

Feedbacks between vegetation pattern and resource loss dramatically decrease ecosystem resilience and restoration potential in a simple dryland model

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Received: 17 August 2012 / Accepted: 1 March 2013 / Published online: 17 March 2013
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Abstract Conceptual frameworks of dryland degradation commonly include ecohydrological feedbacks between landscape spatial organization and resource loss, so that decreasing cover and size of vegetation patches result in higher water and soil losses, which lead to further vegetation loss. However, the impacts of these feedbacks on dryland dynamics in response to external stress have barely been tested. Using a spatially-explicit model, we represented feedbacks between vegetation pattern and landscape resource loss by establishing a negative dependence of plant establishment on the connectivity of runoff-source areas (e.g., bare soils). We assessed the impact of various feedback strengths on the response of dryland ecosystems to changing external conditions. In general, for a given external pressure, these connectivity-

mediated feedbacks decrease vegetation cover at equilibrium, which indicates a decrease in ecosystem resistance. Along a gradient of gradual increase of environmental pressure (e.g., aridity), the connectivity-mediated feedbacks decrease the amount of pressure required to cause a critical shift to a degraded state (ecosystem resilience). If environmental conditions improve, these feedbacks increase the pressure release needed to achieve the ecosystem recovery (restoration potential). The impact of these feedbacks on dryland response to external stress is markedly non-linear, which relies on the non-linear negative relationship between bare-soil connectivity and vegetation cover. Modelling studies on dryland vegetation dynamics not accounting for the connectivity-mediated feedbacks studied here may overestimate the

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resistance, resilience and restoration potential of drylands in response to environmental and human pressures. Our results also suggest that changes in vegetation pattern and associated hydrological connectivity may be more informative early-warning indicators of dryland degradation than changes in vegetation cover.

Keywords Resource-leakiness feedbacks · Vegetation spatial pattern · Hydrological connectivity · Desertification · Resilience · Restoration potential · Dryland ecosystems

Introduction

The vegetation of dryland ecosystems is typically distributed in patches interspersed within a matrix of bare ground and low vegetation (Aguilar and Sala 1999; Deblauwe et al. 2008). A number of ecosystem models considering spatial interactions (so-called spatially-explicit models) have successfully described the wide variety of vegetation patterns observed in dryland landscapes worldwide (e.g., von Hardenberg et al. 2001; Kéfi et al. 2007a; Manor and Shnerb 2008; von Hardenberg et al. 2010; Rietkerk et al. 2002). Aside from studying the origin of the patterns, several of these modelling works have explored the impacts of changing climatic conditions and disturbance on vegetation cover and pattern with the aim to derive predictive models for critical transitions from vegetated to degraded states. Recent results suggest that changes in vegetation-pattern properties, such as patch-size distributions (Kéfi et al. 2007b, 2011) or spatial regularity (Rietkerk et al. 2004; Kéfi et al. 2010) could predict such undesired transitions ultimately leading to desertification and associated substantial losses in ecosystem services (Schröter et al. 2005).

So far, the main mechanisms considered in dryland vegetation models are resource-concentration (i.e., resource concentration near the plants and depletion further away leading to long-distance negative plant–plant interactions) and local facilitation (i.e., positive plant–plant interaction due to environment amelioration near the plants). Most of the models including resource concentration as a pattern-driving mechanism account explicitly for feedbacks between vegetation and water availability at the local scale, such as the positive feedback between plant biomass and

increased soil infiltration capacity (e.g., von Hardenberg et al. 2001; Rietkerk et al. 2002). In addition to the internal redistribution of resources, the degree of conservation or loss of resources by the landscape (i.e., resource leakiness) is also considered to be crucial in dryland ecosystem dynamics (e.g. Hillerislambers et al. 2001; Rietkerk et al. 2002; Scanlon et al. 2007; Okin et al. 2009). Both vegetation cover and vegetation pattern greatly impact the potential of the ecosystem to conserve key resources such as water, soil, and nutrients (Abrahams et al. 1995; Ludwig and Tongway 1995; Cammeraat and Imeson 1999; Wilcox et al. 2003; Puigdefábregas 2005; Bautista et al. 2007; King et al. 2011). A number of pattern attributes have been reported to affect resource leakiness, including the ratio between runoff-source and runoff-sink areas (Urgeghe et al. 2010), the connectivity of the runoff-source areas (Bautista et al. 2007; Ludwig et al. 2007; Moreno-de las Heras et al. 2012), the degree of aggregation of vegetation patches (Franz et al. 2012), and the dominant shape and orientation of the vegetation patches (Puigdefábregas et al. 1999). Therefore, any given pattern can be associated to a certain potential for conserving resources, which in turn would affect the conditions of the system and therefore the factors that determine vegetation pattern dynamics. Conceptual frameworks of desertification have largely acknowledged these ecohydrological feedbacks (e.g., Brandt and Thornes 1996; Ludwig et al. 1997). According to these frameworks, a significant reduction in the cover and size of vegetation patches due to disturbance is accompanied by an increase in the amount and spatial connectivity of bare-soil interpatches, which increases the potential for higher hydrological connectivity of the system (i.e., the actual connectivity of runoff and sediment flows) (Abrahams et al. 1995; Bautista et al. 2007; Ravi et al. 2010; Ludwig et al. 2007; Turnbull et al. 2010; Moreno-de las Heras et al. 2012). In turn, the depletion of water and soil resources from the landscape driven by runoff may negatively affect plant establishment and functioning of established plants (McIvor et al. 1995; Holm et al. 2002; García-Fayos et al. 2010), resulting in a positive feedback to the loss and fragmentation of the vegetation patches. Thus, along a degradation path driven by increasing anthropic or climatic pressure on the system, we expect that feedbacks between vegetation pattern and resource leakiness accelerate the transition to a

