Linking spatial self-organization to community assembly and biodiversity

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Abstract Drier climates impose environmental stresses on plant communities that may result in community reassembly and threatened ecosystem services, but also may trigger self-organization in spatial patterns of biota and resources, which act to relax these stresses. The complex relationships between these counteracting processes - community reassembly and spatial self-organization - have hardly been studied. Using a spatio-temporal model of dryland plant communities and a trait-based approach, we study the response of such communities to imposed water stress of increasing degrees. We first show that spatial patterning acts to reverse shifts from fast-growing species to stress-tolerant species, as well as to reverse functional-diversity loss. We then show that spatial re-patterning buffers the impact of further stress on community structure. Finally, we identify multistability ranges of uniform and patterned community states and use them to propose forms of non-uniform ecosystem management that integrate the need for provisioning ecosystem services with the need to preserve community structure.

Introduction

The structure of plant communities - their composition and diversity - forms the foundation of many ecosystem services on which human well-being crucially depends. These include provisioning services such as food, fresh water, wood and fiber; regulating services such as flood regulation and water purification; cultural services such as recreation and aesthetic enjoyment; and supporting services such as soil formation, photosynthesis, and nutrient cycling (Duraiappah and Naeem, 2005). These services are at risk due to potential changes in the composition and diversity of plant communities as a result of global warming and the development of drier climates (Harrison et al., 2020; Grünzweig and et al., 2021). Understanding the factors that affect community structure in varying environments calls for integrated studies of mechanisms operating at different levels of organization, from phenotypic changes at the organism level, through intraspecific interactions at the population level, to interspecific interactions at the community level (Gratani, 2014; Falik et al., 2003; Bertness and Callaway, 1994; Pérez-Ramos et al., 2019). Of these mechanisms, the role of intraspecific interactions in driving community dynamics through spatial self-organization, has hardly been studied (Vandermeer and Yitbarek, 2012; Bonanomi et al., 2014; Cornacchia et al., 2018; Zhao et al., 2019; O'Sullivan et al., 2019).

Spatial self-organization in periodic and non-periodic patterns of biota and resource, driven by intraspecific competition that leads to partial plant mortality, is widely observed in stressed
environments (Rietkerk and van de Koppel, 2008). An important class of these phenomena are vegetation patterns in drylands. In sloped terrains these patterns commonly appear as parallel vegetation stripes oriented perpendicular to the slope direction (Lefever and Lejeune, 1997; Valentín et al., 1999; Bastiaansen et al., 2018). In flat terrains, with no preferred direction imposed by slope or wind, stripe-like configurations often appear as labyrinthine patterns. However, in such terrains two additional pattern morphologies are often observed; nearly periodic patterns of bare-soil gaps in otherwise uniform vegetation, and nearly periodic patterns of vegetation spots in otherwise uniform bare soil (Rietkerk et al., 2004; Deblauwe et al., 2008; Borgogno et al., 2009; Meron, 2018). Spatial self-organization may not necessarily result in periodic patterns; according to pattern-formation theory (Meron, 2015; Knobloch, 2015) it can also result in non-periodic patterns, such as single or randomly scattered vegetation spots in otherwise bare soil, randomly scattered bare-soil gaps in otherwise uniform vegetation and others (Tlidi et al., 2008; Dawes and Williams, 2015; Parra-Rivas and Fernandez-Oto, 2020; Jaibi et al., 2020; Zelnik et al., 2015). The driving mechanisms of these self-organized vegetation patterns are scale-dependent positive feedback loops between local vegetation growth and water transport toward the growth location (Rietkerk and van de Koppel, 2008; Meron, 2019).

Vegetation patterns involve not only spatial distributions of plant biomass, but also less-visible distributions of soil-water, nutrients, soil biota, and possibly toxic substances (Paz-Kagan et al., 2019; Inderjit. and Duke, 2003; De Deyn et al., 2004; van der Putten et al., 2013). The various habitats that these self-organizing distributions form lead to niche differentiation and community reassembly (Weiher et al., 2011). Thus, spatial self-organization and community dynamics are intimately-coupled processes that control community composition and diversity. Understanding this unexplored coupling is essential for assessing the impact of global warming and drier climates on community structure and ecosystem services.

