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## Spatial instabilities untie the exclusion-principle constraint on species coexistence

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## HIGHLIGHTS

- Spatial patterns allow coexistence of two species, competing on one resource.
- Competition increases the precipitation range that supports spatial patterns.
- Invasion of a strong competitor can drive a patterned system to extinction.

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## ABSTRACT

Using a spatially explicit mathematical model for water-limited vegetation we show that spatial instabilities of uniform states can lead to species coexistence under conditions where uniformly distributed species competitively exclude one another. Coexistence is made possible when water-rich patches formed by a pattern forming species provide habitats for a highly dispersive species that is a better competitor in uniform settings.

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## 1. Introduction

Species coexistence and diversity are fundamental aspects of community dynamics widely explored in the context of resource-limited ecosystems (Shmida and Ellner, 1984; Chesson, 2000; Levin, 2000; Turchin, 2003; Herben and Hara, 2003; Scheiter and Higgins, 2007; Pronk et al., 2007; Nevai and Vance, 2007; May et al., 2009; Díaz-Sierra et al., 2010). One of the main theoretical results is the competitive exclusion principle, stating that two species competing for the same limiting resource cannot coexist if other ecological factors are constant (Hardin, 1960). This easily verifiable mathematical statement rarely holds in real ecosystems, which are often characterized by a wide abundance of different species, apparently exploiting the same limiting

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resource. Many mechanisms have been suggested to explain this discrepancy between theory and reality, including niche differentiation due to heterogeneous space and time (Goldberg and Novoplansky, 1997; Tilman, 1994; Amarasekare, 2003), species specific predation (Takeuchi and Adachi, 1984; Hulme, 1996), species that affect each other directly (Vance, 1984) and others. All these explanations make a step towards reality in breaking the main assumption of the exclusion principle – uniform environmental conditions and similar species behavior in all aspects beside competition on a resource (Barot, 2004).

Despite the significance of environmental heterogeneity for species diversity, studies of species coexistence have largely overlooked an important driver of such heterogeneity – spatial instabilities leading to *self-organized* patchiness (Gilad et al., 2007a; Meron, 2012). A well studied context of such patchiness is vegetation pattern formation in water limited ecosystems (Deblauwe et al., 2008). Model studies of water-limited ecosystems have identified local biomass-water feedbacks capable of inducing instabilities of uniform vegetation that result in global

regular and irregular vegetation patterns (Rietkerk et al., 2002; Barbier et al., 2006; Gilad et al., 2007b; von Hardenberg et al., 2010). These patterns can form even in the absence of any environmental heterogeneity, such as micro-topography or differences in soil type.

Associated with vegetation pattern formation are resource redistribution and ecosystem engineering, which may affect inter-specific interactions (Gilad et al., 2004, 2007b). Studies of a two species model representing a water-limited woody-herbaceous system with a pattern-forming woody engineer, have demonstrated transitions from competition and exclusion of the herbaceous life form at high rainfall to facilitation and coexistence at low rainfall (Gilad et al., 2007a), consistently with field observations (Holzapfel et al., 2006). These studies, however, assumed the existence of a maximal standing biomass, a parameter representing constraints on above-ground biomass growth such as plant-shoot architecture. This assumption, which breaks the conditions of the exclusion principle, allows for species coexistence even in uniform systems. In this paper we study whether self-organized patchiness alone can induce species coexistence. That is, we consider a system that satisfies all the assumptions of the exclusion principle, except that it is spatially extended. We show that although the system's environment is assumed to be homogeneous, spatial instabilities leading to patterned states can induce species coexistence. This result is implicit in a recent study on savanna ecosystems (Baudena and Rietkerk, 2013), but has not been spelled out. We further show various realizations of species exclusion and coexistence and we uncover the conditions that are required to yield these realizations.

## 2. The model

Vegetation pattern formation in drylands has been studied using a wide range of mathematical models (see for example Borgogno et al., 2009; Lefever and Lejeune, 1997; O. Lejeune and Lefever, 2004; Rietkerk et al., 2002; Gilad et al., 2004). While representing the soil-vegetation-atmosphere feedbacks at different degrees of detail, most models produce the same basic characteristics of vegetation patchiness, including the sequence of vegetation states (uniform and patterned) along environmental gradients, and bistability ranges between any consecutive pair of vegetation states. This is largely due to the universal behavior of dynamical systems near instability points. The relevant instability in the present case is a stationary nonuniform instability of a uniform vegetation state, which leads to stripe patterns and two forms of hexagonal patterns (Cross and Greenside, 2009), representing spot and gap patterns.

A similar degree of universality is expected in models for two competing species. We therefore use a fairly simplified version of the model which was introduced in Gilad et al. (2007a) and Meron (2011) for a pattern-forming species and a non-pattern forming species that compete for a single limiting resource – soil water. We first omit the maximum standing biomass limitation to regain the validity of the exclusion principle in the absence of a pattern forming instability. This will allow us later on to attribute species coexistence to spatial self organization. We further keep only one pattern forming feedback – a larger infiltration rate of surface water into vegetated soil compared to bare soil, dropping the positive feedback associated with root-shoot relations (Gilad et al., 2007b). An additional simplification is the replacement of the nonlinear diffusion term in the equation for the surface-water variable by a linear diffusion term, as we will further explain below. Under these simplifications the model can be regarded as an extension of the model introduced by HilleRisLambers et al. (2001) to two species.

