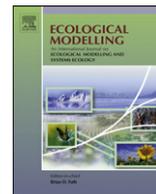




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Pattern-formation approach to modelling spatially extended ecosystems

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ABSTRACT

Self-organization processes leading to pattern formation phenomena are ubiquitous in nature. Intensive theoretical and experimental research efforts during the past few decades have resulted in a mathematical theory of pattern formation whose predictions are well confirmed by controlled laboratory experiments. There is an increasing observational evidence that pattern formation plays a significant role in shaping dryland landscapes. Supporting these observations are studies of continuum vegetation models that have reproduced many of the observed patterns. Such continuum models consist of partial differential equations and lend themselves to the powerful methods of pattern formation theory. Indeed, vegetation pattern formation has been identified with mathematical instabilities of uniform vegetation states, occurring at threshold degrees of aridity. This paper describes applications of this modelling approach to problems in landscape, community, ecosystem and restoration ecology, highlighting new open questions and research directions that are motivated by pattern formation theory. Three added values of this approach are emphasized: (i) the approach reveals universal nonlinear elements for which a great deal of knowledge is already available, (ii) it captures important aspects of ecosystem complexity, and (iii) it provides an integrative framework for studying problems in spatial ecology.

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1. Introduction

The significance of spatial heterogeneity in understanding ecological processes has been recognized long ago. One of the earliest expressions of this recognition is the habitat heterogeneity hypothesis that links spatial heterogeneity to niche formation and species coexistence (Tews et al., 2004). The increasing interest in spatial aspects of ecological processes has led to the emergence of an independent research field, landscape ecology. Numerous studies have been devoted to the definition and quantification of landscape heterogeneity, to the identification and study of its drivers (Turner, 2005), and to the implications for community dynamics, ecosystem processes and ecosystem function (Holyoak et al., 2005; Loreau, 2010; Ritchie, 2010). Yet, an important if not crucial aspect of landscape heterogeneity has escaped deep consideration, that is, the possible occurrence of spatial instabilities leading to *self-organized* heterogeneity (Rietkerk et al., 2004).

Self-organized heterogeneity, or *pattern formation*, is ubiquitous in nature. Cloud streets, sand ripples, geological column formation, and banded vegetation (Fig. 1) are a few examples of pattern-formation phenomena. Underlying these phenomena are positive

feedbacks operating at small scales that destabilize uniform states and lead to large-scale regular or irregular patterns. Although we generally cannot prove the emergence of patterns in nature from such instabilities, we often do make this association, relying on experimental studies of model systems and on mathematical analyses of model equations. This approach has partially been pursued recently in the context of dryland vegetation. Most notably, model studies have identified instabilities that induce vegetation patterns, and tracked pattern changes along environmental gradients that are consistent with field observations (Borthagaray et al., 2010; Borgogno et al., 2009; Gilad et al., 2004, 2007a, 2007b; Klausmeier, 1999; Lefever and Lejeune, 1997; Rietkerk et al., 2002; Sherratt, 2005; Saco et al., 2006; Deblauwe et al., 2008; Valentin et al., 1999; von Hardenberg et al., 2001). These studies, however, have hardly addressed ecosystem and community aspects of vegetation pattern formation, nor have they used the powerful tools of pattern formation theory (Cross and Hohenberg, 1993; Pismen, 2006; Cross and Greenside, 2009).

Two main modelling approaches are currently prevalent in the context of resource limited vegetation landscapes, discrete, agent-based or individual-based models (Grimm and Railsback, 2005), and continuum, partial-differential-equations (PDEs) models. Discrete models are numerical algorithms that go down to the level of *individual plants* and often describe them in great detail. Continuum models consist of spatially continuous variables satisfying sets of coupled PDEs. The lowest level of description in

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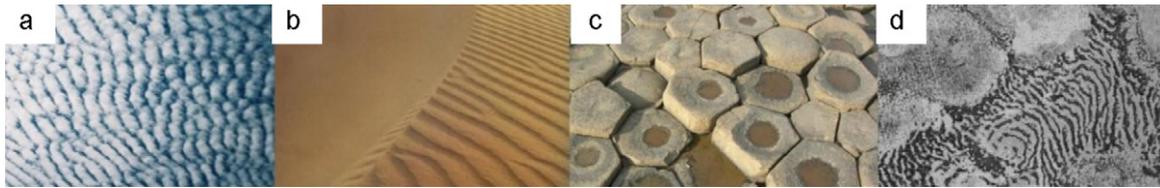


Fig. 1. Patterns in nature. (a) Cloud streets (courtesy of Hezi Yizhaq), (b) sand ripples (courtesy of Arie Barlev), (c) hexagonal column formation in the Giant's Causeway, Northern Ireland (from Goehring et al., 2009), (d) banded vegetation in Niger (from Valentin et al., 1999).

continuum models does not involve individual plants but rather processes at *small scales*. In this approach plants are described by the biomass they form per unit ground area, which may result from a single or many individuals. While the continuum modelling approach does not capture information items related to the life cycle of an individual, it is capable of describing continuous processes such as overland water flow, soil-water dynamics, fog advection, erosion-deposition processes, etc.

From the implementation point of view discrete models are formulated in terms of algorithms that are executed by numerical computations, whereas continuum PDEs models are amenable to mathematical analysis besides numerical computations. This is an important difference between the two modelling approaches; continuum models lend themselves to the powerful tools of pattern formation theory (Cross and Hohenberg, 1993; Pismen, 2006; Cross and Greenside, 2009), whereas no mathematical theory of this kind is available for discrete models.

The main purpose of this paper is to describe a few applications of pattern formation theory to spatial ecology, highlighting new open questions and research directions, and emphasizing the added values of this approach. The results and the open questions to be discussed are particularly relevant to clonal plant growth, the topic of this special issue.

2. A glimpse into pattern-formation theory

Spatially extended systems that are driven far from equilibrium often show ordered patterns with characteristic length scales. Numerous natural examples of this phenomenon exist, a few of them are shown in Fig. 1. A fascinating aspect of this phenomenon is that the order is not imposed by any external factor; it rather results from positive feedbacks operating at small scales, that give rise to self-organization and pattern formation at large scales. Associated with these phenomena are a few principles:

- **Symmetry breaking:** A uniform force that drives a uniform system out of equilibrium can break the spatial uniformity (or symmetry to translations) of the system and induce spatially periodic patterns. The transition to the patterned state is not gradual; spatial variability appears only beyond a critical force strength at which the stabilizing and destabilizing factors just balance one another. We call such a phenomenon a symmetry-breaking instability.
- **Universality:** Symmetry-breaking instabilities lead to patterns that are to a large extent universal. The same patterns can appear in completely different physical, chemical or biological contexts if they are induced by the same type of instability. Stripe-like patterns, for example, appear in cloud streets and in banded vegetation on hill slopes (Fig. 1a and d), although the local feedbacks that drive the common instability are obviously different.
- **Emergence:** Pattern formation is an emergent property (Anderson, 1972), that is, a property that appears at the system level, i.e. the level of clouds or patchy landscapes, and has no meaning at the level of the system's constituents (water molecules, plants). It is a bottom-up self-organization process, whereby small-scale interactions give rise to large-scale order, but large-scale pat-

tern dynamics can also feed back on small-scale interactions. Top-down processes of this kind can be interpreted as adaptive behavior of the system's constituents (Levin, 1998).

The pattern-forming instabilities that a uniform state can go through are commonly classified according to the nature of the perturbations or modes that grow from the unstable state and the new states they lead to. Thus, four main types of instabilities are distinguished:

1. *Stationary uniform instability*, in which a monotonously growing uniform mode leads to a stationary uniform state.
2. *Stationary nonuniform instability*, in which a monotonously growing nonuniform mode leads to a stationary spatial pattern.
3. *Oscillatory uniform instability*, in which a uniform mode with oscillatory growth leads to uniform oscillations.
4. *Oscillatory nonuniform instability*, in which a nonuniform mode with oscillatory growth leads to traveling waves.

The second and fourth instability types directly lead to spatial patterns as the growing modes are already spatially structured. The first and third instability types do not lead directly to spatial patterns as the growing modes are uniform. Spatial patterns can still result from these instabilities if they involve the creation of multiple stable states, for then patterns consisting of domains of different states can be formed.