In this paper we incorporate spatial self-organization into community-assembly studies, using a mathematical model of dryland plant communities. Our model study provides three new insights, illustrated in Fig. 1: (i) Spatial self-organization acts to reverse community-structure changes induced by environmental stress, (ii) it buffers the impact of further stress, and (iii) it offers new directions of ecosystem management that integrate the need for provisioning ecosystem services with the need to conserve community structure. More specifically, using a trait-based approach (Díaz and Cabido, 2001), we show that drier climates shift the composition of spatially uniform communities towards stress-tolerant species, and reduce functional diversity. By contrast, self-organization in spatial patterns, triggered by these droughts, shift the composition back to less tolerant species that favor investment in growth, and increase functional diversity. Once patterns are formed, spatial self-organization provides various pathways to relax further stresses without significant changes in community composition and diversity. Furthermore, multistability ranges of uniform and patterned states open up new opportunities for grazing and foddering management by forming mixed community states of increased functional diversity.

Results

A model for spatial assembly of dryland plant communities

The model we study largely builds from foundations introduced earlier (Meron, 2016). These foundations capture three pattern-formation mechanisms associated with three forms of water transport: overland water flow, soil-water diffusion, and water conduction by laterally spread roots (Meron, 2019). In this study we focus, for simplicity, on a single mechanism associated with overland water flow. The mechanism induces a stationary nonuniform (Turing) instability of uniform vegetation, leading to periodic vegetation patterns. The instability can be understood in terms of a positive feedback loop between local vegetation growth and overland water flow towards the growth location: an area with an incidental denser vegetation draws more water from its surrounding areas than the latter do, which accelerates the growth in that area and decelerates the growth.
in the surrounding areas, thus amplifying the initial nonuniform perturbation. This feedback loop is also called a scale-dependent feedback because of the positive effect on vegetation growth at short distances and negative effect at longer distances (Rietkerk and van de Koppel, 2008). The reason why an area of denser vegetation draws more water from its surroundings is rooted in the differential infiltration of overland water into the soil that develops – high in denser vegetation and low in sparser vegetation, as illustrated in Fig. 2. Several factors contribute to this process, including denser roots in denser-vegetation areas, which make the soil more porous, and lower coverage of the ground surface in denser-vegetation areas by physical or biological soil crusts, which act to reduce the infiltration rate. The differential infiltration induces overland water flow towards areas of denser vegetation that act as sinks.

We quantify the plant community by introducing a dimensionless trait parameter (Nathan et al., 2016; Tzuk et al., 2019; Yizhaq et al., 2020), \( \chi \in (0, 1) \), that represents a tradeoff between plant investment in shoot growth vs. investment in tolerance to water stress, so that \( \chi \to 0 \) represents plants that invest mostly in growth, while \( \chi \to 1 \) represents plants that invest mostly in tolerating water stress. Using this parameter, the pool of species is divided into \( N \gg 1 \) functional groups, where all species within the \( i \)th group have \( \chi \) values in the small interval \( \Delta \chi = 1/N \) that precedes \( \chi_i = i\Delta \chi \). Spatial self-organization is captured by including a pattern-forming feedback associ-
Figure 2. Illustration of overland water flow towards vegetation patches (horizontal arrows), induced by differential infiltration: low in bare soil (short vertical arrows) and high in vegetation patches (long arrows). The round arrows denote the positive feedback loop between vegetation growth and overland water flow towards the growth location. This feedback loop destabilizes uniform vegetation to form vegetation patterns, and acts to stabilize these patterns once formed.

