



Vegetation pattern formation in a fog-dependent ecosystem

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ABSTRACT

Vegetation pattern formation is a striking characteristic of several water-limited ecosystems around the world. Typically, they have been described on runoff-based ecosystems emphasizing local interactions between water, biomass interception, growth and dispersal. Here, we show that this situation is by no means general, as banded patterns in vegetation can emerge in areas without rainfall and in plants without functional root (the Bromeliad *Tillandsia landbeckii*) and where fog is the principal source of moisture. We show that a simple model based on the advection of fog-water by wind and its interception by the vegetation can reproduce banded patterns which agree with empirical patterns observed in the Coastal Atacama Desert. Our model predicts how the parameters may affect the conditions to form the banded pattern, showing a transition from a uniform vegetated state, at high water input or terrain slope to a desert state throughout intermediate banded states. Moreover, the model predicts that the pattern wavelength is a decreasing non-linear function of fog-water input and slope, and an increasing function of plant loss and fog-water flow speed. Finally, we show that the vegetation density is increased by the formation of the regular pattern compared to the density expected by the spatially homogeneous model emphasizing the importance of self-organization in arid ecosystems.

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1. Introduction

Vegetation pattern formation has been empirically and theoretically studied in numerous ecological systems including arid and semi-arid ecosystems (Macfadyen, 1950; Klausmeier, 1999; Couteron and Lejeune, 2001; HilleRisLambers et al., 2001; von Hardenberg et al., 2001; Rietkerk et al., 2002; Barbier et al., 2006), peatlands (Rietkerk et al., 2004) and salt marshes (Van de Koppel et al., 2005a). In arid and semi-arid zone ecosystems, in particular, the interaction between a limited amount of water and the vegetation can lead to the emergence of a spontaneous spatial arrangement of the vegetation or pattern formation (von Hardenberg et al., 2001; Rietkerk et al., 2004; Deblauwe et al., 2008).

An interesting common feature in these ecosystems is that the physical landscape (i.e. topography and geomorphology) impose constraints on the orientation and rates of flows of materials like water, nutrients, sediments and seeds (Thiery et al., 1995; Gilad et al., 2004; Saco et al., 2006). In response, the vegetation tends to

produce specific spatial patterns with a clearly defined geometry (Thiery et al., 1995; Gilad et al., 2004). One striking example, are the banded vegetation patterns generally described in systems with gentle slopes, that restrict water and nutrients flows along one spatial direction (Thiery et al., 1995; Valentin et al., 1999; Sherratt, 2005; Ursino, 2005) along which vegetation bands, perpendicular to the direction of the flow, usually develop.

Several hypotheses have been proposed to understand the formation and maintenance of banded vegetation patterns in water-limited ecosystems (see Rietkerk and van de Koppel, 2008; Borgogno et al., 2009 for a review). In general, these patterns are thought to emerge as a consequence of the interaction between two components acting at slightly different spatial scales. On one hand, there is local cooperation among neighboring individuals to concentrate scarce resources in certain zones (by intercepting the flow of materials), which enhances the probability of plant establishment, growth and survival (Thiery et al., 1995; Borgogno et al., 2009). On the other hand, the depletion of resources by the vegetation results in a net negative effect on their growth rates at a slightly larger spatial scale. Typically, positive effects favor environmental conditions like reduction in soil moisture losses or protection against herbivores while negative effects are attributed to competition for resources via mainly the root system (von Hardenberg et al., 2001; Barbier et al., 2008).

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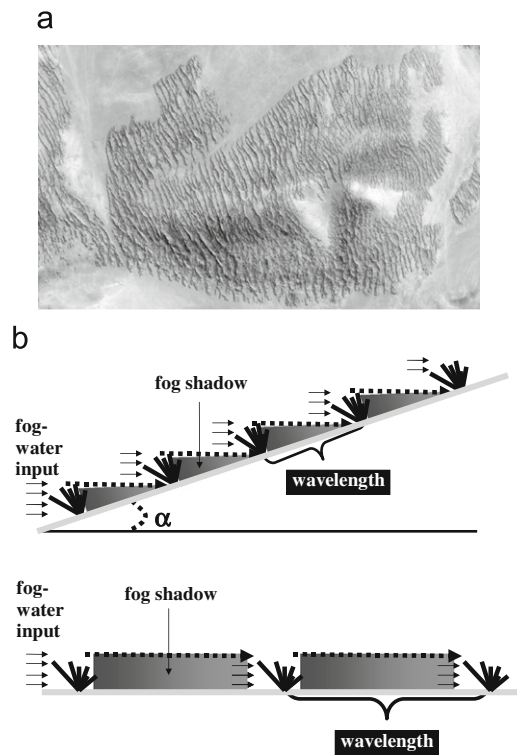


Fig. 1. (a) Aerial photograph of a vegetation pattern in the Atacama Desert, North of Chile. The scale is about 400×200 m. The photograph was taken from Google Earth. (b) Conceptual model of the pattern formation with the parameters as in the mathematical model (see the text for more details and Table 1 for abbreviations).

However, this situation is by no means general. As we show in this work, banded patterns in vegetation can emerge in areas without rainfall and in plants without functional root as is the case in the Atacama Desert in northern Chile, the most arid ecosystem in the world (precipitation average < 2 mm between 1905 and 2001 Pinto et al., 2006). Here fog-water is the main source of humidity which is moved inland from the Pacific Ocean by the westerly winds (the prevailing wind system along the west coast of South America) (Heinz, 1998). The interplay between the fog and the local topography of the system gives rise to the formation of isolated patches consisting of parallel vegetated bands of the bromeliad *Tillandsia landbeckii*, an epiarenic species that lacks functional roots.