The universal behavior of systems close to instability points is rooted in the mathematical theory of pattern formation. Starting from the specific equations that describe any system near an instability point, it is possible to derive new equations that look alike for all systems that share that type of instability. The new equations, often called normal form or *amplitude equations*, differ from one system to another only in the coefficients of the various terms that appear in the equations, which are expressed in terms of parameters that are specific to the system in question. This is a powerful result of pattern formation theory; the normal form equations for various instabilities have thoroughly been studied, and the identification of an instability in a particular system makes that information available at once.

3. The pattern-formation approach applied to dryland vegetation

3.1. Modelling dryland vegetation

Vegetation pattern formation is a result of positive feedbacks operating at local scale. We focus here on two important feedbacks (Gilad et al., 2007a, 2007b; Meron et al., 2007a,b). The first, illustrated in Fig. 2a, is a positive feedback between above-ground and below-ground biomass (hereafter the *root-augmentation feedback*) and is related to the root-to-shoot ratio, a characteristic trait of plant species. As a plant grows its root zone extends to new soil regions where water can be taken up from. As a result the amount of water available to the plant increases and the plant grows even further. The second feedback, illustrated in Fig. 2b, is a positive

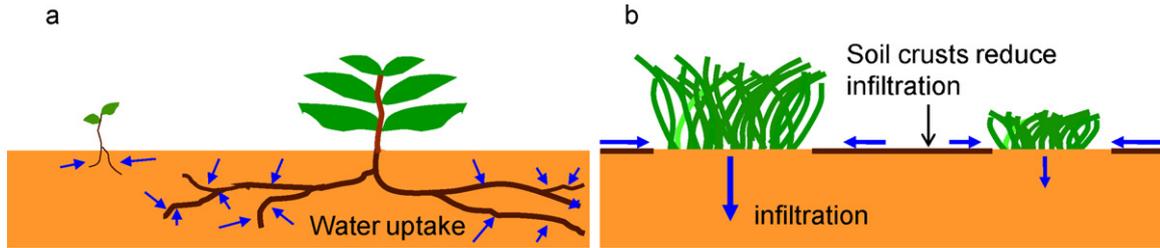


Fig. 2. Schematic illustrations of the root-augmentation feedback (a) and the infiltration feedback (b).

feedback between biomass and water (hereafter the *infiltration feedback*). Bare soils in arid regions are often covered by biological soil crusts which reduce the infiltration rate of surface water into the soil relative to the infiltration rate in vegetation patches (Eldridge et al., 2000). As a consequence vegetation patches act as sinks for runoff water generated by their crusted neighborhoods. This accelerates their growth, sharpens the infiltration contrast and increase even further the soil moisture in the patch areas. Soil erosion in bare areas and deposition in vegetation patches is another mechanism that can induce or enhance infiltration contrast (Saco et al., 2006).

Both feedbacks involve water transport towards the growing vegetation patches, and therefore provide pattern formation mechanisms, for while they help the vegetation patches grow, they inhibit the growth in the patches' surroundings. For this reason they are often referred to as mechanisms of short-range activation and long-range inhibition.¹ Positive feedbacks that do not involve water transport, such as reduced evaporation in patch areas due to shading, are not pattern forming.

Several continuum models have been proposed for studying vegetation patchiness (Borgogno et al., 2009). We choose to present here the Gilad et al. (2004, 2007a, 2007b) model because it is the only model that captures the two feedbacks discussed above, and, unlike most other models, describes satisfactorily overland water flow for arbitrary topographies by deriving it from shallow water theory. The model, hereafter the Gilad et al. model, consists of one or more biomass variables, $b_i(\vec{r}, t)$, where $\vec{r} = (x, y)$, representing species belonging to different functional groups, and two water variables, $w(\vec{r}, t)$ and $h(\vec{r}, t)$, representing the soil-water content per unit ground area and the height of a thin surface water layer above ground level, respectively. The equations for the biomass variables include diffusion-like terms which account for clonal growth or short-distance seed dispersal. The model equations have already been presented and described in detail in earlier publications (Gilad et al., 2007a, 2007b). We refer the reader to these earlier works and limit the discussion here mostly to the manner by which the root-augmentation and the infiltration feedbacks are modelled.

The root-augmentation feedback is captured by representing the spatial extents of the root zones of plants located at a point \vec{r} by means of a localized kernel function

$$g\left(\frac{|\vec{r} - \vec{r}'|}{S}\right),$$

whose width, $S = S_0(1 + \eta b + \dots)$, grows monotonously with the above ground biomass, $b(\vec{r}, t)$. The root-to-shoot ratio can then be quantified by the parameter $\eta = S_0^{-1} dS/db|_{b=0}$. Gilad et al. (2004, 2007a) have used a Gaussian function for the kernel g , but other

forms can be considered (Barbier et al., 2008). The infiltration feedback is captured by assuming an increasing biomass dependence of the infiltration rate of the form (Gilad et al., 2007a, 2007b; Rietkerk et al., 2002):

$$I(\vec{r}, t) = A \frac{b(\vec{r}, t) + Qf}{b(\vec{r}, t) + Q},$$

where A and Q are constant parameters and f is another parameter representing the infiltration contrast. The value $f=1$ corresponds to an infiltration rate which is biomass independent, $I=A$, i.e. no infiltration contrast between bare soil and vegetated area. This case may approximate sandy soils. Small values, $f \ll 1$, on the other hand represent high infiltration contrasts: low infiltration rate in bare soil, $I(0) = Af$, and high infiltration rates in vegetated patches that asymptote to $I(\infty) = A$.

The parameters η and f quantify the strengths of the root-augmentation and infiltration feedbacks and therefore strongly affect the system's spatial behavior. Another significant parameter is the precipitation or rainfall rate p , which, in general, is time dependent. However, when the characteristic growth time of the vegetation is significantly longer than the time scales of rainfall variability, the vegetation responds to the time-average precipitation and p can be taken as a constant parameter. Woody vegetation, for example, grows slowly compared to seasonal variability and in that case p can represent the annual rainfall. In the following we will consider p to be constant, disregarding inter-annual rainfall variability. We refer the reader to Kletter et al. (2009) for an analysis of a time-dependent intermittent rainfall. On a slope, a topography function, $\zeta(\vec{r})$, measuring ground level height at a point \vec{r} , should be specified.

It is worth noting that the information that is used in building a continuum model pertains to small spatial scales, within a single patch, and to low organization levels, mostly the organism level, while the information that is extracted from the model pertains to large landscape scales and to high organization levels – population, community and ecosystem. Once the model has been built, solving it numerically requires specifying initial conditions, that is, initial spatial distributions of the biomass and water variables. The solutions then provide the spatial distributions at any time in the future.

3.2. Vegetation pattern formation

Vegetation pattern formation is the manner by which dryland vegetation can cope with water deficit. It does so by increasing water availability to vegetation patches at the expense of their neighborhoods. Depending on rainfall rate, soil properties, species traits, topography, consumer pressure and other factors, different spatial patterns are formed. The pattern formation approach provides an invaluable tool for investigating these patterns.

Consider first the Gilad et al. model for a single species, with biomass b , that may represent woody vegetation. The simplest model solutions are time-independent, spatially uniform solutions. There are two solutions of that kind representing bare soil ($b=0$)

¹ An alternative terminology that is often used is short-range facilitation and long-range competition. While the long-range inhibition is generally due to competition (over a limiting resource), the short-range activation is not necessarily associated with facilitation. We therefore prefer the terms activation and inhibition over facilitation and competition.

