

Ecosystem Engineers: From Pattern Formation to Habitat Creation

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Habitat and species richness in drylands are affected by the dynamics of a few key species, termed “ecosystem engineers.” These species modulate the landscape and redistribute the water resources so as to allow the introduction of other species. A mathematical model is developed for a pair of ecosystem engineers commonly found in drylands: plants forming vegetation patterns and cyanobacteria forming soil crusts. The model highlights conditions for habitat creation and for high habitat richness, and suggests a novel mechanism for species loss events as a result of environmental changes.

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Ecosystems are threatened today more than ever; climatic changes [1] and human action [2] have led in the past three decades to an unprecedented loss of habitats and species. The structure and dynamics of ecosystems are extremely complex due to the interactions among the many species they contain, the food-web connections across trophic levels, and the landscape modulations induced by biotic-abiotic interactions [3]. While interactions among species and food-web interconnections have been studied extensively [4], the roles of symmetry-breaking landscape modulations in creating habitats has largely been ignored.

Landscape modulations are often governed by a few key species—animals, plants or microorganisms—known as “ecosystem engineers” [5]. In modulating the landscape they change the flow of resources and affect the number of other species in the ecosystem. An example of ecosystem engineering in water limited systems is the cooperative action of cyanobacteria and shrubs to accumulate soil-water for the benefit of other species. Cyanobacteria alter the water regime by forming biological soil crusts which enhance runoff generation, whereas shrubs increase the infiltration capacity of surface water into the soil and act as sinks for runoff water [6].

In this Letter we propose a mathematical model for the engineering effects of shrubs and cyanobacteria in water limited systems. Applying concepts of pattern formation, such as symmetry breaking, instabilities, and coexistence of stable states, we highlight conditions for habitat creation, habitat diversity, and resilience of the system to perturbations. We also suggest a novel mechanism for species loss events as a result of environmental changes. The suggested mechanism is an emergent property [7] associated with symmetry breaking and cannot be deduced from the properties of individual species and their mutual interactions alone.

Recent models of vegetation growth [8–12] and field observations [13,14] indicate that plant species can modulate the landscape by forming symmetry-breaking patterns of biomass. The instabilities that induce these patterns result from two positive feedback mechanisms between biomass and water: (a) increased surface-water infiltration induced by vegetation, and (b) soil-water uptake by the plants’ roots. According to the first mechanism, a growing plant induces further local infiltration of surface water which accelerates its growth. According to the second mechanism, as a plant grows its roots become longer. The longer the roots the more soil-water they take up and the faster the plant grows. In both mechanisms, the depletion of soil-water from the plant surrounding, and the plant competition for water resource, lead to symmetry breaking and pattern formation.

The importance of the first positive feedback mechanism depends to a large extent on the infiltration properties of the bare soil; the lower the rate of infiltration the stronger the feedback. The infiltration rate, in turn, is significantly reduced if the soil is covered by biological soil crusts. These crusts, typically 1–3 mm thick, contain cyanobacteria (as well as other microorganisms) that exude mucilaginous materials and “glue” organic matter and soil grains in place [15]. The swelling capacity of the organic and inorganic matter greatly reduce the water infiltration rate. The crusts do not develop under vegetation, partly because the vegetation and the litter it produces block sunlight [16].

The model we present is the first to take into account the two positive feedback mechanisms between biomass and water. It contains three dynamical variables: density of biomass above ground level, $b(\mathbf{r}, t)$, soil-water density, $w(\mathbf{r}, t)$, describing the amount of soil-water available to the plant per unit area of ground surface, and the height, $h(\mathbf{r}, t)$, of a thin layer of surface water above ground level.

The model equations in nondimensional form are

$$\begin{aligned} b_t &= G_b b(1-b) - \mu b + \delta_b \nabla^2 b, \\ w_t &= I - (1-\rho b)w - \beta G_w w + \delta_w \nabla^2 w, \\ h_t &= p - I + \nabla^2(h^2) + 2\nabla h \cdot \nabla \zeta + 2h \nabla^2 \zeta, \end{aligned} \quad (1)$$

where the subscript t denotes partial time derivative and $\nabla^2 = \partial_x^2 + \partial_y^2$. The quantity G_b represents biomass growth rate and βG_w the rate of soil-water consumption by the vegetation. The quantity I represents the infiltration rate of surface water into the soil, and the parameter p stands for the precipitation rate. The parameter μ describes the rate of biomass loss due to mortality and disturbances (e.g., grazing), and ρ represents reduced evaporation due to shading. Finally, the term $\delta_b \nabla^2 b$ represents seed dispersal while the term $\delta_w \nabla^2 w$ describes soil-water transport in a nonsaturated soil [17]. The ground surface need not be flat—its height is given by the topography function $\zeta(\mathbf{r})$. The equation for h has been derived using shallow-water theory [18]. The equations for b and w are phenomenological.

