptotic patterns that develop, starting from multiple (circular) fronts of the same structure (a), and from a single front structure (b-d), where time proceeds from left to right. In (a), an initial state of multiple circular fronts, moving outward (see illustration with orange circle and arrows), eventually converges to a nearly stationary polygonal pattern, because of repulsive front interactions (adapted from Zelnik and Meron [53]). In (b) a longitudinal instability of a perturbed front results in two front segments moving in opposite directions (see arrows) that develop into a steadily rotating spiral wave. In (c) a transverse instability of a perturbed front results in a stationary labyrinthine pattern through fingering, tip splitting and repulsive front interactions (fingers do not merge) (adapted from Yochelis et al. [197]). In (d) a combination of longitudinal and transverse front instabilities results in fingering, followed by repeated events of merging and splitting of domains to form a chaotic pattern in space and time.

come close to one another and interact. These interactions can be attractive, repulsive or combinations of attractive and repulsive interactions at different distances between the fronts [16,181]. We focus on repulsive front interactions [189], as this case is more applicable to vegetation patterns [190,191]. Repulsive interactions slow down front motion, but the outcomes of this effect depend on the strength of the interactions and on the existence of additional front structures [55]. When repulsive interactions are sufficiently weak the fronts "collide" and the domain between the fronts disappears. In bi-stable systems, this process eventually results in a uniform state. In higher multi-stable systems simpler patterns involving fewer states result. When repulsive interactions are sufficiently strong the fronts may come to a stop and form stationary patterns (Figs. C.1a, c). When an additional front structure moving in an opposite direction exists, the fronts may bounce and form complex pattern dynamics (Fig. C.1d).

Multi-stable systems can give rise to fronts that differ in the pairs of stable states that they separate. Tri-stable systems, for example, consisting of three stables states, denoted A, B and C, can give rise to three front types: fronts separating A and B, B and C, and C and A. Combinations of such fronts may result in a variety of multi-state patterns, including multi-state spiral waves [168]. An interesting ecologically-relevant context that gives rise to multi-stability is periodically forced oscillating systems. In such systems, the number of stable states is determined by the ratio of the forcing frequency to the oscillation frequency of the unforced system. When that ratio is close to an integer number n, and the forcing is strong enough, n alternative stable symmetric states can result. The states oscillate at the same

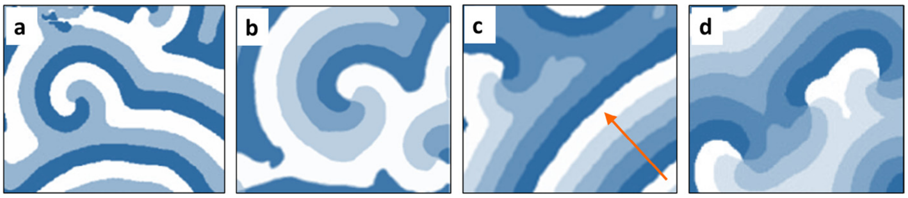

Fig. C.2. Multiphase traveling waves, including rotating spiral waves, in a periodically illuminated photosensitive oscillating chemical reaction. Shown are snapshots of n-phase patterns with n – the ratio of oscillation period to forcing period - equals 3,4,5,6 in panels a, b, c, d, respectively. Darker blue shades invade lighter shades until a whole cycle (2π) is completed, as the orange arrow in panel c illustrates (adapted from Lin et al. [192,198]).

period (n times the forcing period) but differ in their phase of oscillations by a constant amount $2\pi/n$. Fig. C.2 shows multiphase traveling and spiral waves for different n values observed in experiments on forced chemical reactions [192]. Successive spiral arms correspond to oscillating domains separated by moving phase-fronts that shifts the oscillation phase by $2\pi/n$. These phase-fronts can also be stationary (non-moving) in which case standing-wave patterns develop. Multiphase patterns of this kind are highly relevant to ecosystems with mechanisms acting to induce oscillations (possibly only damped oscillations) that are subjected to seasonal forcing [169,193,194].

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