degraded state, therefore decreasing the maximum perturbation that the system can stand without shifting to an alternative stable state (i.e., decreasing the resilience of the system, *sensu* Holling 1973). Similarly, the restoration potential of a degraded system can also be affected by these feedbacks, as high resource leakiness in degraded stages could hamper recovery. Despite the existing consensus on the crucial role of such connectivity-mediated feedbacks in the behavior of dryland ecosystems, their impact on dryland response to land degradation drivers has been barely tested and assessed in experimental or modeling studies (but see Helldén 2008).

Our background assumption is that current spatially-explicit models on vegetation-pattern dynamics that focus on the interplay between vegetation pattern and critical transitions would derive more realistic predictions if feedbacks mediated by changes in the hydrological connectivity of the bare soil, and the associated redistribution and export of resources, are considered. In this study, we extended the model of Kéfi et al. (2007a), which already includes local facilitation among plants, to study how these connectivity-mediated feedbacks between vegetation pattern and ecosystem resource leakiness shape the ecosystem response to changing environmental and human pressure. The original model of Kéfi et al. (2007a) exhibits bistability, meaning that two alternative stable states (vegetated and bare) can be reached for the same parameter values depending on the initial conditions. In such bistable systems, the shift from a vegetated to a desert state in response to gradual increasing pressure is sudden (i.e., discontinuous transition), and returning the conditions to those existing before the shift is not sufficient to recover the vegetated state. Thus, degradation and recovery trajectories do not overlap, which is known as hysteresis. In this work, we specifically aim to assess the effect of various connectivity-mediated feedback intensities on the response of dryland ecosystems to changing external conditions in terms of (i) resistance, as the amount of change in the ecosystem state at equilibrium; (ii) occurrence of critical shifts (i.e., presence of bistability); (iii) resilience, as the amount of pressure that the ecosystem can stand without shifting to a degraded stable state; and (iv) restoration potential, as the ecosystem ability to recover from that shift (i.e., size of the bistability region or hysteresis loop).

Methods

The model

The model of Kéfi et al. (2007a) is a stochastic cellular automaton that was built to analyze the links between vegetation patchiness and local facilitation among plants in drylands. Local facilitation is defined here as the combination of physical and biological processes occurring in the local environment of a plant patch that favors the establishment of other plants in the neighborhood of that patch. The model simulates typical patchy landscapes of dryland ecosystems as lattice-structured habitats in which each cell is occupied by vegetation (+), empty (0), or degraded (−). Empty cells have fertile soils where seeds can germinate whereas degraded cells have eroded soils unsuitable for recolonization. The processes and parameters of the model, and the values of the parameters used in this work, are defined in Table 1. The fundamental processes that occur in the model are mortality of vegetated cells, degradation of empty cells, recovery of degraded cells, and colonization of empty cells, which occur, respectively, at the following rates at each time step

$$w_{\{+,0\}} = m, \quad (1)$$

$$w_{\{0,-\}} = d, \quad (2)$$

$$w_{\{-,0\}} = r + fq_{+|-}, \quad (3)$$

$$w_{\{0,+\}} = [\delta\rho_+ + (1 - \delta)q_{+|0}](b - c\rho_+). \quad (4)$$

Local facilitation is modeled as an increased recovery rate of degraded cells when these have more vegetated cells in their neighborhood (Eq. 3), while the spontaneous or basal regeneration rate of a degraded site (r) is assumed to depend on soil type. The colonization rate (Eq. 4) depends on a parameter representing the probability of recruitment of an empty cell, the so-called plant establishment (b). To include feedbacks between vegetation pattern and the global loss of resources from the landscape driven by hydrological connectivity, we modified the model by including a negative impact of landscape resource loss on plant establishment. This loss was estimated with Flowlength (Mayor et al. 2008), a spatial metric designed to be used as a surrogate for the loss of resources on hillslopes where runoff is the main agent of sediment transport and deposition. Flowlength is

Table 1 Process rates and parameters of the model. With the exception of α and FL , parameter values are from Kéfi et al. (2007a)