The two positive feedback effects between biomass and water are included in the explicit forms of the infiltration term I and the biomass growth rate G_b . The infiltration I is assumed to depend on the biomass b according to [10,11]

$$I = \alpha h(\mathbf{r}, t) \frac{b(\mathbf{r}, t) + qf}{b(\mathbf{r}, t) + q}, \quad (2)$$

where α , q , and f are constants. The parameter f quantifies the infiltration property of the soil. Small values, $f \ll 1$, model the existence of a soil crust, as the infiltration rate in bare soil ($b = 0$) is much smaller than the rate in a vegetated soil. As f gets close to 1 the infiltration term becomes independent of biomass, representing the absence of a soil crust. The biomass growth rate is modeled by

$$\begin{aligned} G_b(\mathbf{r}, t) &= \int_{\Omega} g(\mathbf{r}, \mathbf{r}', t) w(\mathbf{r}', t) d\mathbf{r}', \\ g(\mathbf{r}, \mathbf{r}', t) &= \frac{1}{2\pi\sigma_0^2} \exp\left[-\frac{|\mathbf{r}-\mathbf{r}'|^2}{2[\sigma_0(1+\eta b(\mathbf{r}, t))]^2}\right], \end{aligned} \quad (3)$$

where the integration is over the entire domain Ω . According to this form the biomass growth rate depends not only on the amount of soil-water at the plant location, but also on the amount of soil-water in the neighborhood which the plant's roots extend to. The positive feedback effect due to water uptake by the roots is captured by the dependence of the root length on biomass, $\sigma(\mathbf{r}, t) = \sigma_0[1 + \eta b(\mathbf{r}, t)]$; the bigger the biomass the longer the roots and the higher the water uptake. The water consumption rate at a point \mathbf{r} is similarly given by

$$G_w(\mathbf{r}, t) = \int_{\Omega} g(\mathbf{r}', \mathbf{r}, t) b(\mathbf{r}', t) d\mathbf{r}'. \quad (4)$$

Note that $g(\mathbf{r}', \mathbf{r}, t) \neq g(\mathbf{r}, \mathbf{r}', t)$. The soil-water consumption rate at a given point is due to all plants whose roots extend to this point.

Equations (1) have two stationary uniform states representing bare soil and uniform vegetation, as well as patterned states. Uniform solutions and their linear stability have been studied analytically while nonuniform solutions were obtained by solving Eqs. (1) numerically using a pseudospectral code with periodic boundary conditions. Figure 1 shows the uniform states and their stability properties for two choices of parameters, corresponding to plants that differ in their root extension rates, η , in their growth rates and in their maximum standing biomass densities. The bare-soil state, \mathcal{B} ($b = 0, w = p, h = p/\alpha f$), loses stability as the precipitation p exceeds a threshold p_c . Depending on the parameters the bifurcation at $p = p_c$ is super or subcritical. Plants characterized by small η appear in a supercritical bifurcation