In this work, we develop a model that describes the biomass dynamics of (*Tillandsia landbeckii*) and of fog-water supply and explains the emergence of the banded vegetation pattern observed in the Atacama Desert ($20^{\circ}29'S$ – $20^{\circ}26'S$, Fig. 1a).

2. Methods

2.1. Conceptual model

The conceptual model to explain the pattern formation by *Tillandsia landbeckii* in the Atacama Desert is as follows (see Fig. 1b). The fog-water is advected by the wind and is intercepted by plant biomass. The increased water interception facilitates the vegetation growth over a local range. Since *T. landbeckii* does not have a functional root system, we assume that the amount of fog intercepted is directly associated with the canopy or the above ground biomass. So higher vegetation density enables higher water interception. Further, vegetation spread is slow as compared to the fog-water flow, which results in fog-water depletion by the vegetation and this creates a fog-shadow or an area where

fog-water input does not allow plant growth. When the availability of fog-water supply is again enough for the plant establishment and growth (i.e. at certain distance from the band ahead of the flow) a new band is developed. We provide support to this hypothesis by means of a spatially explicit model.

2.2. Mathematical model

We use the model proposed by Klausmeier (1999) for a runoff-dependent ecosystem, but modified it to include an advective flow of fog-water. We also incorporate in our model a parameter, α , that weights the topography or slope of the terrain, which modifies the effective capture of water (hereafter called ECW) by the plant biomass. Such that ECW is lower in a flat terrain, while the inverse effect is expected on a sloped terrain. In this last case, an increase in the plant biomass in contact with fog-water inputs enhances ECW. Our model is composed of a set of two partial differential equations describing the rate of change in plant biomass, B (g m^{-2}), and fog-water, W (mm), in space and time. The dynamic of each state variable is expressed by a reaction term and a diffusion or advection term as follows:

$$\frac{\partial W(x,t)}{\partial t} = W_0 - RW(x,t) - \alpha cW(x,t)B(x,t)^2 + V \frac{\partial W(x,t)}{\partial x}, \quad (1)$$

$$\frac{\partial B(x,t)}{\partial t} = e\alpha cW(x,t)B(x,t)^2 - MB(x,t) + D \frac{\partial^2 B(x,t)}{\partial x^2} \quad (2)$$

Eq. (1) contains a source term W_0 that represents the fog-water inputs assumed to be constant and uniform, and two loss terms: one biomass independent RW , representing evaporation, and a second one αcWB^2 which represents the plant water uptake, such that an increase in biomass is associated with an increase in the amount of intercepted water. The parameter c is the consumption constant and α is related with the effect of the topography (slope) on ECW. It is an adimensional parameter that ranges between 0 and 1 and corresponds to a normalized slope defined as $\text{slope}(\circ)/90^{\circ}$. The movement of water-fog by the wind is modeled by an advection term $V \partial W(x,t)/\partial x$, where V is the wind speed.

In Eq. (2) the term αcWB^2 multiplied by the parameter e that converts water uptake by plants to plant growth. We assume density-independent mortality given by MB where M is a mortality constant. The lateral or vegetative growth what enables the bands to expand laterally, thus allowing the growth of parallel bands, is modeled by a diffusion term $D \partial^2 B/\partial x^2$, where D is a diffusion coefficient for the biomass.

A list of parameters of the model with their units and numerical values obtained from the literature are presented in Table 1.

2.3. Analysis of the model

We analyze our model using the reaction–diffusion theory (of morphogenesis) developed by Turing on 1952, which has also been applied in ecology by others authors to relate ecosystem spatial patterns to the underlying driven mechanisms (e.g. Segel and Jackson, 1972; HilleRisLambers et al., 2001; Murray, 2002; Sole and Bascompte, 2006; Rietkerk and van de Koppel, 2008; Borgogno et al., 2009). Briefly, Turing suggested that, under certain conditions, two chemical species can react and diffuse in such a way as to produce heterogeneous spatial patterns in their chemical concentrations (Murray, 2002). This implies that in absence of diffusion the chemicals tend to a stable uniform steady state but under certain conditions, a spatially inhomogeneous pattern can evolve by diffusion driven instability (Murray, 2002). In our model, the instability that promotes the formation of the banded pattern is not induced by diffusion but by the advection

Table 1
Interpretation of symbols and parameter values used.

Symbols	Interpretation	Units	Numerical value
B	Plant biomass	g m^{-2}	–
W	Fog-water	mm	–
t	Time	day	–
x	Space	m	–
W_0	Fog-water supply	mm day^{-1}	0.07
R	Water evaporation	day^{-1}	1
α	Topography effect on capture of water	no. units	0.05
c	Water uptake	$\text{m}^4 \text{g}^{-2} \text{day}^{-1}$	0.3
e	Conversion of water uptake	$\text{g mm}^{-1} \text{m}^{-2}$	12
M	Loss of plant density due to mortality	day^{-1}	0.0007
V	Diffusion coefficient for water-fog	$\text{m}^2 \text{day}^{-1}$	85,000
D	Plant dispersal or lateral growth	$\text{m}^2 \text{day}^{-1}$	0.00005

Note: Parameter values were obtained or derived from empirical studies in the literature (González, 2007, Pinto, 2005 and the Official Meteorological Station of Diego Aracena, Chile). The slope (deg.) values were determined in the field to determine α .

term related to the fog-water flow. However, while the mathematical description of the dynamics may be different, it is essentially the same physical mechanism, early described by Turing (1952), that induce the pattern formation (Borgogno et al., 2009), which is commonly called symmetry-breaking instability.