Symbol	Definition	Value
$w_{\{0,+\}}$	Colonization rate of an empty site	
$w_{\{-,0\}}$	Regeneration rate of a degraded site	
$w_{\{+,0\}}$	Mortality rate of a vegetated site	
$w_{\{0,-\}}$	Degradation rate of an empty site	
ρ_+	Density of vegetated sites	
q_{ij}	Probability of finding a site i in the neighborhood of a site in state j	
m	Mortality probability of a vegetated site	0.005–1
f	Local facilitation strength: maximum effect of a neighboring vegetated site on the regeneration of a degraded site	0.9
β	Intrinsic seed production rate per vegetated site; “survival probability”, “germination probability”	
ε	Establishment probability of seeds on an empty site in a system without competition	
b	Establishment probability of plants on an empty site in a system without competition ($=\beta\varepsilon$). Measures the severity of the environmental conditions; a lower b value reflects a higher aridity level	0–1
δ	Fraction of seeds globally dispersed	0.1
g	Competitive effect of the global density of vegetated sites on the establishment of new individuals	
c	βg	0.2
r	Regeneration probability of a degraded site without vegetation in its neighborhood	0.01
d	Degradation probability of empty sites	0.1
α	Strength of connectivity dependence or strength of feedback between plant pattern and resource leakiness	0–1
FL	Flowlength index	0–26.7

based on the assumption that bare-soil areas (i.e., either empty or degraded cells in the model) behave as sources of runoff and sediments that are trapped by downslope vegetated areas, which behave as sinks of resources. This contrasting behavior of bare and vegetated areas has been confirmed by many studies in drylands worldwide (e.g., Dunkerley and Brown 1995; Reid et al. 1999; Mayor et al. 2009). Flowlength measures the connectivity of bare-soil areas by calculating the average of the runoff pathway lengths from all the cells in the system. The flowpath from each cell is constrained so that it can only progress downslope from pixel to pixel via the neighboring steepest descent cell, as determined by the topography, until it reaches a vegetation patch or flows out of the area of interest (see Mayor et al. 2008 for further details). In this way, the flowpath lengths for the vegetated cells are zero and Flowlength varies with

both vegetation pattern and vegetation cover, with higher values representing higher hydrological connectivity of bare-soil areas. Flowlength has been found to be highly correlated with hillslope and catchment measures of water and soil losses from patchy drylands of Spain and Australia (Mayor et al. 2008; Muñoz-Robles et al. 2011). As knowledge about the type of relationship between plant establishment and bare-soil connectivity, as surrogate of resource leakiness is still not conclusive, we assumed a linear relationship between these two processes, defined as:

$$b' = b \left(1 - \alpha \frac{FL}{FL_{\max}} \right) \quad (5)$$

where b' is the actual plant establishment as affected by the global leakiness of resources from the system; b is the potential plant establishment, which coincides with plant establishment in the original version of the

model of Kéfi et al. (2007a); α modulates the dependence of plant establishment on bare-soil hydrological connectivity, and thus, it represents the strength of the feedback between vegetation pattern and resource leakiness; FL is the Flowlength index; and FL_{\max} is the maximum value of the index, which is obtained from a lattice without vegetated cells. Plant establishment is negatively affected by increased bare-soil connectivity for $\alpha > 0$. For $\alpha = 0$ (i.e., null connectivity-mediated feedbacks), $b' = b$, and thus, the original form of the Kéfi et al. (2007a) model is a particular case of the extended model presented in this work. The strength of the connectivity-mediated feedback (α) lumps factors that may influence either the actual loss of resources from the landscape for a given bare-soil connectivity or the impact of a given loss of resources on plant functioning and establishment. Thus, for low α values the global loss of resources would be low, even if the spatial connectivity of the bare areas is high. Conversely, for high α values, changes in bare-soil connectivity would greatly affect the actual loss of resources. Factors such as soil type, slope angle, and rainfall regime could modulate the strength of the feedbacks for any given bare-soil connectivity, while factors such as the vegetation community composition and diversity, the phenological state of the species, etc. could modulate plant establishment for any given amount of resource loss. For example, the actual hydrological connectivity of the landscape for a given vegetation pattern and bare-soil spatial connectivity will be higher, and closer to its maximum potential, in areas with frequent intense rainfalls, soils prone to generate runoff, and steep slopes (see several examples in Bracken and Croke 2007).

The extended model also considers the topography of the landscape, which together with the plant spatial pattern is used to derive the flow paths needed to calculate the Flowlength index. In this work, we used an idealized planar slope with an angle of 20°. All the simulations were carried out on grids of 100×100 cells with a cell-size of 0.5 m. The corresponding FL_{\max} value for this setting is 26.7 m. The extent of this grid (50×50 m) represents a medium length of a dryland hillslope, which serves us to illustrate the effect of various connectivity-mediated feedback intensities for a given modeled hillslope. However, as it would be expected in real landscapes, the impact of bare-soil connectivity in landscape leakiness

decreases with slope length due to the scale-dependent variation of water and soil losses in drylands (see, for example, Mayor et al. 2011).