The simplified model version reads

$$\begin{aligned} \partial_t B_1 &= (C_1 W - M_1) B_1 + D_1 \nabla^2 B_1 \\ \partial_t B_2 &= (C_2 W - M_2) B_2 + D_2 \nabla^2 B_2 \\ \partial_t W &= J(B_1) H - W(N + \Gamma_1 B_1 + \Gamma_2 B_2) + D_W \nabla^2 W \\ \partial_t H &= P - J(B_1) H + D_H \nabla^2 H \end{aligned} \quad (1)$$

with  $J(B_1) = A(B_1 + Qf)/(B_1 + Q)$ . The model represents vegetation densities for two species,  $B_i$  ( $i=1,2$ ), the first pattern-forming and the second not, with growth rates  $C_i$ , mortality rates  $M_i$ , and diffusion (dispersal) rates  $D_i$ . The two species compete for a single resource, water, which is modeled by two layers. One is soil water,  $W$ , which contributes linearly to biomass growth of both species. The soil water is reduced by evaporation at a rate  $N$  and by water uptake due to each species with rates  $\Gamma_i B_i$ . The soil water density increases by infiltration from the surface water layer,  $H$ , at a rate  $J(B_1)$ . This biomass dependence simulates the higher infiltration rate in vegetated areas due to the absence of a soil crust and, in some cases, the formation of a soil mound that intercepts runoff, as explained in Gilad et al. (2007b). In principle, the infiltration rate should also depend on  $B_2$ . However, in order for  $B_2$  to remain non-pattern forming this dependence should be weak enough and for simplicity we omit it. We verified that introducing a weak dependence on  $B_2$ , while remaining in a parameter range where  $B_2$  alone does not form patterns, does not change our qualitative results. In the surface water equation overland water flow is represented by a simple diffusive term  $\nabla^2 H$ . This term, together with the  $J(B_1)H$  term, is responsible for the instability to periodic vegetation patterns; the surface water flow towards vegetation patches, because of higher infiltration rates at the patch areas, provides a mechanism for short range facilitation and long-range competition that favors nonuniform vegetation. In other papers, such as Gilad et al. (2007b), a nonlinear diffusion term of the form  $\nabla^2 H^2$  has been used. While this form is better motivated from a physical point of view, the linear version used here allows for a simpler numerical and analytical solution of the equations and we verified that our results do not depend crucially on this detail.

As a first step in our analysis we non-dimensionalize the equations and reduce the parameter space, using the mortality, dispersal and growth rates of the first species to define scales for time, space and water, respectively, and using the soil-water uptake rates of both species to rescale their biomasses

$$\begin{aligned} \partial_t b_1 &= (w-1)b_1 + \nabla^2 b_1 \\ \partial_t b_2 &= (c_2 w - \mu_2) b_2 + d_2 \nabla^2 b_2 \\ \partial_t w &= I(b_1) h - w(n + b_1 + b_2) + d_w \nabla^2 w \\ \partial_t h &= p - I(b_1) h + d_h \nabla^2 h, \end{aligned} \quad (2)$$

where  $I(b_1) = \alpha(b_1 + qf)/(b_1 + q)$ ,  $\alpha = A/M_1$ ,  $n = N/M_1$ ,  $p = PC_1/M_1^2$ ,  $\mu_2 = M_2/M_1$ ,  $c_2 = C_2/C_1$ ,  $d_2 = D_2/D_1$ ,  $d_w = D_W/D_1$ ,  $d_h = D_H/D_1$ ,  $q = Q\Gamma_1/M_1$ ,  $b_1 = B_1\Gamma_1/M_1$ ,  $b_2 = B_2\Gamma_2/M_1$ ,  $w = WC_1/M_1$ ,  $h = HC_1/M_1$ ,  $x = \sqrt{M_1/D_1}X$ ,  $t = M_1 T$ .

We study solutions of these model equations for different parameter values, addressing the question how pattern formation affects the community dynamics of the two competing species. We will limit our analysis to one-dimensional systems and concentrate on the parameters which control water stress and competition. These are the precipitation rate  $p$  and the parameters defining the second species,  $c_2, \mu_2, d_2$ . The parameters  $n, \alpha, q, f, d_w$  and  $d_h$ , which control soil water dynamics and overland flow are kept constant and appropriate values to represent dryland water-vegetation interactions are chosen. The specific values we choose,  $\alpha = 40$ ,  $q = 0.1$ ,  $f = 0.1$ ,  $n = 1$ ,  $d_w = 100$ ,  $d_h = 10\,000$ , have been employed and discussed in Gilad et al. (2004, 2007b). We fix the non-dimensional domain size to 400, equivalent to a domain of  $D=9.1$  m in dimensional units when realistic values are chosen for the dimensional parameters. The parameters  $c_2$  and  $\mu_2$  both

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