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\[ \text{bi} \]

\[ \left( \frac{\partial}{\partial t} \right) \text{bi} = \Lambda_i \left( W \text{bi} - M_i \text{bi} + D_i \frac{\partial^2}{\partial x^2} \text{bi} + D_i \frac{\partial}{\partial x} \text{bi} \right), \quad (1a) \]

\[ \left( \frac{\partial}{\partial t} \right) W = I H - L W - \Gamma W \sum_{j=1}^N B_j \Delta \chi + D_w \frac{\partial^2}{\partial x^2} W, \quad (1b) \]

\[ \left( \frac{\partial}{\partial t} \right) H = P - I H + D_H \frac{\partial}{\partial x} \left( H^2 \frac{\partial}{\partial x} H \right), \quad (1c) \]

where the second 'trait derivative', \( \frac{\partial^2}{\partial x^2} \text{bi} \equiv N^2 (\text{bi} - 2 \text{bi} + \text{bi}) \), represents mutations at a very small rate \( D_i \). In these equations the growth rate of the \( i \)th functional group, \( \Lambda_i \), the infiltration rate of above-ground water into the soil, \( I \), and the evaporation rate, \( L \), are given by the expressions:

\[ \Lambda_i = \frac{\Lambda_0 K_i}{B + K_i}, \quad I = \frac{\Lambda (\bar{B} + f \bar{Q})}{\bar{B} + \bar{Q}}, \quad L = \frac{L_0}{1 + RB}. \quad (2) \]

where \( B = \sum_{i=1}^N \text{bi} \Delta \chi \) and \( \bar{B} = \sum_{i=1}^N \bar{Y}_i \text{bi} \Delta \chi \).

The biomass dependence of the growth rates, \( \Lambda_i \), models competition for light and accounts for growth attenuation due to shading. That attenuation is quantified by the parameters \( K_i \); high \( K_i \) values represent plant species investing preferably in shoot growth that are less affected by shading. Note that the growth rate also includes attenuation due to self-shading (Noy-Meir, 1975). The parameter \( \Lambda_0 \) represents the growth rate at low biomass values for which competition for light is absent. The biomass dependence of the infiltration rate, \( I \), is responsible for differential infiltration, quantified by the dimensionless parameter \( 0 \leq f \leq 1 \) and the parameter \( Q \). Low \( f \)
values represent highly differential infiltration, low in bare soil and high \((Q\text{-dependent})\) in vegetation patches, and constitute an important element in the pattern-forming feedback associated with overland water flow towards denser vegetation patches \((\text{Meron, 2019})\). The biomass dependence of the evaporation rate, \(L\), accounts for reduced evaporation in vegetation patches due to shading, quantified by the parameter \(R\). The parameter \(L_{\omega}\) represents evaporate rate in bare soil. Tolerance to water stress is modeled through the mortality parameters \(M_i\) – a plant investment in tolerating stress reduces the mortality rate. For simplicity, we choose to describe here overland water flow as a linear diffusion problem by setting \(a = 0\). Although that process is nonlinear, the qualitative results and conclusions reported here do not depend on that choice \((\text{see Gilad et al. (2004)})\) for the choice \(a = 1\). Additional model parameters are \(P\), representing mean annual precipitation, \(\Gamma\), representing the rate of water uptake by plants’ roots, \(D_i\) representing seed dispersal rate, \(D_W\) quantifying lateral soil-water diffusion, and \(D_H\) quantifying overland water flow.

As pointed out earlier, we distinguish between different species through the different tradeoffs they make between shoot growth and tolerance to water stress. We capture this tradeoff using the parameters \(K_i\) and \(M_i\) through the tradeoff relations:

\[
K(\chi) = K_{\text{max}} + \chi \left( K_{\text{min}} - K_{\text{max}} \right),
\]

\[
M(\chi) = M_{\text{max}} + \chi \left( M_{\text{min}} - M_{\text{max}} \right),
\]

where \(K_i = K(\chi_i)\) and \(M_i = M(\chi_i)\). According to these relations, \(\chi \to 0\) represents the functional group \((K_{\text{max}}, M_{\text{max}})\) with highest investment in growth and lowest investment in tolerance (highest mortality), while \(\chi = 1\) represents the functional group \((K_{\text{min}}, M_{\text{min}})\) with lowest investment in growth and highest investment in tolerance. This tradeoff is likely to affect the contributions, \(Y_i\), of the various functional groups to the infiltration rate \(I\); denser roots associated with lower-\(\chi\) species (increased investment in shoot growth) make the soil more porous and increase the infiltration rate. An additional contribution to that effect is lower soil-crust coverage in patches of lower-\(\chi\) species. We therefore assume the following form for \(Y\):

\[
Y_i = Y(\chi_i) = Y_{\text{max}} + \chi_i (Y_{\text{min}} - Y_{\text{max}}).
\]