Analyses

Our analyses were based on the comparison of the ecosystem state at equilibrium (measured as the proportion of vegetated cells in the steady-state lattice) and the degradation and recovery trajectories for a number of α values representing a gradient of feedback strengths between vegetation pattern and resource leakiness, being the case for $\alpha = 0$ the conditions considered by the original model of Kéfi et al. (2007a).

In a first experiment, we analyzed the ecosystem state at equilibrium for varying disturbance and environmental conditions (i.e., resistance). The gradient of disturbance (i.e., vegetation removal) was simulated by varying the probability of mortality (parameter m) between model runs. The gradient of environmental conditions was simulated by varying the probability of plant establishment (parameter b ; the worsening of environmental conditions, e.g., higher aridity, leads to lower plant establishment). For each parameter combination, simulations were run until steady-state bare-soil hydrological connectivity (i.e., Flowlength index) was reached. For this experiment, we started all the simulations by randomly introducing in the lattice 50 % of vegetated cells, 25 % of empty cells, and 25 % of degraded cells.

In a second experiment, we analyzed the effect of varying α values on (i) the occurrence of critical shifts from vegetated to desert states (i.e., bistability), (ii) the amount of stress that the system stands before shifting to a degraded state (i.e., resilience), and (iii) the reversibility of this shift (i.e., restoration potential). We obtained the pathways to collapse and recovery of the vegetation in response to decreasing and increasing trends in b values. For every value of α , we started the experiment from a densely vegetated state (random distribution of 90 % vegetated cells, 5 % empty cells, and 5 % degraded cells) and performed simulations for decreasing values of b . We repeated this until b reached a critical threshold at which vegetation collapsed. We proceeded similarly for the recovery path (increasing values of b), starting the experiment from a random lattice with 1 % of vegetated cells, 5 % of empty cells, and 90 % of degraded cells. We repeated this experiment for increasing values of m . As

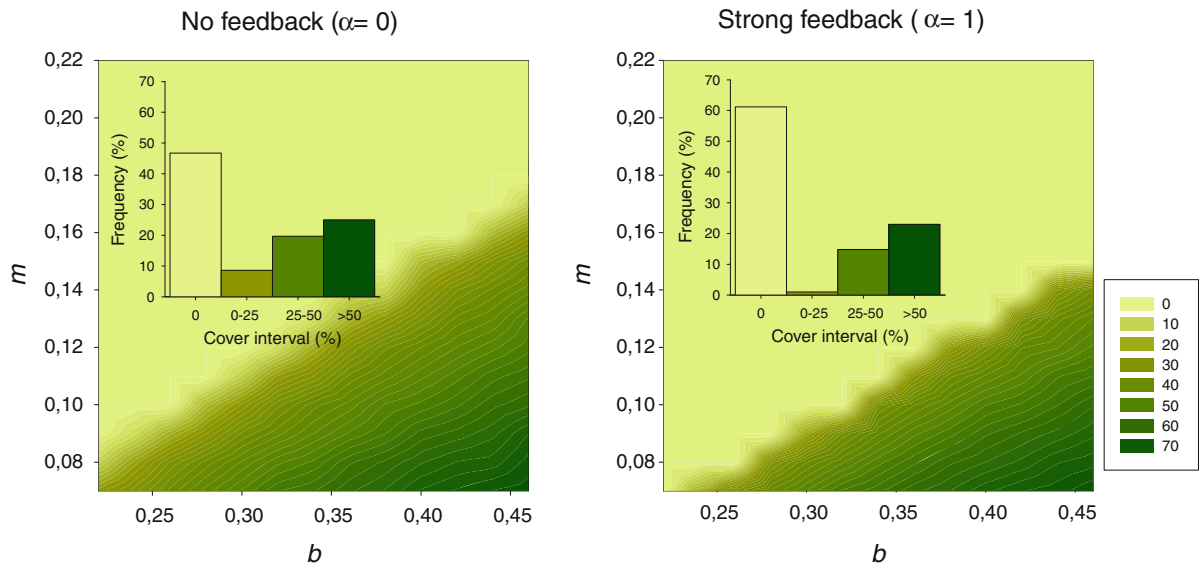


Fig. 1 Vegetation cover at equilibrium predicted by the model with null and strong feedbacks between vegetation pattern and resource leakiness ($\alpha = 0$ and $\alpha = 1$, respectively) for a gradient of disturbance (m) and of environmental conditions

in the former experiment, each simulation was run until the hydrological connectivity of the system reached equilibrium (i.e., steady-state of Flowlength). The values of the other parameters were kept the same in all simulations (see Table 1).