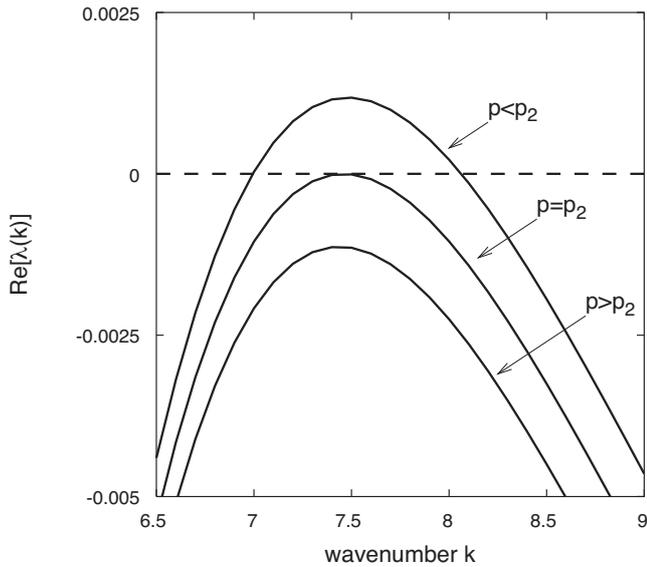


Fig. 3. Stationary nonuniform instability of uniform vegetation. A result of linear stability analysis of the Gilad et al. model showing the growth rates of sinusoidal perturbations with different wave numbers. Above a critical precipitation, p_2 , all perturbations have negative growth rates and uniform vegetation is stable. Slightly below p_2 , a narrow band of wave numbers have positive growth rates, implying an instability to a vegetation pattern. From Gilad et al. (2007a).

and uniform vegetation. The first question pattern-formation theory motivates concerns the stability of these uniform solutions. A uniform state is *linearly stable* if any infinitesimally small perturbation, uniform or non-uniform, decays to zero in the course of time. It is linearly unstable if there exists a perturbation that grows in time. The dynamics of small perturbations are studied by means of *linear stability analysis*. Applying such an analysis to the uniform vegetation state, for plane topography, provides the result shown in Fig. 3 (Gilad et al., 2004, 2007a). The figure shows the growth rates of sinusoidal perturbations with different wavelengths λ or wave numbers $k = 2\pi/\lambda$. Since any perturbation can be represented as a sum of sinusoidal perturbations with different wave numbers (i.e. as a Fourier series), the decay of any sinusoidal perturbation implies the linear stability of the uniform state. This is the case for $p > p_2$ in which the growth rate is negative for any k . At $p = p_2$, however, there is a critical wave number, k_c , for which the growth rate is zero. Slightly below that precipitation rate, $p < p_2$, perturbations with wave numbers k_c and nearby wave numbers grow in time, rendering the uniform vegetation unstable. This is a stationary nonuniform instability (see Section 2) that leads to a stationary pattern state. We note that if we remove the two pattern-forming feedbacks, root-augmentation and infiltration, by setting $\eta = 0$ and $f = 1$, the instability disappears and the uniform vegetation state remains stable whenever it exists.

A linear stability analysis applied to the bare-soil uniform state reveals that it is stable at sufficiently small precipitation rates but becomes unstable in a stationary uniform instability (see Section 2) at a critical value, $p = p_c$ with $p_c < p_2$. At this instability point the uniform vegetation state appears but it is already unstable (unless $\eta = 0$ and $f = 1$) and therefore a pattern state appears. Fig. 4 summarizes the results described for the uniform solutions (Gilad et al., 2004, 2007a). It displays the uniform solutions as functions of the precipitation rate with the convention that solid line represents linearly stable solutions, and dashed and dotted lines represent solutions that are unstable to uniform and non-uniform perturbations, respectively. A diagram of this kind is called a *bifurcation diagram*.

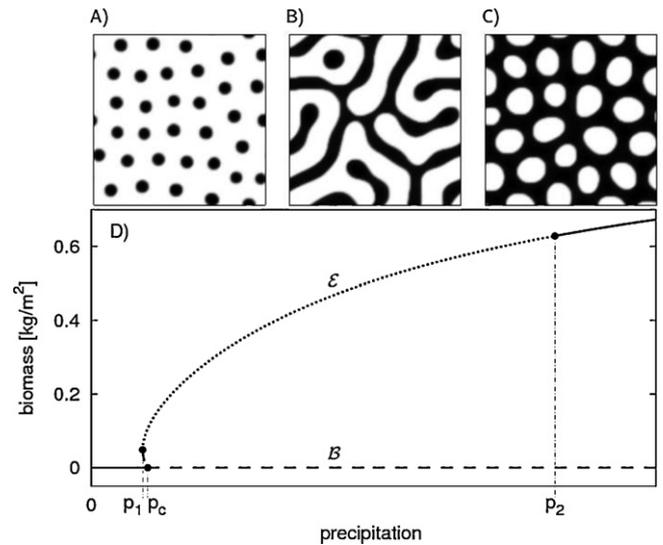


Fig. 4. A bifurcation diagram for stationary uniform solutions of the Gilad et al. (2007b) model. Solid lines represent linearly stable solutions, dashed lines represent solutions that are unstable to uniform perturbations, and dotted lines represent solutions that are unstable to nonuniform perturbations. Bare soil (B) is stable at low precipitation rates ($p < p_c$) whereas uniform vegetation (ϵ) is stable at high precipitation rates ($p > p_2$), as the solid lines indicate. In between stable pattern states exist, examples of which are shown in panels A–C. Dark shades of gray represent high biomass. From Gilad et al. (2007a).

A second question pattern-formation theory motivates is what pattern states appear along the rainfall gradient and are they necessarily regular periodic patterns? The insets in Fig. 4 show numerically computed pattern solutions along the precipitation axis for a plane topography. The uniform vegetation state destabilizes at $p = p_2$ to a periodic gap pattern consisting of a hexagonal array of gaps in uniform vegetation. At lower precipitation rates a new regular pattern state appears, consisting of vegetation stripes. Depending on initial conditions, periodic stripe patterns or labyrinthine patterns are formed. At yet lower precipitation rates a periodic spot pattern appears, consisting of a hexagonal array of vegetation spots (Gilad et al., 2004, 2007a). On a slope, a similar solution structure holds with two major differences. First, stripes are oriented perpendicular to the slope because this way they intercept more runoff water. Second, they can migrate uphill, as most of the runoff is intercepted at the top part of the stripe, while the bottom part losses runoff to the next lower stripe (Gilad et al., 2007a; Sherratt, 2005). Note that in plane topography the stripes often assume the form of labyrinthine patterns; in the absence of a preferred direction random initial conditions induce different orientations at different locations. An instability of stripe patterns to transverse modulations, i.e. to wavy modulations of the stripes (Cross and Hohenberg, 1993) can enhance the labyrinth nature of the patterns. The full bifurcation structure of these periodic pattern solutions has not been evaluated yet.

The overall picture that has emerged so far is of five basic vegetation states along the rainfall gradient: uniform vegetation at high rainfall rates, periodic gap, stripe and spot patterns at decreasing rainfall rates, and bare soil at low rainfall rates. This sequence of basic vegetation states is consistent with field observations (Deblauwe et al., 2008; Valentin et al., 1999), although many more patterns are observed too. Indeed, the Gilad et al. model, as well as other models, predict a wide variety of vegetation states in precipitation ranges where two stable basic states coexist. Such *bistability* ranges are found between any pair of consecutive states: bare-soil and spots, spots and stripes, stripes and gaps and gaps and uniform vegetation. In these ranges spatial mixtures of the different states

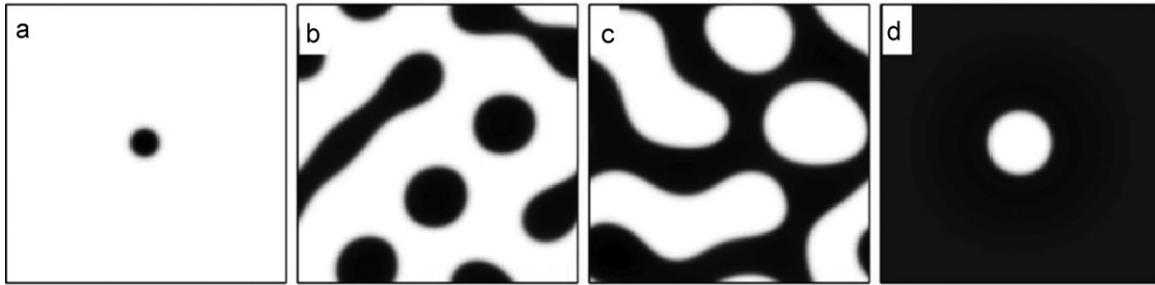


Fig. 5. Mixed patterns predicted by the Gilad et al. model. Shown are numerical solutions of the model equations in bistability ranges of bare soil and spots (a), spots and stripes (b), stripes and gaps (c) and gaps and uniform vegetation (d). Darker gray shades denote higher biomass. From Kletter et al. (2011).