We use numerical continuation methods \((\text{AUTO (Doedel, 1981)})\) to study the model equations for single functional groups, and numerical time-integration in the composed trait-space plane to study the full community model. We use periodic boundary conditions in \(x\) and zero-flux conditions in \(y\). Initial conditions are chosen to contain all functional groups, even if at diminishing small biomass values. Such small values represent the presence of seeds that remain viable even when they cannot germinate \((\text{DeMalach et al., 2021})\). Throughout the paper we use the following parameter values: \(N = 128\), \(L_0 = 0.032 \text{ m}^2/(\text{kg} \cdot \text{y})\), \(\Gamma = 20.0 \text{ m}^2/(\text{kg} \cdot \text{y})\), \(A = 40.0 \text{ m}^{-1}\), \(R = 10.0 \text{ m}^2/\text{kg}\), \(L_0 = 4.0 \text{ y}^{-1}\), \(f = 0.01\), \(Q = 0.06 \text{ kg/m}^2\), \(K_{\text{min}} = 0.1 \text{ y}^{-1}\), \(K_{\text{max}} = 0.6 \text{ kg/m}^2\), \(M_{\text{min}} = 0.5 \text{ y}^{-1}\), \(M_{\text{max}} = 0.9 \text{ y}^{-1}\), \(Y_{\text{min}} = 0.5\), \(Y_{\text{max}} = 1.5\), \(D_B = 1.0 \text{ m}^2/\text{y}\), \(D_W = 10^2 \text{ m}^2/\text{y}\), \(D_H = 10^4 \text{ m}^2/\text{y}\), \(D_L = 10^{-6} \text{ y}^{-1}\). Values of other parameters are as stated in the following.

We wish to point out that the results presented here are not sensitive to this particular choice of parameter values, and similar results have been obtained with other sets of parameter values.

The main constraint on this choice is the need to capture the Turing instability of the uniform vegetation state, and the need to define the tradeoff relations such that the Turing threshold split the community into functional groups that form and do not form periodic patterns. Since vegetation patterns are observed on spatial scales that differ by orders of magnitude, from periodicity of tens of centimeters for herbaceous vegetation to periodicity of tens of meters for woody vegetation \((\text{Rietkerk et al., 2004})\), we focus on generic community aspects associated with vegetation patterning, rather than attempt to model a particular ecosystem with a specific spatial scale.

**Single functional-group states**

It is instructive to consider first solutions of a model for a single functional group, \(\chi = 1\). As the bifurcation diagram in Fig. 3a shows, a uniform vegetation solution \((UV)\) exists and is stable at sufficiently high precipitation \((P)\), but loses stability in a subcritical Turing bifurcation \((\text{Meron, 2018})\) as
Figure 3. Existence and stability ranges of various solutions of a model for a single functional group. (a) A bifurcation diagram showing the \( L_2 \)-norm of the biomass density vs. precipitation for \( \chi = 1 \). The colors and corresponding labels denote the different solution branches: uniform vegetation (UV), periodic patterns at different wavelengths (PP), hybrid states consisting of pattern domains in otherwise uniform vegetation (HS), and bare soil (BS). Solid (dashed) lines represent stable (unstable) solutions. Example of spatial profiles of these solutions are shown in the panels on the right. (b) Instability thresholds of uniform vegetation, \( P_T \), and of bare soil, \( P_B \), as functions of \( \chi \).