The conditions required for the occurrence of the pattern formation is that the full model tends to a stable uniform steady state in the absence of any spatial effect but to an unstable state when it is spatially perturbed (Murray, 2002; Edelstein-Keshet, 2005). A linear stability analysis is used to determine if regular patterns can form (Edelstein-Keshet, 2005; Ellner and Guckenheimer, 2006; Otto and Day, 2007). To do this we use a simplified, non-dimensional, version of our model.

2.3.1. Scaling of the model

Model Eqs. (1) and (2) are simplified by the following non-dimensionalisation:

$$\begin{aligned} u &= Bc^{1/2}R^{-1/2}, \\ w &= Wec^{1/2}R^{-1/2}, \\ w_0 &= W_0ec^{1/2}R^{-3/2}, \\ m &= MR^{-1/2}, \\ v &= VD^{-1/2}R^{-1/2}, \\ x^* &= xR^{1/2}D^{-1/2}, \\ t^* &= tR. \end{aligned}$$

The resulting dimensionless equations are:

$$\frac{\partial w}{\partial t^*} = w_0 - w - \alpha w u^2 + v \frac{\partial w}{\partial x^*}, \quad (3)$$

$$\frac{\partial u}{\partial t^*} = \alpha w u^2 - m u + \frac{\partial^2 u}{\partial x^{*2}}. \quad (4)$$

Then, in the non-dimensional model the main four parameters that affect the dynamic of the model are: w_0 which measures flow-water inputs, m which measures plant biomass loss due to mortality, α that determines the effect of the topography and v that controls the rate at which the fog-water flows. So, in the remainder of this paper we focus on the conditions for pattern formation and the way in which only these four parameters affect the dynamic and geometry (wavelength) of the resulting pattern. For the sake of clarity, we present the results using W_0 , M , α and V . Notice that the parameter α could also be removed by rescaling w , u and w_0 in Eqs. (3) and (4). However, since α has a clear biological interpretation for the analysis and its later discussion and can be measured in nature to test the model, we prefer to leave it explicitly in the dimensionless equations.

To visualize the effect of the parameters on the dynamic of the model we show diagrams of parameter space showing the transition from one state to another. We solve numerically the equilibrium state, from which the pattern is developed, for different combination of parameters. Also, we show the relationship between the equilibrium biomass and W_0 , R , M by means of bifurcation diagrams to see the dependence of the pattern on that parameters. Then the relationship between the wavelength of the pattern and W_0 , M , α and V is presented.

Finally, to visualize the pattern formation in the space we show a numerical solution of the model using a finite difference method for which we adopted periodic boundary conditions. Numerical simulations were initialized using random perturbations of the homogeneous equilibrium states.

3. Results

3.1. Conditions for pattern formation

First of all, the behavior of the non-spatial model (i.e. with no space derivatives) was resolved. As shown by Klausmeier (1999), the non-spatial model has three steady states corresponding to the spatially homogeneous equilibria of the full model. One of them is a trivial steady state consisting of bare ground without plants ($W=W_0/R$; $B=0$) which is linearly stable. There are two other steady states, one that is always unstable and the other is the key equilibrium from which the pattern is developed. This latter one, which is linearly stable, is:

$$\left(W_{\text{est}} = \frac{eW_0}{2eR} - \frac{1}{2eR} \sqrt{\frac{\alpha c e^2 W_0^2 - 4M^2 R}{\alpha c}}; \quad B_{\text{est}} = \frac{eW_0}{2M} + \frac{1}{2M} \sqrt{\frac{\alpha c^2 W_0^2 - 4M^2 R}{\alpha c}} \right) \quad (5)$$

The next step is to determine when this non-trivial steady state is unstable to small heterogeneous perturbations (Murray, 2002). In matrix notation, from the full model we obtain the characteristic polynomial form

$$[\mathbf{J} + ik\mathbf{V} - k^2\mathbf{D} - \lambda\mathbf{I}], \quad (6)$$

where

$$\mathbf{J} = \begin{bmatrix} \frac{\partial f}{\partial W} & \frac{\partial f}{\partial B} \\ \frac{\partial g}{\partial W} & \frac{\partial g}{\partial B} \end{bmatrix}_{(W_{\text{est}}, B_{\text{est}})}; \quad \mathbf{V} = \begin{bmatrix} V & 0 \\ 0 & 0 \end{bmatrix}; \quad \mathbf{D} = \begin{bmatrix} 0 & 0 \\ 0 & D \end{bmatrix} \quad (7)$$

being $(\partial f / \partial W) = -R - ce\alpha B^2$, $(\partial f / \partial B) = -2ce\alpha WB$, $(\partial g / \partial W) = \alpha B^2$, $(\partial g / \partial B) = 2\alpha WB - M$, with i the imaginary unit, k the wavenumber (the spatial effect; recall that the wavelength is $\zeta = 2\pi/k$) and $\mathbf{I}$ is

the identity matrix. Then, from the roots of this polynomial evaluated in $(W_{est}; B_{est})$, we get the eigenvalues as a function of the wavenumber k , $\lambda(k)$, which is known as the dispersion relation (Borgogno et al., 2009). So, for $(W_{est}; B_{est})$ to be unstable, the solution of $\lambda(k)$ have to exhibit a real positive value for some $k \neq 0$.

Notice that in expression (6), $k=0$ corresponds to a uniform perturbation (or no spatial effect), and since in this case λ is negative (not a function of k , as in the spatial case), the stationary state $(W_{est}; B_{est})$ is classified as a stable state.

