Spatial Interactions and Resilience in Arid Ecosystems

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ABSTRACT: We present a mathematical analysis of the consequences
of spatial interactions between vegetation patches by means of water
flow for the functioning of arid systems. Our model results suggest
that spatial exchange of water improved the resilience to disturbances
and increased the resistance to human-induced loss of cover. Fur-
thermore, spatial exchange of water allowed vegetation to persist at
lower rainfall levels compared to systems that lack spatial interactions.
Our analysis stresses the general importance of spatial interactions
for the functioning of ecological systems.

Keywords: positive feedback, spatial model, spatial scale, vegetation
collapse, vegetation patterns.

Ecological theory predicts that positive feedback may in-
voke catastrophic shifts in ecosystems (May 1977; Scheffer
et al. 1993; van de Koppel et al. 1997; Scheffer et al. 2001).
Small stochastic changes in conditions may result in a
runaway reaction in the ecosystem as a consequence of
feedback loops that amplify the initial change. Positive
feedback has been proposed as an explanation for dramatic
changes in a large number of systems such as shallow lakes,
arid grasslands, and arctic tundras (Wilson and Agnew
1992; Scheffer et al. 1993; Rietkerk and van de Koppel
1997; van de Koppel et al. 1997; Bertness et al. 2002; Handa
et al. 2002). Nevertheless, the concept met with severe
criticism, in particular because of unclear criteria for ex-
perimental testing (Sutherland 1974, 1990; Connell and
Sousa 1983). Especially spatial heterogeneity, evident in all
but the simplest systems, proved to be limiting the ap-
plicability of the concepts proposed to explain catastrophic

shifts (Sutherland 1990; Petraitis and Latham 1999; Schef-
fer et al. 2001; van de Koppel et al. 2002).

Recent studies indicate that, in models with spatial in-
teractions, positive feedback results in the formation of
regular patterns (Klausmeier 1999; HilleRisLambers et al.
2001; Von Hardenberg et al. 2001; Rietkerk et al. 2002b).
These studies suggest that regular patterns potentially buf-
fer the effects of positive feedback and emphasize their
importance in improving the water-harvesting capacity
and productivity of arid vegetation (Ludwig et al. 1999b;
Valentin and d'Herbes 1999). Regular patterns are typically
found on undisturbed, flat, or smoothly sloping landscapes
(Leprun 1999; Valentin et al. 1999). Regular patterns are
uncommon to arid and semiarid systems that, for instance,
are heavily exploited (Ludwig et al. 1999b). The principles
of water exchange, however, are likely to be valid for a
much wider range of arid ecosystems than those that have
regular patterns. A general, conceptual approach toward
spatial interactions and the functioning of arid ecosystems
is still lacking.

Here, we explore the consequences of spatial interaction
between patches for the functioning of arid vegetation. We
compare two models that differ in the way they address
spatial exchanges of water between patches. Our results
suggest that spatial interactions affect the resilience of arid
ecosystems: spatial exchange of water improved the resil-
ience of our model system to disturbances and increased
the resistance to human-induced loss of cover. Further-
more, spatial exchange of water allowed vegetation to per-
sist at lower rainfall levels as compared to systems that
would lack spatial interactions. Our model should apply
both to systems with regular patterns and systems with
irregular patches. Our analysis emphasizes the general im-
portance of spatial interactions for ecosystem functioning.

Resilience in Arid Grassland

Resilience has a multitude of meanings (see, e.g., Peterson
et al. 1998; Carpenter et al. 2001). One definition, adopted
from engineering systems, is defined as the return time to
equilibrium (Holling 1973; Pimm 1984). Many ecosys-
tems, however, do not have a single equilibrium (May
1977; Scheffer et al. 2001), and following a disturbance,

ecosystems do not necessarily return to the exact state that existed before (Peterson 1982). Therefore, resilience has been defined for ecosystems as the magnitude of disturbance that can be absorbed before the system switches to a different equilibrium (Gunderson 2000; Carpenter et al. 2001). This definition has been called "ecological resilience," in contrast to "engineering resilience," which focuses more on return to a precisely defined equilibrium.