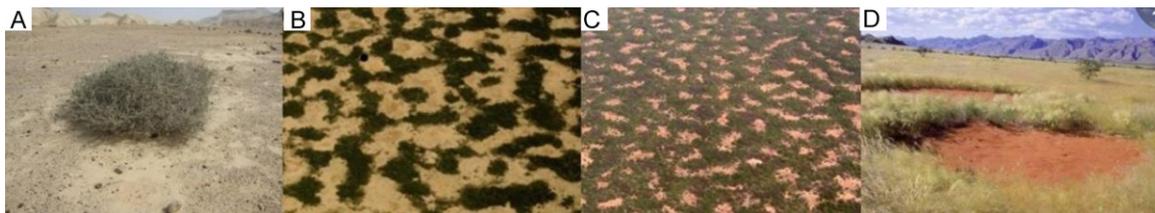


Fig. 6. Mixed patterns in nature: an isolated shrub patch in the northern Negev, Israel (A), mixture of spots and stripes of woody vegetation in Niger (B), mixture of stripes and gaps of woody vegetation in Niger (C), and isolated gaps in the pro-Namib zone of the west coast of southern Africa (D). From Rietkerk et al. (2002) (B and C) and Tlidi et al. (2008) (D).

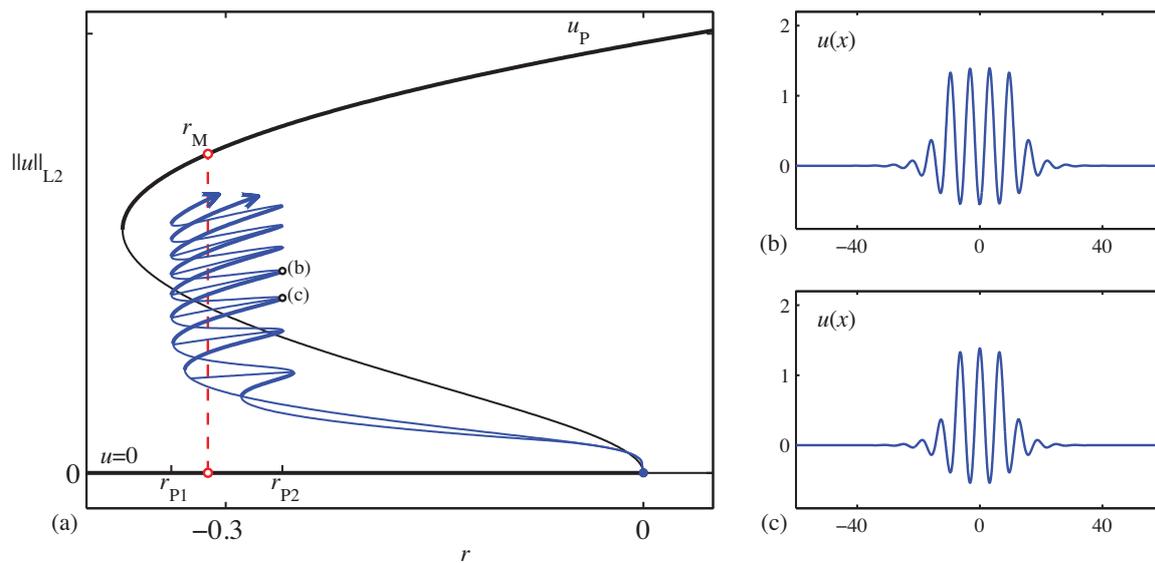


Fig. 7. Homoclinic snaking in the Swift–Hohenberg model. A bifurcation diagram showing intermediate solutions in a bistability range of uniform, $u = 0$, and pattern states $u = u_p$ (a). The intermediate solutions describe localized structures with even (b) and odd (c) numbers of humps. Thick (thin) lines denote stable (unstable) solutions. The parameter range $r_{p1} < r < r_{p2}$ is called the homoclinic snaking range. Courtesy of John Burke.

can form a variety of *irregular* stable patterns (Meron et al., 2004) as Fig. 5 illustrates. Fig. 6 shows similar types of mixed patterns in nature.

The mathematical theory of spatially mixed patterns in bistable systems is far from being complete. However, significant progress has been made recently in the case of bistability of uniform and spatially periodic states. Fig. 7 shows a bifurcation diagram for a simple pattern-formation model, the Swift–Hohenberg equation,² that has a bistability range of a uniform zero state and a periodic pattern.

Apart of the zero solution and the periodic solution there are many intermediate solutions representing spatial mixtures thereof, some of them are shown in the figure (the blue lines). (For interpretation of the references to color in the text, the reader is referred to the web version of the article.) They correspond to localized structures consisting of confined domains of the periodic pattern in a background of the zero state. There are two families of such localized solutions, one with an even number of humps and one with an odd number of humps. The solution families “snake” upward, giving rise to a

² The Swift–Hohenberg equation reads $u_t = ru + bu^2 - u^3 - (\partial_x^2 + k_0^2)u$, where r , b and k_0 are parameters. It can be regarded as the simplest model that captures a

stationary non-uniform instability. In this model the instability destabilizes the zero state, $u = 0$ to a stationary periodic pattern with wave number k_0 .

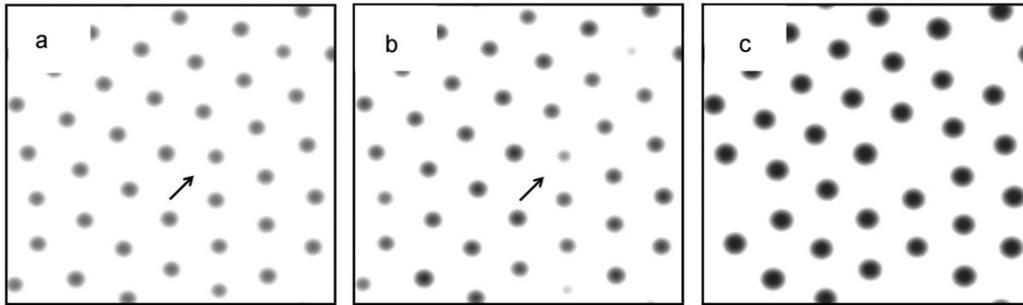


Fig. 8. Transition from a periodic spot pattern to a hole pattern in a bistability range of uniform bare soil and a periodic spot pattern. The transition was induced by a biomass-removal disturbance, uniform across the pattern. Lighter shades of gray denote lower biomass. Time proceeds from left to right. Panel (a) shows the initial disturbed periodic pattern, while panel (c) shows a nearly asymptotic hole pattern whose biomass has recovered except for a few “holes” where the original spots have decayed. The arrows in panels (a) and (b) point towards one of the decaying spot. The patterns were computed using the model introduced by von Hardenberg et al. (2001).

multitude of stable localized structures of increasing sizes. In addition, there is also a multitude of stable “hole solutions”, consisting of holes of increasing sizes in otherwise periodic patterns. Beyond that, there are also stable solutions consisting of several localized structures of various sizes, or of several holes of various sizes, or of combinations of localized structures and holes (Knobloch, 2008).

This mathematical observation, known as *homoclinic snaking*, appears valid, with some variations, for any system in a bistability range of a uniform and a pattern state. It has been observed in various physical contexts, including nonlinear optical systems, convective systems, and magnetic systems (see Burke and Knobloch (2007), Knobloch (2008) and references therein). In particular it applies to the bistability ranges of bare soil and spots and of uniform vegetation and gaps (Tlidi et al., 2008), as the localized solutions in Fig. 5a and d suggest.

These results of pattern formation theory motivate yet another question, pertaining to the nature of transitions between alternate stable states or “catastrophic shifts” (Rietkerk et al., 2004, Scheffer et al., 2001). The common view is of an abrupt transition between the two states in response to a gradual environmental change. This view has been applied to the context of dryland vegetation for explaining desertification. Implicit in this approach is the assumption that the two alternate stable states are spatially uniform, but that is not generally the case because uniform vegetation and bare soil are not adjacent states along the rainfall gradient or along any other environmental gradient. A transition to bare soil is likely to occur from the spot-pattern state and therefore the complex structure of intermediate states due to homoclinic snaking must be taken into account.

The multitude of intermediate states in the bistability range of bare soil and a periodic spot pattern suggests that desertification may not necessarily be abrupt, but rather a gradual process. Fig. 8 shows numerical simulations of the vegetation model introduced by von Hardenberg et al. (2001) in a bistability range of an hexagonal spot pattern and uniform bare soil. The initial state (panel (a)) consists of a nearly hexagonal spot pattern, which is perturbed by uniform partial biomass removal, visualized in the figure as a lighter gray shade. The system responds to the initial perturbation by the decay of several spots, as the arrows indicate. The decay occurs where spots are closer to one another due to (penta-hepta) defects in the (hexagonal) periodic pattern. The final pattern has recovered from the perturbation, as the darker shades of gray in panel (c) imply, but contains “holes” at the locations where spots have decayed. Periodic patterns with holes are among the multitude of intermediate states that exist in the bistability range of uniform and pattern states. Thus, rather than recovering the original spot pattern or decaying to bare soil, the system has relaxed to one of the many available intermediate states.