3.2. Effect of the parameters on the dynamic of the model

The effect of the parameters W_0 , α , M and V on the behavior of the model is shown in Figs. 2 and 3. In all cases, it is indicated the transition from a desert state without vegetation, through a state of striped vegetation, to a homogeneous vegetation state (black arrow in Figs. 2 and 3).

In general, W_0 and α affect the dynamic of the model in the same direction but opposite to the effect of M or V . That is, as W_0 and α are increased the model predicts a transition from a bare state without vegetation, through a state of striped vegetation, to a homogeneous vegetation state (Fig. 2a) and the reverse trend is observed if M and V are increased (Fig. 2b). As expected, an increase in α can give rise to a banded vegetation pattern even if W_0 is low, by increasing the ECW. As shown in Fig. 2b, the limit between the striped pattern and the desert state is independent of

V and is solely determined by M . A similar situation is observed in Fig. 3(a, b) for the effect of V on W_0 and α . Finally, as M decreases and W_0 or α are increased, the model predicts a transition from a bare state to a vegetated homogeneous state (Fig. 3c, d).

The critical values or threshold points at which a sudden shift between the desert and the vegetated states occur are presented in Fig. 4. That critical points are $W_{0c}=0.001 \text{ mm day}^{-1}$ (Fig. 4a), $R_c=5.400 \text{ day}^{-1}$ (Fig. 4b) and $M_c=0.05 \text{ day}^{-1}$ (Fig. 4c). When $W_0 > W_{0c}$ or $R > R_c$ and $M > M_c$ only the desert state is possible, while above W_{0c} or before R_c or M_c the second stable state from which the pattern forms is also observed.

3.3. Effect of the parameters on the pattern geometry (wavelength)

Using the parameter values given in Table 1, our model predicts wavelengths for the banded vegetation pattern ranging from 2.5 to 12 m. This wavelength is the length between two consecutive peaks of biomass, which is the distance from the middle of two consecutive bands. The relationship between the pattern wavelength ζ and the four parameters is shown in Fig. 5. The model predicts a negative non-linear relationship between ζ and W_0 (Fig. 5a) and between ζ and α (Fig. 5b). This means that as the fog-water input or the slope of the terrain increase, the expected distance between bands is reduced. On the other hand, a positive non-linear relationship between ζ and M (Fig. 5c) and between ζ and the V is expected (Fig. 5d). In general, the relationship between the pattern wavelength and the parameters shown in Fig. 5 are in agreement with the effects of these parameters on the dynamic of the model as mentioned above.

In our model the parameter α was incorporated to account for the effect of the slope of the terrain on the geometry of the pattern. Note that $\alpha/90$ is the slope in degrees. In Fig. 6 the empirical relationship between pattern wavelength and the slope is shown to be in agreement with the model prediction, that is, a decrease in the wavelength as α increases (Fig. 5b). In the field the banded pattern is observed on hills with slopes ranging, on average, between 1° and 30° which correspond to wavelengths of 3–10 m, respectively.

3.4. Numerical solution

The numerical solution of the model reproduces the regular pattern observed in the field. Along the spatial axis x , biomass shows a periodic pattern with peaks of vegetation density separated by gaps without vegetation. Also, the vegetation density over all the simulated spatial domain is higher than the density predicted by the homogeneous model (Fig. 7a). We extracted the dominant frequencies from the numerical simulation by a power spectrum analysis. Similar results, for the vegetation density and fog-water supply were found. The power spectrum analysis for vegetation density is presented in Fig. 7b. Using the same set of parameters values, in Fig. 7c we show that the wavelength predicted by the numerical simulation is in agreement with the wavelength expected by the analytical dispersion relation. Recall that the wavelength is $\zeta = 2\pi/k$.

4. Discussion

Regular banded patterns have been described in several resource-limited ecosystems around the world and shown to result from a balance of positive and negative feedbacks between water and biomass, coupled with dispersion (Klausmeier, 1999; Rietkerk et al., 2004; Barbier et al., 2006; Deblauwe et al., 2008; Rietkerk and van de Koppel, 2008; van de Koppel et al., 2008).

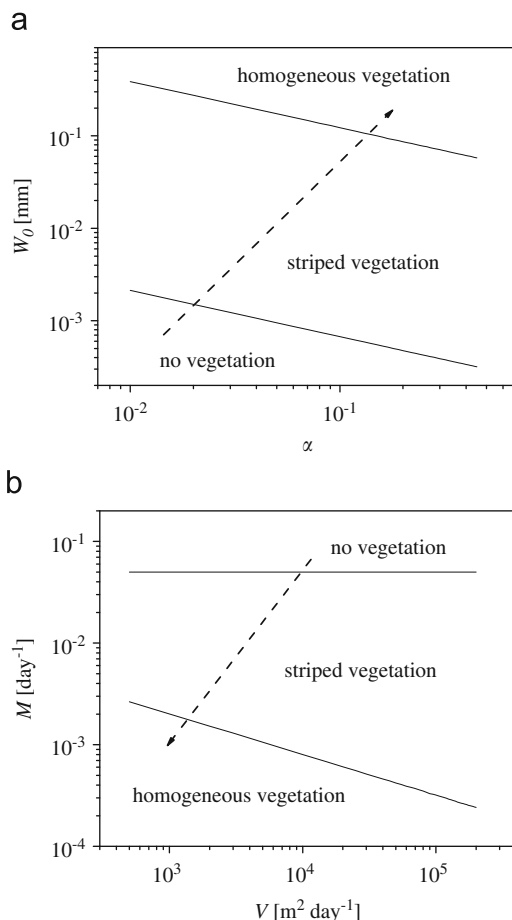


Fig. 2. Parameter space under which the model predicts a transition from a bare state without vegetation to a homogeneous vegetation state, indicated with black arrows. In (a) the transition is achieved as W_0 and α increase while in (b) a similar situation is observed as M and V decrease. All the parameters are in a logarithmic scale.