Results

Figure 1 shows the values of vegetation cover at equilibrium predicted by the model for null and strong connectivity-mediated feedbacks between vegetation pattern and resource leakiness ($\alpha = 0$ and $\alpha = 1$, respectively) for a gradient of initial environmental conditions (b) and disturbance (m). For all parameter combinations, vegetation cover at equilibrium was always equal or lower for $\alpha > 0$ than for $\alpha = 0$ (no feedbacks). The higher the value of α (α values of 0, 0.2, 0.5, and 1 were tested; Fig. 1 only shows the results for the most contrasting α values, $\alpha = 0$ and $\alpha = 1$) the lower the resistance of the system (i.e., larger decrease in vegetation cover at equilibrium for the same b and m values). As showed in the histograms in Fig. 1, bare states were more frequent for $\alpha > 0$. Also, the frequency of systems with low vegetation cover (below ≈ 25 %, for the parameter values used

(b). A lower b value represents harsher environmental conditions. The plots within the lattices show the frequency distribution of the vegetation cover values at equilibrium for several vegetation cover intervals

here) was almost null when feedbacks were strong ($\alpha = 1$).

The analysis of the dynamics towards equilibrium of bare-soil cover and bare-soil connectivity, as measured with the Flowlength index, provides insights about the role of the represented feedbacks in the behavior of the system. Figure 2 displays such data for null and strong feedbacks ($\alpha = 0$ and $\alpha = 1$, left and right graphs, respectively) and two levels of environmental stress ($b = 0.34$ and $b = 0.32$, top and bottom graphs, respectively). Depending on the initial values of environmental stress (b), the impact of the connectivity-mediated feedbacks on the system state at equilibrium greatly varied (e.g., almost no impact for $b = 0.34$ and the collapse of the vegetation cover for $b = 0.32$; Fig. 2). When feedbacks are not considered (Fig. 2, left), a small increase in environmental stress hardly affect the system state at equilibrium. When feedbacks are considered (Fig. 2, right), if the system exceeds critical cover-connectivity values in the transition to equilibrium (around 75 % of bare-soil cover and 2 m of Flowlength index for the parameter setting used in this work; Fig. 2, bottom right), the bare-soil connectivity quickly increases, and its positive feedback with plant establishment quickly leads to the collapse of the system. This non-linear

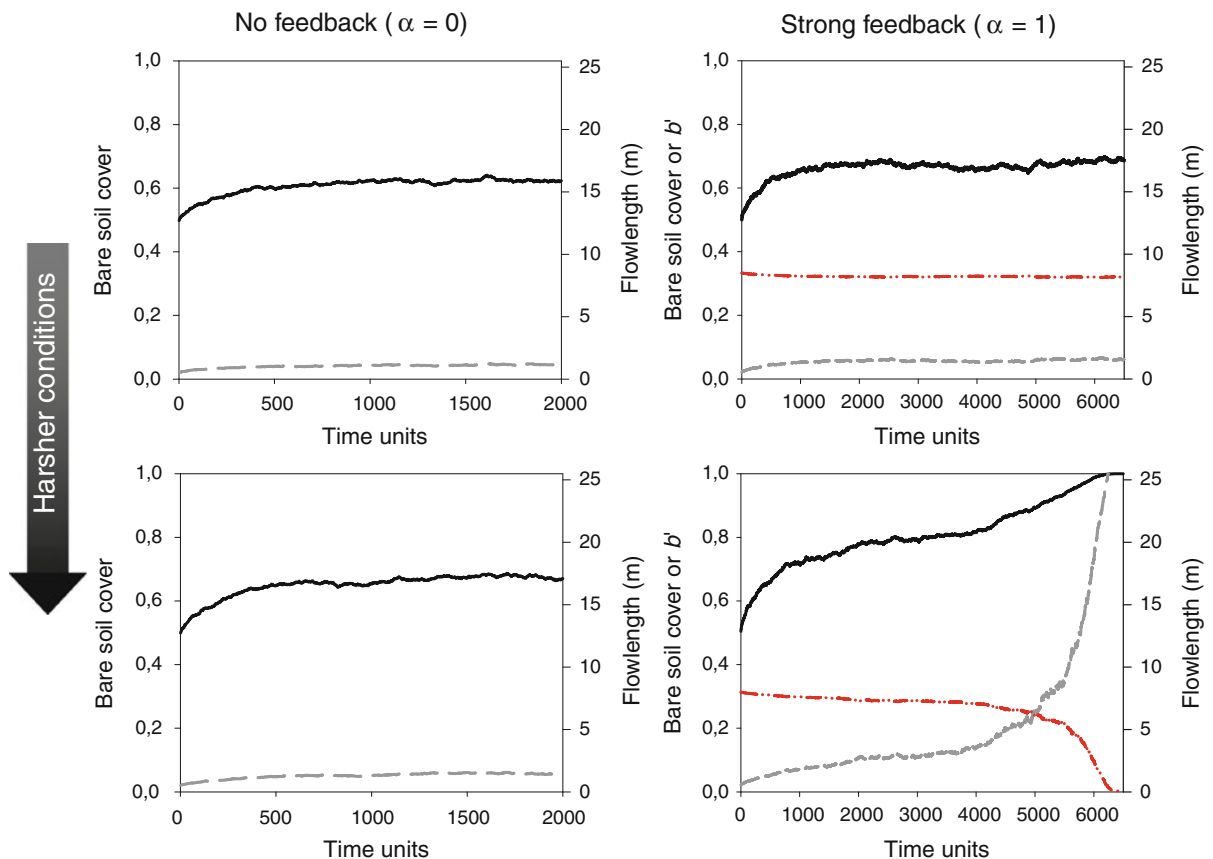


Fig. 2 Variation in bare-soil cover (solid black line), Flowlength index (dashed grey line), and b' , plant establishment as modified by Flowlength index (dash-dotted red line, right plots) along simulations runs for $\alpha = 0$ (left) and $\alpha = 1$ (right),