The variety of patterns discussed so far share one property – they all have a characteristic length scale, whether it is the width of a stripe, the size of a spot or the size of a gap. Recent field studies (Kéfi et al., 2007; Scanlon et al., 2007), however, have reported the observations of patterns with wide patch-size distributions, lacking any characteristic length. Can continuum models account for scale-free patterns of this kind too? Studies of the Gilad et al. model have unraveled biotic and abiotic circumstances under which scale-free patterns emerge as a pattern formation phenomenon. We refer the reader to von Hardenberg et al. (2010) for more details and state here only the main result. Scale-free patterns can develop when the spatial distribution of the water resource is fast relative to processes that exploit or absorb it (Manor and Shnerb, 2008). Two realizations of this condition have been identified, fast surface-water flow relative to the infiltration of surface water into the soil, and fast soil-water diffusion relative to water uptake by plant roots. The first realization is likely to apply to species whose patch sizes are relatively small, such as perennial grasses, and to conditions of strong runoff generation, such as high infiltration contrast and slope. The second realization may apply to woody vegetation in sandy soil.

3.3. Mechanisms of species-diversity change

Dryland vegetation generally involves two major functional groups, woody and herbaceous vegetation. While the woody vegetation often includes only a few species, the herbaceous vegetation may consist of tens or even hundreds of species, depending on the areas considered (Boeken and Shachak, 2006). Since pattern-formation processes of the woody vegetation involve redistribution of the water resource, they may have a significant impact on the diversity of the herbaceous vegetation, and therefore should be taken into account in species-diversity studies. In the following we describe how the Gilad et al. model can be used to study mechanism of species-diversity change associated with vegetation pattern formation.

We use the two-species version of the model with b_1 and b_2 representing the woody and the herbaceous functional groups, respectively. The two functional groups can be distinguished in the model by choosing much higher growth and mortality rates for the herbaceous species and much larger maximum standing biomass for the woody species. This choice of parameters introduces a strong asymmetry; the woody vegetation has a dominant role in the pattern-formation process, whereas the herbaceous vegetation mostly responds to the landscape induced by the woody vegetation without affecting it significantly.

Calculating the existence range of spatially uniform steady states and their stability properties for a woody–herbaceous system we have obtained (Gilad et al., 2007b) the bifurcation diagram

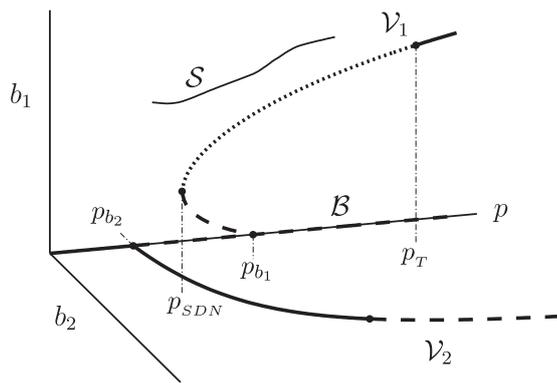


Fig. 9. A bifurcation diagram showing stationary uniform and pattern solutions of a two-species version of the Gilad et al. (2007b) model that describes a woody–herbaceous system. The solution branches B , v_1 and v_2 represent, respectively, uniform bare soil, uniform woody vegetation and uniform herbaceous vegetation. The branch S represents the amplitudes of spots patterns. Solid lines represent stable solutions, and dashed and dotted lines represent solutions unstable to uniform and non-uniform perturbations, respectively. From Gilad et al. (2007b).

shown in Fig. 9. The bare-soil state, B ($b_1 = b_2 = 0$), is stable at low precipitation rates p , but becomes unstable to uniform herbaceous vegetation, v_2 ($b_1 = 0, b_2 \neq 0$), or “grassland”, as p exceeds a threshold value p_{b_2} . The grassland state remains stable up to a second threshold (the beginning of the dashed part of the grassland branch), where an unstable, uniform mixed woody–herbaceous state appears (not shown in the figure). At significantly higher precipitation, uniform woody vegetation, v_1 , becomes stable, but in the intermediate range stable pattern states prevail. Shown in the figure is a numerically calculated solution branch, S , describing a spot pattern of the woody species, representing a “shrubland”. At the high and very low ends of this branch the pattern consist of the woody species only, but the middle part of the branch describes a shrubland with herbaceous vegetation growing understory – a nursing effect to be addressed below.

An important point to stress in Fig. 9 is the existence of a bistability range where both the spot pattern solution, S , and the solution describing uniform herbaceous vegetation, v_2 , are stable. In that range a variety of stable mixed patterns are expected to exist, due to homoclinic snaking, including savanna-like patterns, that is, scattered woody patches in a grassland (see Fig. 11). The association of savanna-like patterns with bistability of woody spot pattern and uniform herbaceous vegetation suggests the possible existence of a simple, general criterion for savanna-like patterns that is met by many of the mechanisms that have been proposed for such patterns (House et al., 2003). This suggestion can be tested by studying continuum models that capture these mechanisms and searching for bistability ranges of S and v_2 solution types.

To better understand the nursing effect of woody patches on herbaceous vegetation let us focus for a moment on a system consisting of a woody species alone. Associated with the biomass patterns are soil-water patterns, and depending on the precipitation the two type of patterns can correlate or anti-correlate, as Fig. 10b and c demonstrate (Gilad et al., 2004, 2007a; Meron et al., 2007a,b). At high precipitation (c) the soil-water content, w , in the woody patch is lower than away from the patch, anti-correlating with the biomass distribution, whereas at low precipitation (b) it is higher in the patch area and correlates with the biomass. The crossover from water depletion to water concentration in the patch area, as the precipitation rate decreases (a), can be understood as follows. Two processes strongly affect the water balance in the patch area, infiltration of surface water, which acts to increase the water content, and water uptake by the plants’ roots, which

acts to deplete it. Let us examine how each of these processes changes with precipitation. Since the patch area decreases significantly as the precipitation is decreased, the water uptake from any unit area in the patch decreases significantly. By contrast, although the biomass decreases too, the infiltration rate hardly decreases. The reason is the saturated growth of the infiltration rate at high biomass values and the slow approach to the asymptote $I(\infty) = A$. Thus, as the precipitation decreases, the loss of soil water per unit area of the vegetation patch decreases significantly while the water gain remains almost unchanged. This tilts the balance between the two processes and induces the crossover shown in Fig. 10a.

A possible response of the herbaceous vegetation to the soil-water pattern induced by the woody vegetation is shown in Fig. 10d and e. At high precipitation the woody species excludes the herbaceous species from its neighborhood, allowing its growth only in the open area away from the woody patch (e). By contrast, at low precipitation the woody species ameliorates its patch area and creates a micro-habitat for the herbaceous vegetation understory (d). Transitions of this kind, i.e. from competition to facilitation along rainfall gradients, have been observed in field studies (Holzapfel et al., 2006; Pugnaire and Luque, 2001). The distinctive ability of an organism not only to respond to its physical environment but also to modify it so as to create habitats for other species has been termed ecosystem engineering (Jones et al., 1994, 1997). This model study therefore suggests that plants can act as ecosystem engineers and identifies biotic and abiotic conditions under which engineering develops. It further suggests that the engineering capacity of woody plants can buffer species-diversity loss along rainfall gradients.

This example demonstrates the utility of the pattern formation approach in unraveling mechanisms of species diversity change. The tilted balance between surface-water infiltration and soil-water uptake along a rainfall gradient would be hard to deduce without the application of the pattern-formation approach to a continuum model. This mechanism may not be the only factor at work, nor even the most significant one in all field realizations of transitions from competition to facilitation along environmental gradients. Soil-moisture increase because of reduced evaporation and transpiration, and nutrient-concentration increase because of litter decomposition, are among the additional factors that ameliorate the micro-environments formed by woody patches and contribute to facilitation in stressed environments (Bruno et al., 2003; Callaway and Walker, 1997; Holmgren et al., 1997). However, the effects of reduced patch size in a woody spot pattern on the spatial distribution of soil water, and thus on the diversity of herbaceous vegetation, can be significant and should be considered, along with other factors, in studies of facilitation along environmental gradients.