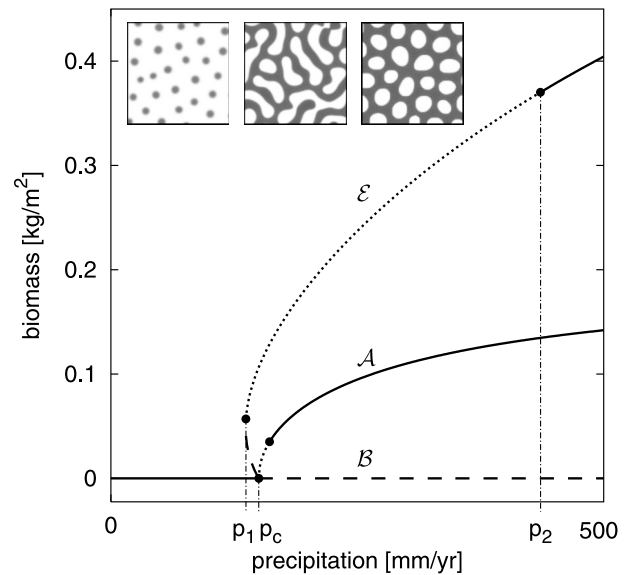


FIG. 1. Biomass b vs precipitation p for plane topography. Solid lines denote stable solutions while dashed (dotted) lines denote solutions which are unstable to uniform (nonuniform) perturbations. The branch \mathcal{B} represents a uniform bare-soil solution; The two branches marked \mathcal{A} and \mathcal{E} represent uniform vegetation states for two different parameter choices, corresponding to (\mathcal{A}) low biomass density, high growth rate, and short root lengths and (\mathcal{E}) higher biomass density, low growth rate, and long root lengths. The insets show typical biomass patterns of the \mathcal{E} species along the precipitation gradient. Dark shades of gray represent high biomass. Parameter values used are $\mu = 0.3$, $\alpha = 10$, $f = 0.1$, $\delta_b = 10^{-4}$, $\delta_w = 10^{-2}$, $\sigma_0 = 0.1$, and (\mathcal{A}): $\eta = 0.7$, $\beta = 1$, $\rho = 0.6$, $q = 0.25$; (\mathcal{E}): $\eta = 3.5$, $\beta = 5$, $\rho = 3$, $q = 0.05$. These values reflect realistic orders of magnitudes for shrubs in water limited systems [17,19]. Nondimensional units have been converted to dimensional quantities using the following scalings (obtained for a particular choice of scaling parameters): precipitation $P = (500 \text{ mm/yr})p$, biomass $B = (1 \text{ Kg/m}^2)b$.

(branch \mathcal{A} in Fig. 1) while plants characterized by larger η appear in a subcritical bifurcation (branch \mathcal{E}). The former may represent annual plants while the latter may be associated with shrubs or trees.

Both vegetation branches are unstable to finite wave number perturbations. Specifically, the \mathcal{E} branch, that appears at the bifurcation point, $p = p_1$, is unstable in the range $p_1 < p < p_2$. In this range patterned states prevail: spots at relatively small p , stripes at intermediate p and gaps at relatively high p , as the panels in Fig. 1 show. The patterned states also extend to values $p < p_1$ (coexistence of spots with bare soil; see Fig. 1) and to values $p > p_2$ (coexistence of gaps and uniform vegetation).

The model equations (1) can be used to study conditions that maximize the accumulation of soil-water for the benefit of other species. We associate the variable b in the model equations with the biomass of a plant engineer, such as shrub, and parametrize the presence of biological crust by the value of f . The upper panels of Fig. 2 show the spatial distributions of b , w , and h for a small value of $f = 0.1$ (crusted soil) for three species characterized by distinct values of η . For $\eta \gg 1$ there is a significant depletion of soil-water in the vicinity of the vegetation patch [Fig. 2(a)]. At intermediate values, $\eta \sim \mathcal{O}(1)$, a pronounced *maximum* is induced at the patch location [Fig. 2(b) and 2(c)]. This maximum may exceed the soil-water level corresponding to the uniform bare state (see dotted line in Fig. 2), thereby creating habitats for plant species that would not grow in the absence of the ecosystem engineer.

The soil-water distribution in Fig. 2(b) has been obtained with low values of the parameter f , corresponding

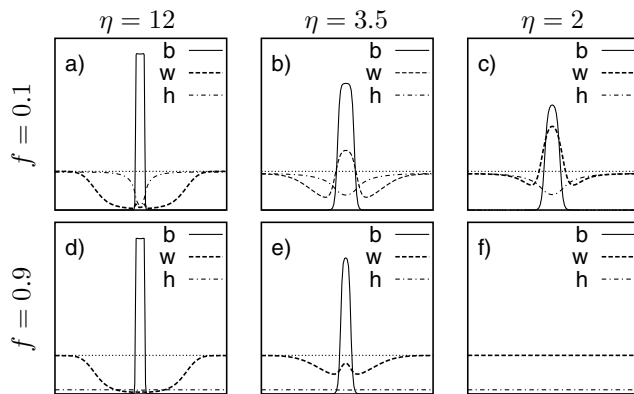


FIG. 2. Spatial profiles of b , w , and h obtained by taking cross sections through two-dimensional numerical solutions of (1). The profiles represent three different species (different η) at two levels of crust coverage, with dimensional precipitation $P = 75$ mm/yr ($p = 0.15$): (a) $\eta = 12, f = 0.1$; (b) $\eta = 3.5, f = 0.1$; (c) $\eta = 2, f = 0.1$; (d) $\eta = 12, f = 0.9$; (e) $\eta = 3.5, f = 0.9$; (f) $\eta = 2, f = 0.9$. Other parameters are the same as those of the \mathcal{E} branch in Fig. 1. Panels (a) and (d) span an horizontal range corresponding to 14 m, all others span 3.5 m.

to a crusted soil. Higher values of f can lower the soil-water amount that a plant accumulates below the level of a bare soil as shown in Fig. 2(e). Thus the accumulation of soil-water beyond the bare-soil level, and the consequent creation of habitats, is a combined engineering effect of the plant-cyanobacteria system.