$b = 0.34$ (top) and $b = 0.32$ (bottom). In all cases initial vegetation cover = 50 %, $m = 0.1$, $c = 0.2$, $d = 0.1$, $f = 0.9$, $r = 0.01$, $\delta = 0.1$. (Color figure online)

effect of the connectivity-mediated feedbacks on the resistance of the system to increasing stress results from the non-linear inverse relationship between bare-soil connectivity and vegetation cover (Fig. 3).

Feedbacks between vegetation pattern and resource leakiness increase the occurrence and irreversibility of shifts from vegetated to desert states. These results are illustrated with an example in Fig. 4, which shows the changes in vegetation cover at equilibrium along degradation and recovery trajectories in response to gradual changes in environmental conditions (b) for two values of mortality (m) and several strengths of connectivity-mediated feedbacks (α). For the lowest mortality value ($m = 0.10$; Fig. 4, left), the model outputs for $\alpha = 0$ (no feedbacks) predict a gradual decrease of vegetation cover with the gradual worsening of environmental conditions. However, when connectivity-mediated feedbacks are considered

($\alpha > 0$), the transition from a vegetated to a bare state is sudden, even for low α values. Similarly, when $\alpha = 0$, starting from a bare state, vegetation cover increases progressively if environmental conditions improve (i.e., degradation and recovery trajectories overlap). However, when $\alpha > 0$, the improvement of the environmental conditions back to the level at which the shift occurred did not result in the recovery of the system, which required being under much less harsher environmental conditions (higher b values) to be able to recover. Therefore, in these cases, degradation and recovery trajectories did not overlap (i.e., hysteresis). The larger the α value, the lower the amount of stress required to cause a shift of the system to a bare state (i.e., lower resilience), and the larger the size of this hysteresis loop or bistability region. The recovery of the system is even impossible for the strongest feedback ($\alpha = 1$). For a higher mortality

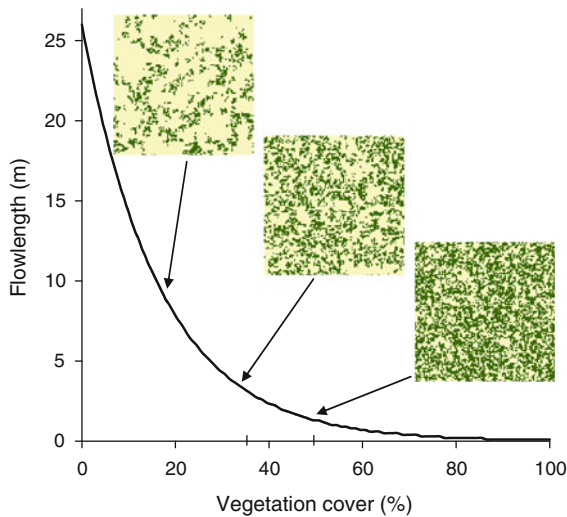


Fig. 3 Relationship between vegetation cover and Flowlength index. The values of vegetation cover and FL in the snapshots (green: vegetated cells; cream: bare-soil cells) are, from right to left: 51, 34, and 17 %, and 0.63, 1.44, and 4.79 m, respectively. (Color figure online)

value ($m = 0.20$; Fig. 3b), the model outputs predict discontinuous transitions for all α values (with and without feedbacks), but the size of the hysteresis loop is larger for $\alpha > 0$. In this latter case, the recovery of the system is not possible even for moderate feedback strength ($\alpha = 0.5$).