\( P \) is decreased below a threshold \( P_T(\chi) \). That instability creates a bistability range of uniform vegetation and periodic patterns (PP) where hybrid states (HS), consisting of patterned domains of increasing size in otherwise uniform vegetation, exist (Knobloch, 2015; Zelnik et al., 2015). Besides the periodic-pattern solution that appears at the Turing bifurcation (\( PP_{W L=81} \)), many more periodic solutions appear, as \( P \) further decreases, with longer wavelengths (WL) (Zelnik et al., 2013; Siteur et al., 2014). The second periodic solution shown in the diagram (\( PP_{W L=150} \)) has a wavelength almost twice as long. A solution describing bare soil (BS), devoid of vegetation, exists at all \( P \) values but is stable only below a threshold value \( P_B \). Similar bifurcation diagrams are obtained for lower \( \chi \) values, but the existence and stability ranges of the various solutions change. As Fig. 3b shows, the uniform-vegetation state of species investing mostly in growth (low \( \chi \)) lose stability to periodic patterns at higher \( P \) values. Also, the bare-soil state remains stable at higher \( P \) values. These results imply that species investing in growth have a stronger tendency to form patchy vegetation, and are more at risk of mortality (collapse to bare soil) as a result of disturbances.

Effects of spatial patterning on community assembly

What forms of community assemblages can emerge when the \( N \) functional groups are allowed to interact and compete with one another? Figure 4 shows the assembly of a spatially uniform community, where all functional groups asymptotically form uniform vegetation (\( P > P_T(\chi \to 0) \), see Fig. 3b). Because of species competition for water and light, a particular community assemblage develops, often characterized by a hump-shape biomass distribution with a most abundant group (maximal biomass) at \( x_{max} \). This distribution contains information about two community-level properties of interest here: the community’s composition, quantified by \( x_{max} \), and its functional diversity. The latter represents the diversity of functional traits around \( x_{max} \) (Diaz and Cabido, 2001).
We measure functional diversity using two metrics, functional richness, \( FR \), and functional evenness, \( FE \) \cite{Mason2005}. The first metric is given by the extent of the biomass distribution around \( x_{\text{max}} \), as Fig. 4 illustrates. The second metric contains information about the abundance of functional groups in the community and how even the abundance is among the groups. We use here the following analogue of the Shannon diversity index,

\[
H = -\sum_{i=1}^{N} b_i \ln b_i, \quad b_i = \frac{B_i}{\sum_{j=1}^{N} B_j},
\]

and the related index of Pielou for functional evenness \cite{Pielou1966},

\[
FE = \frac{H}{\ln N}.
\]

How do plant communities respond to progressively drier climates, mimicked here by precipitation downshifts of increasing strength? Figure 5 shows asymptotic biomass distributions for decreasing precipitation values. At \( P_1 = 150\text{mm/y} \) (panel a), a spatially uniform hump-shape community develops, characterized by a symmetric distribution of functional groups around a most abundant group at \( x_{\text{max}} = x_0 = 0.62 \), and by functional richness \( FR_0 = 0.29 \). Lowering the precipitation to \( P_2 = 100\text{mm/y} \) (panel b), results in a spatially uniform community shifted to species that better tolerate water stress (higher \( \chi \)), now distributed around a most abundant function group at \( x_0 = 0.78 \), and reduced functional richness, \( FR_0 = 0.25 \).

Lowering the precipitation further yet to a value, \( P_3 = 80\text{mm/y} \), below the Turing threshold \( P_T \), results in spatial patterning (panel c). Interestingly, the community composition is now shifted back to species that favor investment in growth (lower \( \chi \)) and the functional richness increases rather than continue to decrease; the patterned community is distributed around \( x_0 = 0.68 \) and its functional richness is \( FR_0 = 0.27 \). Panel (c) also shows (in black) the biomass distribution of the unstable spatially-uniform community at \( P_3 = 80\text{mm/y} \), which continues the trend of panels (a,b) and demonstrates the significant change in community structure that spatial self-organization induces.

Once periodic patterns form, a further decrease in precipitation does not result in significant community-structure changes, unlike the case of uniform communities, as Fig. 6 shows. While spatially uniform communities move to higher \( \chi \) values with decreasing precipitation, as the monotonically decreasing graph \( x_{\text{max}} = x_0(P) \) shows, spatially patterned communities remain largely unchanged, as the nearly horizontal graphs \( x_{\text{max}} = x_{\text{h}}(P) \) and \( x_{\text{max}} = x_{\text{t}}(P) \) show. The first graph represents the periodic pattern that emerges at the Turing instability point \( P_T \). Along this graph, as \( P \) is reduced, the number of vegetation patches remains constant, but their size (along the \( x \) axis) significantly reduces (compare the insets at \( P = P_3 \) and \( P = P_4 \) in Fig. 6). Furthermore, the patches...
span the same range of functional groups (patch extension along the $x$ axis), i.e. retain their functional richness, and their most abundant functional group, $x_{\text{max}} = x_{\text{max}}(P)$, does not change. Thus, as $P$ is reduced, the patterned community that emerges at the Turing instability hardly changes in terms of pattern wavenumber $k_1$ or wavelength $2\pi/k_1$, and in terms of community structure, but the abundance of all functional groups reduces significantly as the vegetation patches become thinner along the $x$ axis.