Transitions from competition to facilitation can also be induced at constant precipitation by increasing the woody-patch density (Gilad et al., 2007b). Patterns of highly dense as well as sparsely scattered woody patches can be realized in the bistability range of periodic spot patterns and uniform herbaceous vegetation. As Fig. 11 shows, in the case of sparse woody patches the herbaceous species is excluded from the woody patches and grows in the open area only (a), whereas in the case of dense woody patches the growth of the herbaceous species is facilitated by the woody species and occurs understory (b). The mechanism is similar to that described for a single patch along a precipitation gradient, except that the decline in soil water is due to higher uptake in dense patterns and not due to lower precipitation.

This observation suggests another mechanism of species diversity change, associated with nonuniform dilution of woody patches in a bistability range of uniform herbaceous vegetation and a periodic spot pattern consisting of mixed woody–herbaceous patches. The two types of vegetation states and various spatial mixtures thereof, differ in the niches they form for herbaceous

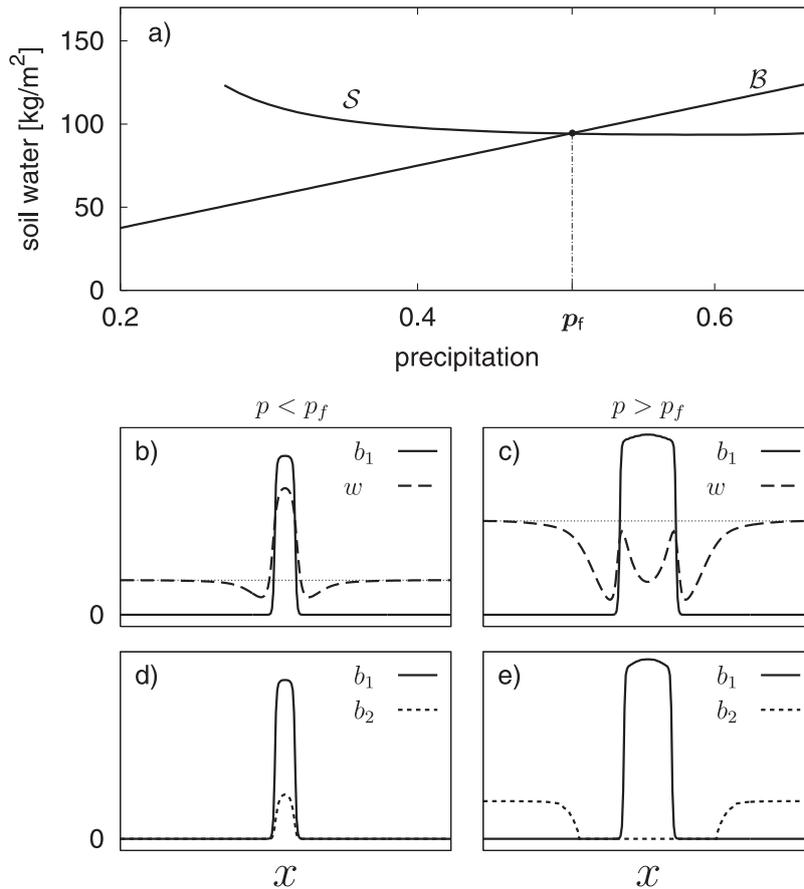


Fig. 10. Model solutions for a woody–herbaceous system, showing a transition from competition to facilitation as precipitation decreases. The lines B , and S in panel (a) show, respectively, the soil-water content (per unit ground area) in bare soil and in a woody (b_1) patch as functions of precipitation, in the absence of herbaceous vegetation, b_2 . Above (below) a threshold precipitation p_f , the water content under the woody patch is lower (higher) than in bare soil, implying competition (facilitation). Examples of soil-water distributions, $w(x)$, above and below p_f are shown in panels (b) and (c) respectively. Possible responses of the herbaceous vegetation to the soil-water distributions are shown in panels (d) and (e). From Gilad et al. (2007b).

vegetation. Consider for example herbaceous species that differ from one another with respect to two traits, tolerance to shading and tolerance to grazing (Gilad et al., 2007b). These species can be divided into three groups: (i) species that are intolerant to both shading and grazing, (ii) species intolerant to shading but tolerant to grazing, (iii) species intolerant to grazing but tolerant to shading. A landscape consisting of a periodic dense pattern of woody patches will accommodate only group (iii), while an open-area landscape, free of woody patches, will accommodate only group (ii). However, in the bistability range of both landscape types all three groups can be accommodated by appropriate removal and dilution of woody patches. In this range there exist stable spatially mixed patterns that contain three different habitats as Fig. 12 illustrates: areas of dense woody patches accommodating group (iii), open areas accommodating group (ii), and open areas enclosed by dense woody patches that restrict grazers access and therefore accommodate group (i). Mathematically, areas of dense woody patches surrounded by open areas correspond to solutions describing localized structures, whereas open areas enclosed by dense woody patches correspond to solutions describing combinations of localized structures with holes in periodic patterns (see Section 3.2).

We stress that bistability of uniform herbaceous vegetation and a periodic spot pattern is a necessary condition for the coexistence of the three groups of herbaceous species. In a higher precipitation range where the spot pattern is the only stable solution, multi-species patterns as in Fig. 12 will converge in the course of time

to a single herbaceous species, residing in the woody patches, or to no herbaceous vegetation at all. The bistability condition, however, is not a sufficient condition, because the solution branches of localized structures and holes in periodic patterns may occupy only part of the bistability precipitation range (see Fig. 7). Identifying the biotic and abiotic conditions that control the size of these solution branches, is a significant open problem that can be addressed with continuum models.

3.4. Rehabilitation of degraded vegetation

A common rehabilitation practice of degraded vegetation on hill slopes is based on runoff harvesting by means of parallel contour bunds or embankments that intercept water runoff and along which the vegetation is planted. The optimal distance between adjacent bunds, however, is unknown, nor their minimal effective depth. Since under favorable rainfall conditions the vegetation tends to self-organize in banded patterns anyway, restoring vegetation by runoff harvesting is a resonance problem, the spatial counterpart of time-periodic forcing of oscillatory systems, in which the bunds provide the periodic force. Resonant response in this context means the success of the system to follow the spatial pattern even if there is a mismatch between the forcing pattern and the pattern that the unforced system tends to form.

Little is known about this spatial resonance problem, but recent studies of the Swift–Hohenberg equation subjected to a parametric

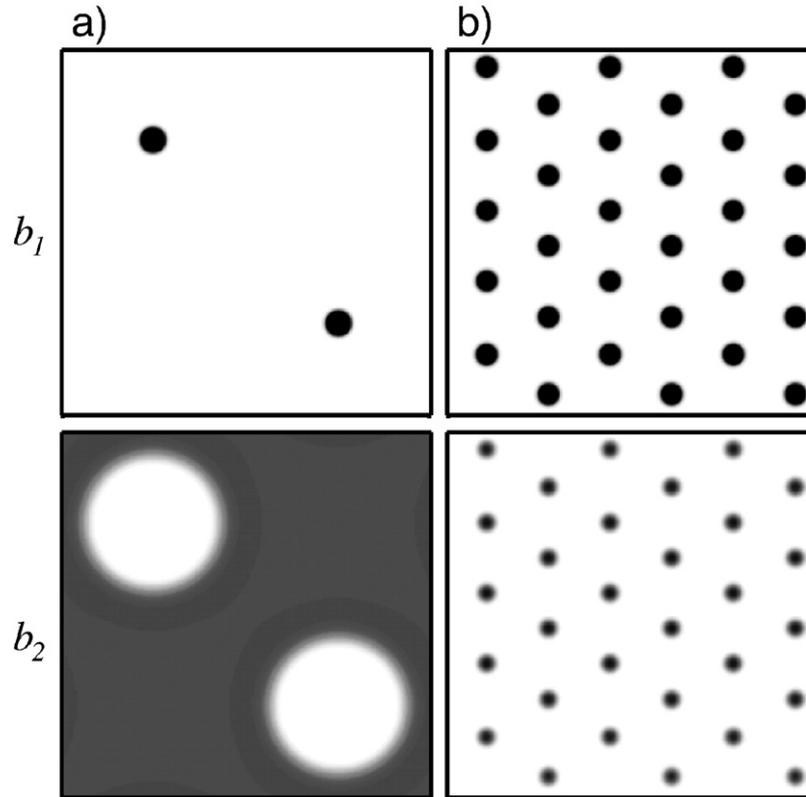


Fig. 11. Transition from competition to facilitation in woody (b_1) – herbaceous (b_2) system, induced by a change of woody-patch density in a bistability range of uniform herbaceous vegetation and a woody spot pattern. At low density herbaceous vegetation grows in the open areas (a), while at high density understory (b). Darker gray shades denote higher biomass. From Gilad et al. (2007b).