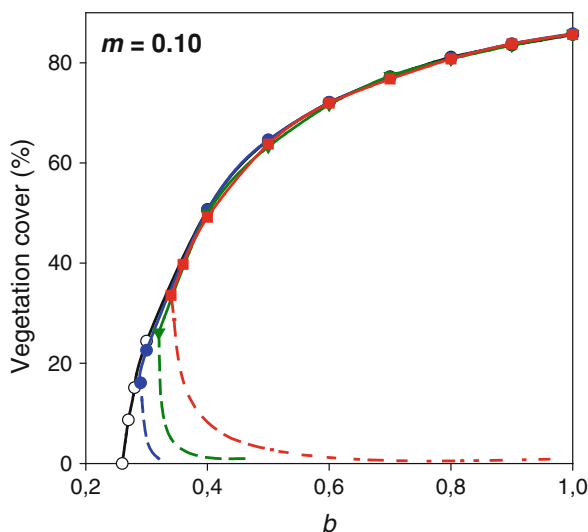
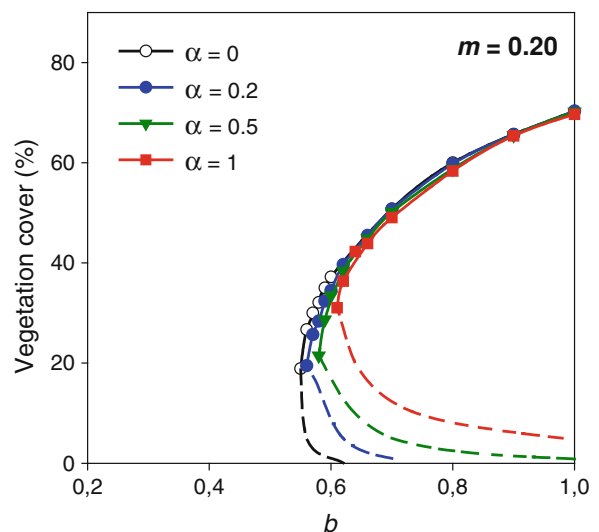


Fig. 4 Bifurcation diagrams: variation in vegetation cover at equilibrium in response to changing environmental conditions (b , a lower value represents harsher conditions) and two levels of disturbance ($m = 0.1$, left plot; $m = 0.2$, right plot) as a

Discussion

We extended an existing spatial model of dryland vegetation dynamics by including feedbacks between vegetation pattern and resource loss that are mediated by changes in the connectivity of the bare-soil. Using this model, we analyzed the role of these connectivity-mediated feedbacks in the response of drylands to changing environmental and human pressure. The extended model mimics that increasing bare-soil connectivity (i.e., increasing spatial connectivity of runoff sources and increasing potential for resource loss) has a negative impact on plant establishment, which in turn may increase the amount and spatial connectivity of the bare-soil areas, completing a positive feedback loop. These important ecohydrological feedbacks are one of the fundamental assumptions of many conceptual frameworks synthesizing the interactions between landscape patterns and processes in semiarid ecosystems (e.g., Brandt and Thornes 1996; Ludwig et al. 1997). However, in spite of their wide recognition, their influence in ecosystem dynamics has been barely assessed in previous experimental or modelling work, and thus our study constitute one of the first attempts to do it.

Our results show that feedbacks between vegetation pattern and connectivity-mediated resource loss decrease the resistance and resilience of the system



function of the strength of the feedback between plant pattern and resource leakiness (α). Continuous lines represent stable equilibria and dashed lines represent unstable equilibria

to environmental and human pressure (e.g., aridity, overgrazing), leading to a dramatic increase in the risk of sudden discontinuous transitions and their irreversibility. The impact of these feedbacks depends on the initial potential for plant establishment, the magnitude of external pressures, and the strength of the feedbacks. Quantification of the actual impacts of these connectivity-mediated feedbacks in natural dryland dynamics is lacking. However, a growing body of literature suggests that both sudden and gradual variations in resource availability (e.g., due to drought and/or temperature increase) can lead to sudden shifts in dryland ecosystems (Foley et al. 2003; Breshears et al. 2005).

Our model outputs show that the influence of the mimicked feedbacks in the response of the system to external stress (i.e., resistance) is markedly non-linear. This result is linked to the also non-linear increase in hydrological connectivity with increasing bare-soil cover. According to this relationship, if bare-soil cover increases in a densely vegetated system, the connectivity of the system, and hence resource conservation/loss, are barely affected and the impact of the feedback on vegetation cover and pattern will be small. However, if bare-soil connectivity increases above certain values, a significant loss of resources would take place, greatly limiting plant establishment and causing the system to shift into a degraded state. Indeed, when moderate to strong feedbacks are considered, our model predicts that, for any level of external stress, the only possible stable system below a vegetation cover value around $\approx 25\%$ (which roughly corresponds with a Flowlength value of 2 m for the patterns tested in this work) is a bare state. This critical cover-connectivity value could be interpreted as a resilience threshold, beyond which the systems would enter into a desertification loop that ends in a stable degraded state (cf. Rietkerk and Van de Koppel 1997).

According to the model outputs, the loss of resources in degraded states may hamper the natural recovery of the ecosystem even if the external pressure is released. The influence of connectivity on plant establishment makes more difficult that the recovery rate of the system outbalances the loss rate. A recent coupled human-environment dynamic model for desertification (Helldén 2008), suggests that feedbacks between vegetation cover and erosion may increase the recovery period of a degraded system (10–20 years without feedbacks and 20–40 years with

feedbacks) but will not lead to an irreversible stage, unless the soil becomes extremely thin. However, recent results from long-term observational studies support the existence of such ecological thresholds for irreversible degradation. Gao et al. (2011) studied natural recovery of degraded forest areas in China during 25 years after the suppression of grazing disturbance, finding that natural recovery of the sites was possible where initial vegetation cover was above 20 %. On the contrary, if the system had crossed this threshold, vegetation cover continued decreasing slowly throughout the study period despite the lack of disturbance.