The second graph $x_{\text{max}} = x_{\text{max}}(P)$ represents a periodic vegetation pattern consisting of fewer patches (along the $x$ axis). Their extension along the $x$ axis remains approximately constant (functional richness hardly changes), and the same holds for the most abundant functional group, $x_{\text{max}} = x_{\text{max}}(P)$. Thus, the effect of further precipitation decrease is a transition to periodic pattern of longer wavelength and reduced abundance, but the community structure (composition and richness) remains almost unaffected.

**Effects of multistability on community assembly**

The discussion so far focused on spatial self-organization in periodic patterns. However, the bifurcation diagram of Fig. 3, obtained for a single functional group, suggests the possible existence of non-periodic or disordered patterns as well, associated with (i) homoclinic snaking (Knobloch, 2015) in the bistability range of uniform and periodic vegetation, which gives rise to a multitude of additional non-periodic hybrid states (Meron, 2019), (ii) multiplicity of stable periodic patterns of different wavenumbers within the Busse balloon (Sherratt, 2013; Zelnik et al., 2013; Siteur et al., 2014; Bastiaansen et al., 2018). We focus here on the first form of multistability and show in Fig.
Figure 6. The buffering effect of spatial patterning on community structure. Shown is a partial bifurcation diagram depicting different forms of community assembly along the precipitation axis, as computed by integrating the model equations in time. Stable, spatially uniform communities, $\chi_{0}(P)$ (solid dark-green line), shift to stress-tolerant species (higher $\chi$), as precipitation decreases. When the Turing threshold, $P_T$, is traversed, spatial self-organization shifts the community back to growth species (lower $\chi$), and keep it almost unaffected as the fairly horizontal solution branches, $\chi_{k_1}(P)$ (light green line), representing periodic patterns of wavenumber $k_1$, and $\chi_{k_2}(P)$ (yellow line), representing patterns of lower wavenumber $k_2$, indicate. The insets show biomass distributions in the ($\chi$, $x$) plane for representative precipitation values. The unstable solution branch describing uniform vegetation (dashed line) was calculated by time integration of the spatially-decoupled model.

Discussion and conclusion

The results described above provide three insights into the intimate relationships between spatial self-organization, community assembly and ecosystem management, as illustrated in Fig. 1 and explained below.

Insight I: Spatial patterning acts to reverse community-structure changes induced by environmental stress

According to Fig. 5, reduced precipitation shifts spatially uniform communities to stress-tolerant species (higher $\chi$ values), but when the Turing threshold is traversed and self-organization in periodic spatial patterns occurs, this trend is reversed and a shift back to species investing in growth takes place. This surprising change of community structure reflects the complex nature of ecosystem response to varying environments, which can employ mechanisms operating in parallel at different organization levels. The composition shift to higher $\chi$ values, as $P$ decreases but still remains...
Figure 7. Increased functional diversity of hybrid states and evenness control. Left panels show biomass distributions of different hybrid states in the trait ($\chi$) – space ($\chi$) plane. Right panels show biomass profiles along the $\chi$ axis averaged over space. The functional richness, $FR$, of all hybrid states is almost equal and higher than that of purely uniform or purely patterned states (compare with panel b in Fig. 5), but their functional evenness, $FE$, differs – high for patterned and uniform domains of comparable sizes (b) and low for small (a) and large (c) pattern-domain sizes. Calculated for a precipitation rate $P = P_3 = 100$ mm/y.

above the Turing threshold $P_T$, is driven by community-level processes, whereby interspecific competition results in a community consisting of species that are better adapted to water stress, and of lower functional richness. By contrast, the composition shift to lower $\chi$ values, once the Turing threshold is traversed, is driven by population-level processes of spatial self-organization, whereby intraspecific competition results in partial mortality and the appearance of bare-soil patches. These patches provide an additional source of water to adjacent vegetation patches, besides direct rainfall, through overland water flow (Meron, 2019). That additional resource compensates for the reduced precipitation and relaxes the local water stress at vegetation patches. The resulting ameliorated growth conditions favor species investing in growth (lower $\chi$), and increase functional richness.