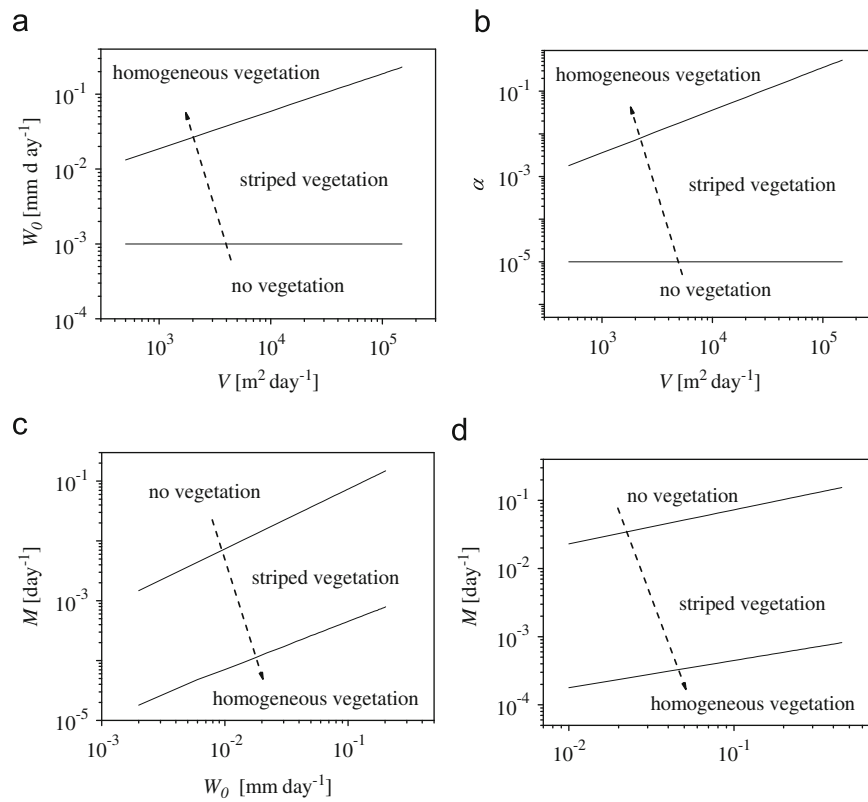


Fig. 3. Parameter space under which the model predicts a transition from a bare state without vegetation to a homogeneous vegetation state, indicated with black arrows. In (a, b) the transition is achieved as W_0 or α increase and V decreases while in (c, d) as W_0 or α increase and M decreases. All the parameters are in a logarithmic scale.

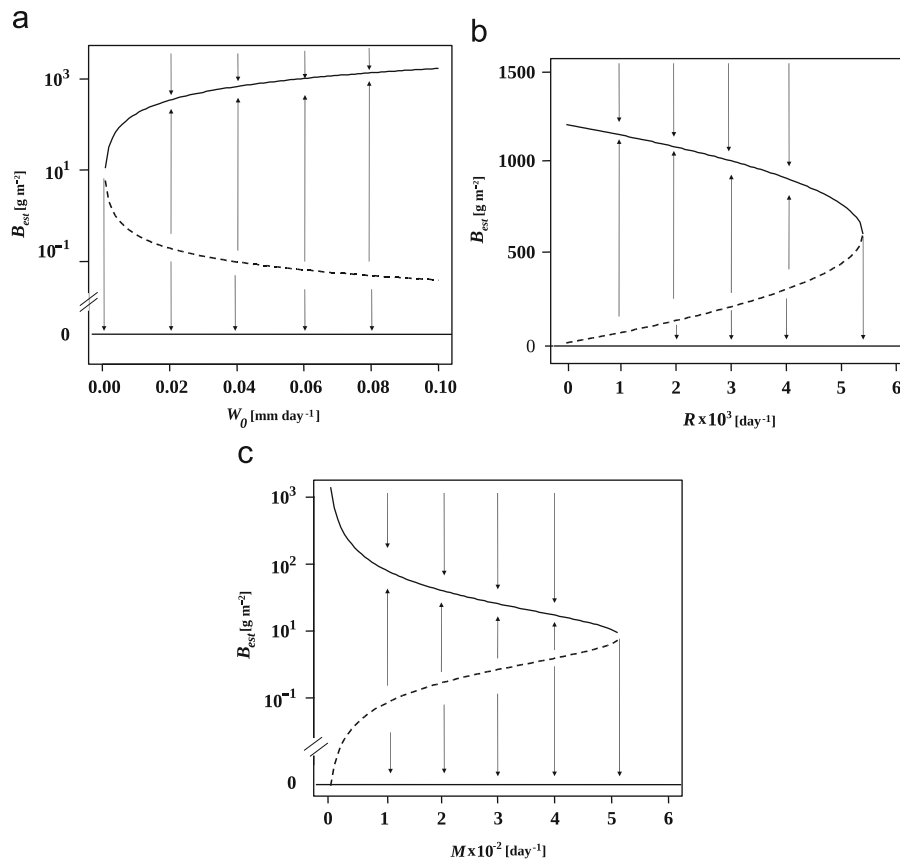


Fig. 4. Bifurcation diagrams for: (a) W_0 , (b) R and (c) M . The solid lines represent the stable states whereas the dashed lines represent the unstable states. In all cases the arrows indicate the direction of change in plant biomass (see text for the threshold values at which the bifurcation in the model is observed). In (a) and (c) B_{est} is in logarithmic scale.