The acceleration of the hydrological connectivity of the system for low cover values that was observed in our study (Fig. 3) has been described by previous works (e.g., Ludwig et al. 2007), and it is also consistent with conceptual models of soil loss based on percolation theory, which assume that critical threshold values of bare-soil cover lead to sharp changes in the probability of runoff-source areas being connected (e.g., Davenport et al. 1998). Numerous works support the non-linear, and often threshold-driven relationship between resource conservation and vegetation cover for a wide range of dryland environments (e.g., Elwell and Stocking 1976; Francis and Thornes 1990; Abrahams et al. 1995; Ludwig and Tongway 1995; Davenport et al. 1998; Ludwig et al. 2007). Our results point to feedbacks mediated by changes in the hydrological connectivity of the system as the causative mechanism for this markedly non-linear and threshold-like behavior that has often been observed in dryland ecosystems. These results are supported by a recent analysis of remotely sensed Australian mulga landscapes, which indicates that small reductions in plant cover near a threshold can cause abrupt changes in ecosystem function driven by nonlinear changes in hydrological connectivity measured with Flowlength (Moreno-de las Heras et al. 2012). Cross-scale interactions and feedbacks with other drivers can also affect vegetation pattern dynamics in drylands, either amplifying or buffering the risk of sudden regime shifts (Peters et al. 2004; Allen 2007; Browning et al. 2012). Further, degrading landscapes may alter the relative importance of wind versus water erosion in dryland ecosystems (Ravi et al. 2010), which highlights the need to improve our understandings of cross-scale interactions among degradation drivers to better predict degradation

impacts at multiple scales. At any given scale, the role of additional factors such as the diversity of vegetation responses to environmental pressure, feedbacks between individual vegetation patches and local inter-patch connectivity, coevolution of plant pattern and microtopography, and potential anisotropy in vegetation growth also deserve further research.

Interestingly, our results suggest a higher sensitivity of the bare-soil connectivity index (Flowlength index) to changes in the spatial organization of the vegetation during the transition to a degraded state, in comparison with bare-soil (or vegetation) cover, which shows a rather linear evolution during this transition (Fig. 2d). Thus, the acceleration of bare-soil connectivity from spatially-explicit time-series data may provide an early warning of imminent shift. This bare-soil connectivity index could be of special interest for management, since it helps identifying the critical point at which measures should be adopted to prevent drastic changes in ecological conditions (Bestelmeyer 2006). Several promising early-warning signals of critical transitions between alternative stable states have recently been proposed, such as changes in the size distribution of vegetation patches (Kéfi et al. 2007b, 2011) and general indicators of critical slowing down (i.e., slower recovery of a system to equilibrium after a perturbation close to a transition), such as increasing variance, autocorrelation, and skewness (Dakos et al. 2011, 2012). The very limited field testing of these indicators suggests that they may have more or less utility as warning signals depending on the ecosystem type and transition type (Maestre and Escudero 2009; Kéfi et al. 2010; Moreno-de las Heras et al. 2011; Lindegren et al. 2012), pointing to the potential advantages of developing multi-method approaches, tailored to local conditions, to better inform ecosystem management (Dakos et al. 2012; Lindegren et al. 2012).

Some recent empirical works support the main mechanisms and processes involved in the feedbacks studied with our extended model. Thus, there is increasing field evidence on the impact of vegetation cover and pattern on global leakiness of resources (Bautista et al. 2007; Ludwig et al. 2007; Turnbull et al. 2010; Moreno-de las Heras et al. 2012) as well as on the impact of the loss of resources from the landscape on vegetation cover and performance (e.g., García-Fayos et al. 2010). However, empirical knowledge on how these mechanisms feedback each other and how the

intensity of this feedback may be modulated by different factors is still a research frontier.

Conclusions

Our modelling work highlights that simple connectivity-mediated feedbacks between vegetation spatial pattern and the potential net loss of resources from the system can play a crucial role in determining system dynamics and critical shifts in dryland ecosystems. These positive ecohydrological feedbacks dramatically decrease the resistance and resilience to external stress and the recovery potential of the ecosystem, fostering threshold dynamics that are associated to a non-linear increase in hydrological connectivity with decreasing vegetation cover. Thus, ignoring such feedbacks can lead to incorrect conclusions about the risk of critical transitions and their reversibility. Our results suggest that changes in bare-soil connectivity, which result from changes in both vegetation cover and pattern, along degradation trajectories may be more informative than changes in vegetation cover as early-warning indicators of dryland degradation.

Acknowledgments This work was supported by the research projects PATTERN (AGCL2008/-05532-C02-01/FOR) and FEEDBACK (CGL2011-30515-C02-01) funded by the Spanish Ministry of Innovation and Science, the EC-funded projects PRACTICE (GA226818) and CASCADE (GA283068), and the project RESINEE funded by the ERA-Net on Complexity. AGM was supported by a postdoctoral contract (APOSTD/2011/005) from the Valencia Regional Government (Generalitat Valenciana), Spain.

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