Insight II: Spatial re-patterning buffers community-structure changes

Once periodic patterns form, a further decrease of precipitation does not result in significant community-structure changes, as Fig. 6 shows. This is because of additional forms of spatial self-organization that buffer the impact of decreasing precipitation. The first of which is partial plant mortality that results in vegetation patches of reduced size (compare the insets at $P = P_1$ and $P = P_3$ in Fig. 6). These patches benefit from increased water availability due to the larger water-contributing bare-soil patches that surround them. This response form does not involve a change in the number of patches or pattern's wavenumber, and occurs along the branch of any periodic solution, including those shown in Fig. 6, $\chi_k(P)$ and $\chi_k(P)$. A second form of spatial self-organization involves plant mortality that results in patch elimination and wavenumber reduction (Yizhaq et al.,
2005; Siteur et al., 2014), such as the transition from $\chi_{1}(P)$ to $\chi_{2}(P)$ in Fig. 6 (see insets at $P = P_4$ and $P = P_5$). Like in the first form, any remaining vegetation patch benefits from larger bare-soil patches surrounding it and, thus, from higher water availability.

These forms of spatial self-organization apply also to two-dimensional systems, especially to gently sloped terrains, where quasi-one-dimensional patterns of stripes oriented perpendicular to the slope direction occupy wide precipitation ranges (Deblauwe et al., 2010) and are widely observed in nature (Valentin et al., 1999; Deblauwe et al., 2012; Bastiaansen et al., 2018). Two-dimensional systems, however, allow for additional forms of patterning and re-patterning, which we have not studied in this work (von Hardenberg et al., 2001; Rietkerk et al., 2002; Lejeune et al., 2004; Gowda et al., 2014; Meron, 2019). In flat terrains uniform vegetation responds to reduced precipitation, below the Turing threshold $P_t$, by forming hexagonal gap patterns. These patterns consist of periodic arrays of circular bare-soil gaps, where any gap is surrounded by six other equidistant gaps. Further decrease in precipitation, below a second threshold, results in a morphology change, where bare soil gaps grow and merge to form patterns of parallel stripes or labyrinthine patterns. Below a third precipitation threshold, a second morphology change takes place, where vegetation stripes breakup to form hexagonal spot patterns. These patterns consist of periodic arrays of circular vegetation spots, where any spot is surrounded by six other equidistant spots.

The common denominator underlying these morphology changes is the increase in bare-soil areas adjacent to vegetation patches, as precipitation is reduced; from bare-soil gaps to bare-soil stripes in the first morphology change, and from bare-soil stripes to bare-soil areas surrounding vegetation spots in the second morphology change. Increasing bare-soil areas compensate for the reduced precipitation by providing an extra source of water – water transport to adjacent vegetation patches through overland water flow, soil-water diffusion, or water conduction by laterally extended roots. These processes act to retain the amount of water available to vegetation patches and buffer the impact of decreased precipitation. As a consequence, and like the one-dimensional case discussed earlier, community structure is expected to remain largely unaffected.

Insight III: Multiplicity of stable community states and ecosystem management

The multitude of stable hybrid states, i.e. patterned domains of different sizes in otherwise uniform vegetation, open up novel directions for sustainable management of stressed ecosystems that integrate the need for provisioning ecosystem services with the need to preserve species diversity, as explained below.