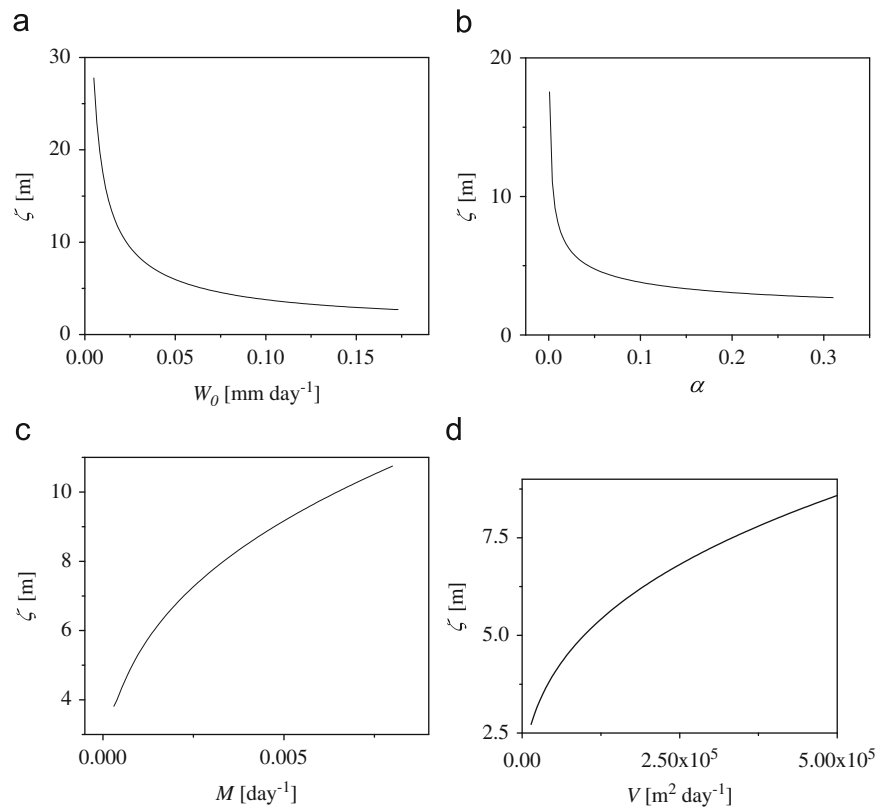


Fig. 5. Expected relationship between the wavelength ζ of the pattern and W_0 , α , M and V .

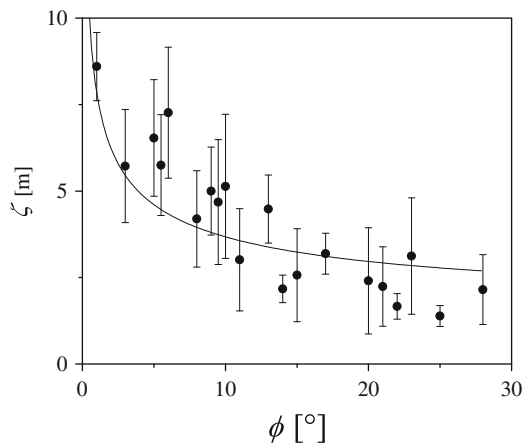


Fig. 6. Relationship between the wavelength ζ of the banded pattern and the slope of the terrain for *T. landbeckii* bands (dots), and the relationship between the wavelength expected by 500 the model and the parameter α 90° (entire line). The bars are the 95% confidence intervals.

Until now, most modeling examples of banded pattern formation came from ecosystems where water flow is unidirectional and driven by gentle sloped terrains (Macfadyen, 1950; Klausmeier, 1999; Valentin et al., 1999; Rietkerk et al., 2002; Sherratt, 2005; Rietkerk and van de Koppel, 2008, but see Couteron and Lejeune, 2001). Herein, using a modified version of the model proposed by Klausmeier (1999) we demonstrated that a simple model based on the displacement of fog-water by wind and its interception by vegetation can reproduce the banded pattern observed in *Tillandsia landbeckii* stands in the Coastal Atacama desert. This is the first time that a banded vegetation pattern produced by the advection of fog-water input is mathematically modeled, contributing to the theoretical hypothesis of spatial self-organization

as the main explanation for the occurrence of regular spatial patterns in resource-limited ecosystems.

As emphasized above, two key differences of this ecosystem to others that show banded vegetation patterns are: (1) it is a fog-dependent system, so the sloping of the terrain takes a different structural role that of intercepting the horizontal advective flow of fog, in comparison to previous models for ecosystems where slope of the terrain modulates the flow of water downhill (Rietkerk et al., 2002), and also, (2) the plants do not have a functional root systems (Rundel and Dillon, 1998) implying that spatial differences in the infiltration rate between vegetated areas and bare soil is not important to induce the pattern formation as has been proposed in previous models (HilleRisLambers et al., 2001; Rietkerk et al., 2002). *T. landbeckii* plants have multiple narrow leaves covered by dense water absorbing trichomes in their surface (Rundel and Dillon, 1998). Thus, the interception of fog-water by the vegetation surface is the key process that gives raise to a regular banded pattern. Since the slope of the terrain modulates the interception of advective fog-water we also incorporate in the model a parameter, α , that weights the effect of the local topography on the vegetation pattern formation. This is an important difference with previous models in which the development of the vegetation pattern is controlled by the terrain slope to the extent that it affects the surface water flow downhill (Klausmeier, 1999; Rietkerk et al., 2002; but see Sherratt, 2005; Ursino, 2005).