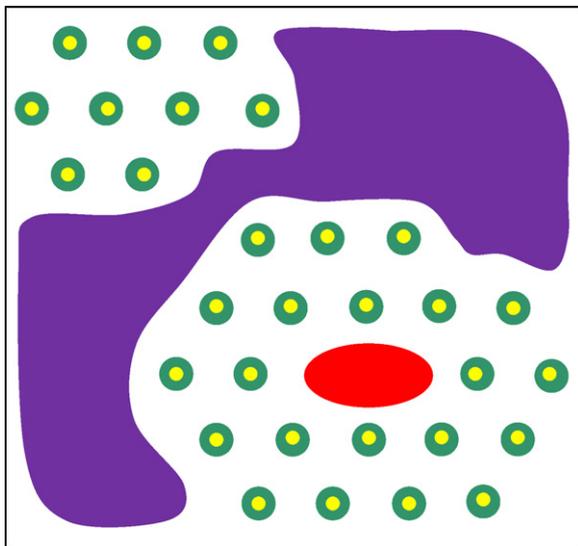


Fig. 12. Schematic illustration of herbaceous-species coexistence in a bistability range of uniform herbaceous vegetation and periodic woody spot pattern (green spots). The variety of intermediate patterns in this range provides niches for herbaceous species that are intolerant to both shading and grazing (red open area), intolerant to shading but tolerant to grazing (purple open area), and tolerant to shading but intolerant to grazing (yellow spots understory of woody patches). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

spatially periodic weak force, shed some light on the intricate nature of vegetation restoration (Manor et al., 2008, 2009). Applying a stripe-like forcing pattern, with a forcing wave-number k_f (or wavelength $\lambda_f = 2\pi/k_f$), to a system that supports stripe patterns with wave-numbers centered around k_0 , does not necessarily reinforce stripe patterns, even if k_f is close to k_0 . Instead, two-dimensional oblique and rectangular patterns generally form as Fig. 13 shows. This surprising response of the system is related to the type of forcing, parametric or multiplicative rather than additive, and to the freedom of a two-dimensional system to respond in a direction perpendicular to the forcing. The forcing exerted by the parallel bunds results in periodic soil-water concentration which affects the biomass growth rate, and is therefore a form of parametric forcing. The parametric forcing favors a resonant response at a wave-number $k_f/2$. As a consequence, the system locks its wave-vector component in the forcing direction, x , to one-half of the forcing wave-number, $k_x = k_f/2$, and compensates for the unfavorable wave-number by building a wave-vector component, k_y , in the orthogonal direction, y , forming a two-dimensional pattern.

The view of vegetation restoration as a spatial resonance problem can be pursued using continuum vegetation models that are subjected to spatially periodic forcing. The forcing can be simulated by modulating the topography function, $\zeta(\vec{r})$, or the infiltration rate $I(\vec{r})$. Such studies may prove invaluable in devising cost-effective restoration practices. The practices currently used involve strong forcing, i.e. substantial landscape modulations, which are costly. Can practices involving weak landscape modulations, such as periodic soil-crust removal, achieve the same goal? Studies addressing this question require the application of pattern-formation theory, for, as discussed above, the response of the vegetation to the weak forcing may not be trivial.

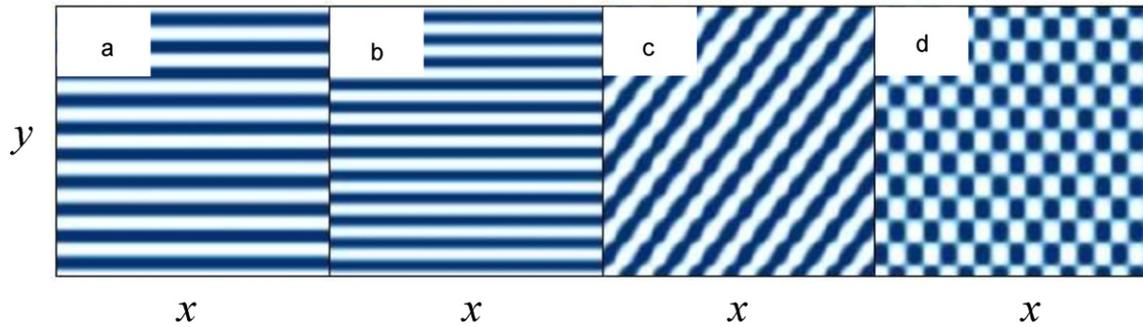


Fig. 13. Two-dimensional response to a one-dimensional spatial force in the Swift–Hohenberg equation. A system that supports a stripe pattern with wave-number k_0 (a), responds to a stripe-like force with a wave-number $k_f = 1.2k_0$ (b), by forming an oblique pattern when the force is sufficiently weak (c), or a rectangular pattern with stronger force (d). Both two-dimensional patterns are resonant since their wave-vector components in the forcing direction are exactly half the forcing wave number. Adopted from Manor et al. (2008).

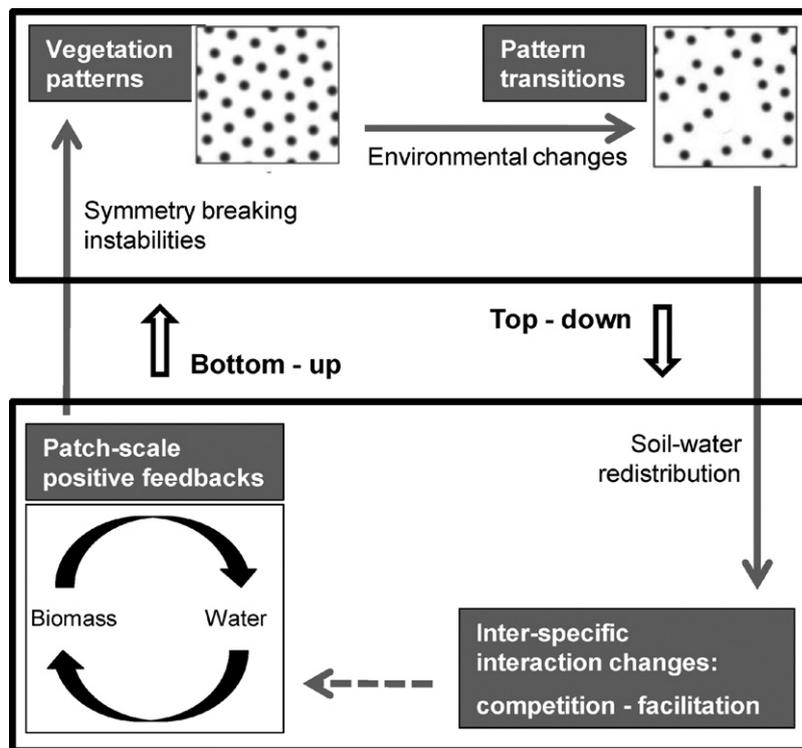


Fig. 14. Examples of bottom-up and top-down processes that are captured by the pattern-formation modelling approach. Local biomass–water feedbacks (lower frame) can induce symmetry-breaking instabilities that lead to vegetation pattern formation at the landscape scale (upper frame). Environmental changes at the landscape scale induce transitions to other alternate stable vegetation patterns (upper frame). These pattern transitions change the local soil–water distributions and thereby affect inter-specific interactions (lower frame). In woody–herbaceous systems these interaction changes may induce transitions from competition to facilitation. In other systems they may feed back on vegetation pattern formation (dashed arrow).

4. Added values of the pattern-formation approach

4.1. Universality

Nonlinear dynamical phenomena are to a large extent universal. Synchronized oscillations, chaotic dynamics and catastrophic shifts are all examples of universal behaviors shared by many different systems. Unraveling the nonlinear elements that are responsible for universal behavior in a given system is important because it helps associating the system with known and often well understood dynamical behaviors. Modelling approaches which make these elements transparent are therefore advantageous over other approaches.

Instabilities are the most fundamental elements responsible for universal behavior. This is grounded in the mathematical theory of normal forms which associates a set of characteristic dynamical

equations with each instability type, and provides the machinery of deriving these equations from any continuum model that contains this type of instability. Continuum models lend themselves to stability analyses and thereby allow the identification of instabilities and their normal forms.