The model equations can also be used to study conditions that make the plant-cyanobacteria system resilient to environmental changes. Resilience to climatic fluctuations, such as droughts, is achieved by a wide coexistence range of spots with bare soil. This coexistence range becomes wider as η is increased. Resilience to disturbances, such as crust removal, is also affected by η as illustrated by the lower panels of Fig. 2. The habitats that a plant species with $\eta = 3.5$ creates (thanks to the infiltration feedback) are destroyed when the crust coverage is reduced, but the plant species itself survives (thanks to the roots feedback) and is capable of restoring the habitats once the crust recovers [Figs. 2(b) and 2(e)]. A plant species with lower η ($\eta = 2$) may outperform in accumulating soil-water but, as Figs. 2(c) and 2(f) show, makes the system fragile. Crust removal not only destroys the habitats; it also leads to the disappearance of the plant species itself, making the system no longer recoverable. A plant species with higher η ($\eta = 12$) survives the crust removal but does not accumulate soil-water [Figs. 2(a) and 2(d)]. This suggests that optimal tuning of η , and possibly other parameters, is required for a plant-cyanobacteria system to act as an effective and resilient ecosystem engineer. The model provides an excellent tool for identifying the optimal parameter ranges.

So far we were concerned with habitat creation by the plant-cyanobacteria system. The *diversity* of created habitats, and consequently species richness [6], depends to a large extent on the types of patterns formed by the ecosystem engineers. Periodic patterns provide only one type of habitat—the unit cell that repeats itself periodically. Aperiodic or disordered patterns provide many more habitats. Such patterns arise in coexistence ranges of different stable states. An earlier study [9,12] predicted a variety of coexistence ranges along the precipitation axis: bare soil and spots, spots and stripes, stripes and gaps, gaps and uniform vegetation. In these ranges long lived (if not asymptotic) patterns involving arbitrary spatial mixtures of the coexisting states can be realized.

We conclude by proposing a novel mechanism of species loss events: An environmental change inducing a transition between different pattern states of the ecosystem engineers can lead to the local disappearance of species if the transition involves a habitat loss. We illustrate this mechanism with an example of a banded vegetation on a slope with low infiltration as shown in Fig. 3(a). When the precipitation falls below a critical value the system self-organizes into an hexagonal spot pattern, as shown in Fig. 3(b)]. The new pattern state is

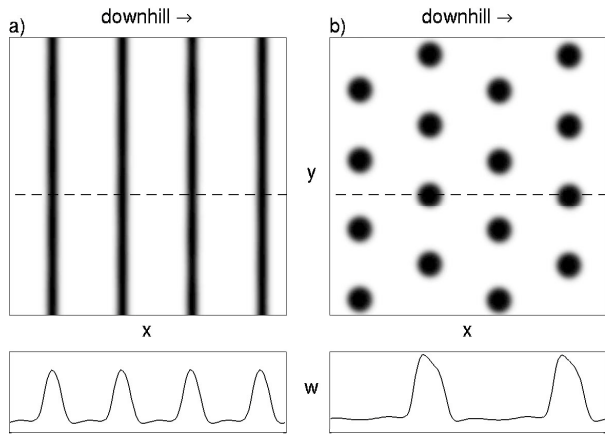


FIG. 3. Habitat change induced by a transition from a banded pattern (a) to a spotted pattern (b), on a slope, in response to a precipitation drop from $P = 175$ mm/yr (a) to $P = 150$ mm/yr (b). The upper frames show two-dimensional biomass patterns (darker gray shades correspond to higher biomass density) obtained by solving numerically Eqs. (1). The lower panels show soil-water profiles along the transects shown by the dashed lines in the upper frames. The soil-water density under spots is higher than the density under bands. Spots may therefore provide habitats to species that bands cannot accommodate. The slope is 10° , $f = 0.1$, and all other parameters are those of the \mathcal{E} branch in Fig. 1. Precipitation has been scaled to dimensional units using $P = (500 \text{ mm/yr})p$.

associated with *increased* soil-water density under vegetation patches as the soil-water profiles at the bottom of Fig. 3 show, because of the larger bare areas uphill. Conversely, increased precipitation, which induces a transition from spots to banded vegetation, can lead to habitat loss and species disappearance. This counterintuitive conclusion is not deducible by considering the responses of individual species, and is rooted in the fact that spatial patterns of ecosystem engineers are emergent properties resulting from the collective dynamics of many individual species.

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