Our model predicts how the parameters may affect the conditions under which the banded pattern will emerge. It shows that a transition is expected from an uniform vegetated state, at high water input and/or low plant mortality, to a desert state, at low water input and/or high plant mortality, throughout intermediate banded states. Consistently with that, we also found that the wavelength of the pattern is a non-linear decreasing function of the fog-water input and a non-linear increasing function of

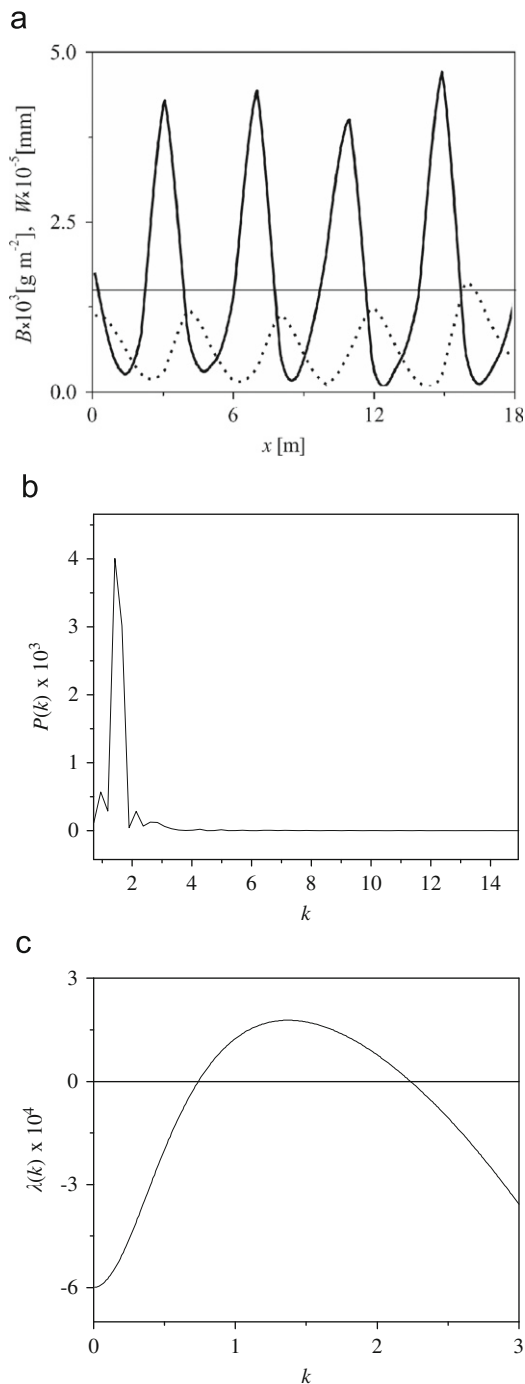


Fig. 7. (a) Regular pattern formation along the spatial axis x . Vegetation density (solid line) and the fog-water supply (dashed line) predicted by the full model. The horizontal line corresponds to the vegetation density predicted by the homogeneous model, $B_{\text{est}} = 1.500$. The parameter values are: $W_0 = 0.06$, $R = 1.2$, $\alpha = 0.05$, $c = 0.3$, $e = 15$, $M = 0.0006$, $D = 0.0001$ and $V = 50.000$. The equations were solved numerically on the domain $0 < x < 200$ m with periodic boundary conditions. (b) Power spectrum analysis showing the dominant wavenumber for the vegetation density data produced by the numerical simulation. (c) The dispersion relation for the same set of parameter values.

plant mortality. These findings are in agreement with model results previously reported by several authors (Klausmeier, 1999; von Hardenberg et al., 2001; Rietkerk et al., 2002; Ursino, 2005; Sherratt, 2005; Liu et al., 2008). Furthermore, Rietkerk et al. (2000) analyzing the effect of varying herbivore impact upon vegetation pattern, provide empirical evidence on the effect of

plant loss on pattern formation. Similarly, van de Koppel et al. (2002) found that the reduction in vegetation cover by herbivores beyond a critical threshold can lead to a collapse of the vegetation, what is consistent with our model predictions. Moreover, these authors have noted that the reduction of vegetation cover, may lead to overgrazing in the remaining vegetated patches. They suggest that the herbivore redistribution creates a positive feedback between reduced cover and increased grazing, which may lead to a desert state.

Most models show that gentle slopes are required for the banded pattern to emerge, as a sloped terrain allow for an unidirectional sheet flow of rainfall water (Klausmeier, 1999; dHerbes et al., 2001; von Hardenberg et al., 2001; Sherratt, 2005; Esteban and Fairen, 2006; Sherratt and Lord, 2007). One of the complications of these analyses is that it is difficult to separate the effect of topography *per se* from the effect of the speed of the water flow on the pattern geometry. Indeed, Sherratt (2005), analyzing the model of Klausmeier (1999), shows that the pattern wavelength is an increasing function of the terrain slope, using the velocity of the downhill flow as indicative of the steepness of the slope. In our case, since water input depends on the advection of fog and is independent of the slope of the terrain we are able to distinguish the effect of slope on the pattern geometry from the effect of the speed of the fog-water flow. Our model predicts that both parameters have opposite effects on the geometry of the pattern. On one hand, the wavelength of the pattern is a non-linear decreasing function of the steepness of the slope, while it is an increasing function of the speed of the fog-water flow. Thus, the slope has a similar effect as the amount of fog-water input, via increasing ECW, while the effect of the speed of the fog-water flow is most similar to the effect of plant loss. This imply that if the slope is steep, the ecosystem could tolerate lower values of water input or higher values of plant loss, compared to a flat scenario, and even so the regular pattern could be observed. Further, our model lead us to hypothesize that plants growing in flat areas would be more physiologically stressed as a result of a lower fog-water input.