Another mathematical construct that contains universal information and is particularly relevant to the subject of this paper is the existence of two alternate stable states of which one state is not spatially uniform. This is the case of desertification; continuum models of dryland vegetation have unraveled bistability ranges of uniform bare-soil state and a spot-pattern state (von Hardenberg et al., 2001; Gilad et al., 2004). Linking this finding with independent studies of simple pattern-formation models, such as the Swift–Hohenberg model (Knobloch, 2008), suggest at once that desertification may not be an abrupt transition, but rather a gradual process involving dynamics across

the multitude of intermediate states that exist between the bare-soil and the spot-pattern states (see Section 3.2). Bistability range of uniform and pattern states is also realized in woody–herbaceous systems. The multitude of intermediate patterns in this range accounts for savanna-like patterns (see Section 3.3). Whether this is a universal mechanism of savanna landscapes is an interesting open question that can be studied by modelling the various mechanisms that have been proposed for savanna landscapes and identifying possible bistability ranges of uniform herbaceous vegetation and woody spot patterns.

It is important to stress that continuum models contain important non-universal information as well. For example, the identification of a stationary non-uniform instability of uniform vegetation implies the appearance of biomass patterns of a universal form (hexagonal gap patterns). Soil-water patterns will also assume that universal form, but the relations between the biomass and soil-water patterns depend on elements which are system-specific – the relative strengths of the infiltration and root-augmentation feedbacks.

4.2. Aspects of complex systems

Ecological systems generally involve processes occurring across different length scales and across different trophic and organizational levels. Two aspects of such processes are particularly significant, the emergence of new properties in bottom-up processes, and the adaptation of the system's constituents to environmental changes in top-down processes. Both the individual-based and the pattern-formation modelling approaches capture these two aspects, but differ in the description of the system's constituents. In individual-based modelling the constituents are individuals plants or other organisms, whereas in pattern-formation modelling the constituents are eco-physical processes, occurring locally at small spatial scales, such as water flow, infiltration of surface water, water uptake by plants' roots, biomass growth, etc.

Vegetation pattern formation is an example of a bottom-up process, whereby positive feedbacks operating at local scales leads to the emergence of periodic patterns at landscape scales. Changes of local woody–herbaceous interactions as a result of rainfall variability or consumer pressure is an example of a top-down process whereby induced woody-pattern transitions at the landscape scale change the local soil-water distribution and, consequently, the colonization of herbaceous vegetation. Fig. 14 provides a schematic illustration of these bottom-up and top-down processes.

The pattern-formation approach provides a powerful tool for studying these and other processes across different length scales and organization levels. Since continuum pattern-formation models are amenable to mathematical analysis they can be used not only to simulate various scenarios of ecosystem dynamics, but also to elucidate mechanisms of such complex processes.

4.3. Integrative framework

Ecology, as an empirical science, has branched into many research fields according to the hierarchical levels and spatio-temporal scales the empirical studies have addressed. As a result, many subdisciplines have emerged, including population ecology, community ecology, ecosystem ecology, landscape ecology, and restoration ecology. Since ecosystem dynamics generally proceed across different organization and trophic levels, and involve different length and time scales, integrative studies that cross the boundaries between these subdisciplines are needed. Indeed, increasing research efforts have been devoted recently to the integration of community and ecosystem ecology (Jones

and Lawton, 1995; Loreau, 2010). Likewise, efforts to incorporate spatial heterogeneity in community dynamics, thus integrating community and landscape ecology, are ongoing (Holyoak et al., 2005; Ritchie, 2010).

We suggest here that the pattern-formation approach to ecology can provide a framework that integrates landscape ecology with other subdisciplines, such as population, community and ecosystem ecology, as well as conservation and restoration ecology. It does so by resolving the ecological and physical processes occurring locally, which are the elements that go into the models, and by providing analytical and numerical tools for upscaling these processes to landscape scales. Thus, the emergence of vegetation patterns from local water-biomass feedbacks integrates aspects of population, ecosystem and landscape ecology. The emergence of rainfall dependent inter-specific interactions in woody–herbaceous systems, the dependence of these interactions on woody patch density and the implications for the coexistence of different herbaceous species, integrates aspects of community, ecosystem and landscape ecology. Finally, the capability of studying the response of woody vegetation to imposed landscape modulations adds aspects of conservation and restoration ecology.

5. Conclusion

The pattern-formation modelling approach seeks to upscale information at the organism level and sub-patch scales, to information at the ecosystem level and landscape scales. The former information is used in building the model equations, while the latter is extracted from the model by means of mathematical analysis and numerical simulations. Unlike individual-based models the basic elements are not individuals, but rather local processes, such as resource flows, clonal propagation of plants, seed dispersal, growth of above and below-ground biomass, etc. These processes are mathematically expressed in terms of space and time dependent dynamical variables, such as biomass and limiting resources. Since no reference to individuals is made, questions related to the life-cycle of an individual or to age distributions cannot be addressed. On the other hand, pattern-formation models can properly handle the continuous flow of matter and lend themselves to the powerful mathematical methods of pattern-formation theory.

Three added values of the pattern-formation modelling approach have been emphasized: (i) It reveals universal elements such as instabilities, bistability ranges, and resonant responses, for which a great deal of knowledge is already available. (ii) It captures processes across different length scales and organization levels, thereby revealing bottom-up processes and emergent properties, as well as top-down processes and adaptive response to environmental changes. (iii) It provides an integrative framework for studying problems in spatial ecology, coupling aspects of landscape, population, community and restoration ecology.

Applications of the pattern-formation approach to water-limited landscapes predict the possible emergence of spatial heterogeneity as a self-organization phenomenon. The predicted spatial patterns can be periodic (spots, stripes and gaps), irregular with a characteristic length scale, or scale free. The pattern formation approach provides clear criteria for the realizations of these different pattern types in terms of environmental conditions, such as precipitation rate, infiltration rate, water-ground friction force, topography and disturbances, and in terms of species traits, such as biomass growth rate, uptake rate and root-to-shoot ratio. Further model studies, however, are needed. In particular, the extent of the snaking range, within the bistability range of bare soil and spot pattern, has not been calculated yet using vegetation models. Understanding the dependence of this range on biotic and abiotic factors is important for studies of desertification and species diversity.

The coupling of biotic and abiotic variables in the pattern-formation modelling approach provide information about resource patterns as well, which can correlate or anti-correlate with biomass patterns. These correlations change not only with environmental conditions and species traits, but also with spatial patterning, and may strongly affect community structure. Inter-specific interactions in woody–herbaceous systems, for example, strongly depend on the soil–water distributions that the woody life form induces. These distributions, in turn, are affected by the root-to-shoot ratio of the woody life form, by the precipitation rate, or by the density of woody patches. Accordingly, woody patches can exclude herbaceous vegetation or facilitate its growth, and for given species these relations can change along rainfall and consumer–pressure gradients. Moreover, the multitude of spatial patterns the woody vegetation can form in bistability ranges of basic vegetation states, increases spatial heterogeneity and thus species diversity. Since the pattern-formation approach provides a fairly good understanding of vegetation pattern formation and how it is affected by environmental conditions, it may also provide information about the response of species diversity to environmental changes taking into consideration the mediating effects of vegetation patterns. Such links between species diversity and vegetation pattern formation have hardly been studied (Gilad et al., 2007b).

The pattern-formation modelling approach also suggests a new view of vegetation restoration by water harvesting methods, that is, restoration as a resonance problem in spatially forced pattern-forming systems. Studies of simple pattern formation models, such as the parametrically forced Swift–Hohenberg equation, clarify conditions under which the response of the system to the forcing may strongly deviate from the forcing pattern. Applying these results to vegetation restoration using continuum vegetation models can shed new light on the applicability of this ancient, but powerful restoration practice, and on possible modifications that can improve the ecological services it provides.

We focused in this paper on dryland vegetation using mostly the Gilad et al. model, but the approach is general and applicable to other models of dryland vegetation, as well as to other contexts, such as vegetation pattern formation in wetlands (van der Valk and Warner, 2009). The specific model to be used in a given ecological context depends to a large extent on the processes and questions that are being addressed. To make the model more tractable with the mathematical methods of pattern formation theory we generally try to simplify it as much as possible. This simplification does not necessarily mean loss of essential information, for despite the overwhelming complexity of ecosystems, not all system processes are equally important in any given context or for any given question. In fact, substantial changes in ecosystem dynamics are often driven by very few processes (Holling, 1992), and the challenge is to identify these few factors and simplify the modelling accordingly. Here too, the theory of pattern formation can be helpful, by providing the mathematical basis for such model simplification.

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