A spatially uniform community state at high precipitation responds to a drier climate by shifting the community composition to stress-tolerant (high $\chi$) species and reducing its functional richness (see Fig. 5a,b). Ecosystem services, such as feeding livestock by grazing, impose further stress and are likely to result in further reduction of functional richness. However, a sufficiently drier climate also induces a Turing instability to periodic patterns and a multitude of stable hybrid states. These states have higher functional richness than those of the uniform and patterned states, separately, and can be even higher ($FR \approx 0.33$) than the functional richness of the original uniform community state before the shift to a drier climate has occurred ($FR = 0.29$, see Fig. 5a). This is because uniform domains give rise to stronger competition and higher water stress, and thus form niches for stress-tolerant species, whereas patterned domains benefit from overland water flow from bare-soil patches, which weakens the competition, and provides niches to fast-growing species.

These results can be used to reconcile the conflicting needs for ecosystem services and preservation of functional diversity, through the management of provisioning ecosystems services by non-uniform biomass removal, so as to induce the formation of hybrid states (Fig. 1c). Moreover, the multitude of stable hybrid states allow to control the relative abundance of fast growing vs. stress tolerant species, and thus the functional evenness, $FE$, of the community; small patterned domains in uniform vegetation (Fig. 7a) or small uniform domains in patterned vegetation (Fig. 7c) give rise to low functional evenness ($FE \approx 0.67$), while domains of comparable sizes give rise to higher evenness ($FE \approx 0.70$).
Concluding remarks

In this work we studied the interplay between spatial self-organization and community reassembly, using a spatial model of dryland plant communities. This model captures a particular pattern-forming feedback, associated with differential infiltration and overland water flow (Fig. 2), but we expect our findings to hold also for models that capture the feedbacks associated with soil-water diffusion, and water conduction by laterally spread roots, since they all lead to the same bifurcation structure (Fig. 3a). We are not aware of empirical studies of dryland ecosystems that address this interplay, and thus of data that can be used to test our theoretical predictions, but the three insights described above can serve as solid hypotheses for new long-term empirical studies.

Spatial self-organization and community reassembly are different pathways by which dryland ecosystems relax an imposed water stress. The former is a population-level process that involves monospecific plant mortality by intraspecific competition, and results in an increase of water availability and stress relaxation for the remaining plants. The latter is a community-level process that involves interspecific competition and stress relaxation through the displacement of fast-growing species by stress-tolerant species. The relative roles of the two pathways in the overall response to an environmental stress, and the factors that control them, are open questions of direct relevance to the management of ecosystems at risk in climates that become drier.

Spatial self-organization is not limited to dryland ecosystems. Periodic and non-periodic vegetation patterns have been observed and studied in a variety of other ecological contexts including non-drylands plant communities with negative plant-soil feedbacks, such as self-toxicity (Bonanomi et al., 2014; Marasco et al., 2014), hydric peat bogs (Weltzin et al., 2000; Eppinga et al., 2008), seagrass meadows (Ruiz-Reynés et al., 2017), salt marshes (Zhao et al., 2019, 2021), aquatic macrophytes in stream ecosystems (Cornacchia et al., 2018), and others (Rietkerk and van de Koppel, 2008). In most of these systems spatial self-organization intermingles with community dynamics; the findings of this work may be relevant to these contexts as well, or motivate new studies along similar lines.

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References


(A) Insight I
Fast-growing community
Spatial patterning
Stress-tolerant community

(B) Insight II
1d patterns
2d patterns

(C) Insight III
bi-stability
Localized patterns

Drier climate
Constant climate
Spatial patterning
Differential infiltration
Functional richness Composition

$B \ [\text{kg/m}^2]$

$\chi_{\text{max}}$

$\chi$

$FR$
$P_1 = 150$
$\langle B(x) \rangle_{\chi_0} = 0.29$
$FR_0 = 0.25$

$P_2 = 100$
$\chi_0 = 0.78$
$FR_0 = 0.25$

$P_3 = 80$
$\chi_0 = 0.90$
$\chi_{k_1} = 0.68$
$FR_{k_1} = 0.27$
$FR_0 = 0.21$
\[ \chi_k(P) \] for various values of \( P \):

- \( P_3 = 30 \)
- \( P_4 = 45 \)
- \( P_3 = 80 \)
- \( P_2 = 100 \)
- \( P_1 = 150 \)