Our model suggest that the slope of the terrain could have a different structural role in the formation of pattern than previously identified. In fog-dependent ecosystems the slope of the terrain determine the effective capture of fog-water by a local plant due to changes in what has been called, a fog-shadow effect (del-Val et al., 2006). Here, the fog-shadow is the negative effect that a band could have on the band immediately behind it because of a reduction in water availability. In general, this inhibitory effect in runoff-dependent ecosystems occurs via the root system, which allows the plant to extend its influence beyond the edges of the aerial crown and so extract water and nutrients from the intercanopy zones (von Hardenberg et al., 2001; Barbier et al., 2008; Ursino, 2009) creating a shadow or a local reduction in resource availability. In the Atacama Desert the plant responsible for the pattern formation does not have a functional root systems (Rundel and Dillon, 1998). However, the negative effects are associated to the fact that the depletion of fog-water by the vegetation in a band is manifested as a decrease in water input up to a distance, beyond which, a new windward facing band can establish. A similar mechanism has been postulated for the emergence of regular spatial pattern described in mussel beds (van de Koppel et al., 2005b, 2008). Consequently, this fog-shadow effect should be more pronounced in flat surfaces while the opposite effect could be expected in steeper slopes determining the geometry, and in particular, the wavelength observed in the banded pattern. Further, since the studied area exhibits a wide range of slopes, we were able to test the model prediction, finding a strong agreement between the model and the observed pattern, thus validating the model.

Other factors, not considered in the model, can affect the formation of a banded vegetation pattern by affecting EWC, and may be associated to the scatter observed in the relationship between slope and wavelength (see Fig. 6). For example, the content of water in the fog decreased from the ocean (where the fog is originated) to the *Tillandsia* stands due to the evaporation of fog droplets when fog is advected over the continental surface (Cereceda et al., 2008). Similarly fog occurs in a well delimited range of altitudes between 500 and 1100 m within which the amount of fog-water also varies thus affecting the amount of water that a *Tillandsia* stand could receive. Indeed, it has been reported in the studied area that the higher the elevation where a plant stand occur the higher would be the water content in the fog (Cereceda et al., 2002, 2008). In addition, wind regimes could play an important role in the amount of water present in fog but mainly due to its temporal variation associated to the differential warming between the sea and the continent experimented during a day (nights vs. morning) or along a year (winter vs. summer) (Cereceda et al., 2008). Finally, apart from these physical factors, the removal of plant biomass by herbivores could also explain the variability observed in the *Tillandsia* stands. However, although herbivore insects have been reported in *Tillandsia* stands, no data has yet been collected on their potential effect. Although, our own observations and monitoring of stems through time suggest that the effect of herbivores is minimal.

The emergence of a banded pattern formation has an important effect on plant productivity. The numerical simulation demonstrates that total amount of biomass that a given area can support is increased by the formation of the regular pattern as compared to the situation expected under a spatially homogeneous model (von Hardenberg et al., 2001; Rietkerk et al., 2002; van de Koppel and Rietkerk, 2004). In a recently study, van de Koppel et al. (2008) provided experimental evidence showing that pattern formation in mussel beds improves individual growth and survival what is reflected, at the pattern scale, in higher productivity and resilience. However, productivity and resilience might not always be positively coupled in pattern formation. Indeed, Yizhaq et al. (2005) found that banded patterns with lower wavelengths are more productive but are also more vulnerable to environmental changes such as a precipitation reduction.

The study of pattern formation may provide a way to better understand and create early warning systems (see Scheffer et al., 2009) for the impacts of global environmental change, one of the major challenges ahead of us. Along this line, ecosystems modeling has allowed considerable advances generating strong predictions about the behavior of real ecosystems under extreme conditions. For example, the desertification phenomenon (an abrupt shift to a desert state), which is irreversible and mainly attributed to a decrease in rainfall (Rietkerk et al., 2004), can also occur due to changes in external conditions that reduce resilience without affecting the equilibrium state of the system, which appears unaltered until it suddenly shifts to a more degraded state (Scheffer et al., 2001; Scheffer and Carpenter, 2003). Several authors have emphasized that the shape of the vegetation pattern should be taken as an early warning signal of the fact that ecosystems may suddenly undergo irreversible shifts (Rietkerk et al., 2004; Kefi et al., 2008; Ursino, 2009). This is specially important if it is considered that arid and semi-arid ecosystems are among the most sensitive to climate change (Kefi et al., 2008).

In summary, we show in this study, for the first time, that the formation of banded vegetation patterns can develop under advective water inputs as in the fog-dependent ecosystems in the Atacama Desert. Further, we show that the mechanisms, based on scale-dependent feedbacks, are common to a variety of arid runoff-dependent ecosystems. We also show that the

emergence of pattern and its geometry depends on a series of parameters, being the most important fog-water input, slope of the terrain, plant loss and speed of the fog-water flow. In particular, we show that a wide range of combination of values of parameters could lead to a regular banded pattern. This results contribute to the growing body of studies that demonstrate the importance of self-organization in arid ecosystems.

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