Intrinsic to the definition of ecosystem resilience is the assumption that disturbances are relatively short-lived, which allows the system to return to its former state after the disturbance has passed. As a consequence, the disturbance does not affect the size of the stability domains. In many ecosystems, human influence is not short-lived but imposes an ever-increasing stress upon the system. Studies on systems with alternate stable states show that the number of stable states and the size of their stability domains are affected by changed conditions or human-induced stresses (e.g., Scheffer et al. 2001; van de Koppel et al. 2001). In semiarid systems, reduced rainfall or increased grazing by domestic cattle (Rietkerk and van de Koppel 1997; Rietkerk et al. 1997; van de Koppel et al. 1997) may lead to catastrophic shifts of the system to other stability domains. The capacity of ecosystems to resist and adapt to such stress without switching to a state characterized by a different set of structuring processes is called the "adaptive capacity" (Gunderson 2000).

Below, we investigate the importance of spatial interactions within the vegetation for both the engineering and ecological resilience and the adaptive capacity of arid ecosystems. Key properties in this respect are ability of the system to adapt to changed rainfall and reduction in plant cover and the ability to resist ecosystem collapse and return to a stable vegetated state after a disturbance. First, we will define our model systems.

Spatial Interactions

The main limiting resource for vegetation in many arid or semiarid regions receiving <550 mm of rain per year is water. Despite the low absolute amount of rainfall, rain in most arid regions typically occurs in intense showers (Wainwright et al. 1999). During such a shower, the infiltration capacity of the soil is exceeded, and as a consequence, rainwater accumulates on top of the soil. Surface water is susceptible to rapid lateral flow, in reaction to small local differences in elevation or infiltration. This may lead to exchanges of water between patches, or water may be lost to drainage through channels. Hence, vegetation in these regions may receive water directly from rain or from lateral exchange between patches.

To investigate the consequences of lateral exchange of water, we compare a nonspatial model with a model that includes spatial flow of water. The models we use differ in only one key aspect. In the nonspatial model, all water that does not infiltrate is lost, and hence no exchange between patches occurs. In the spatial model, water that does not infiltrate locally may also infiltrate in other patches, thus taking into account spatial interactions between patches. Both models are used to compare local plant growth and the stability properties of patches.

A Nonspatial Model

Below, we analyze a slightly modified version of the nonspatial model analyzed by Rietkerk and van de Koppel (1997) and Rietkerk et al. (1997). This model assumes uptake of water by plants to be strongly limited by the low intrinsic infiltration of water in the soil. The rate of infiltration, however, is promoted by the vegetation itself, invoking a positive feedback between increased plant growth and enhanced infiltration. We adopted the formulation used by Walker et al. (1981) to describe the relation between infiltration and plant standing crop. This relation assumes that only a fraction W_0 of the rainfall PPT infiltrates in bare soil. Infiltration W_{in} increases and approaches rainfall rate as plant standing crop P increases, as determined by a constant k:

$$W_{in} = PPT \frac{P + k \cdot W_0}{P + k}. \qquad (1)$$

Changes in the availability of soil water W to plants are determined by infiltration, uptake by plants, and losses to evaporation and seepage to deeper layers:

$$\frac{dW}{dt} = W_{in} - c_{max} \frac{W}{W + k_1} P - r_W W. \qquad (2)$$

Here c_{max} is the maximal specific uptake of water by plants, k_1 is the water availability at which uptake is half maximal, and r_W is the specific rate of loss of soil water to evaporation or seepage. Plant growth is proportional to water uptake, and plants experience density-dependent losses due to senescence and herbivory:

$$\frac{dP}{dt} = g_{max} \frac{W}{W + k_1} P - (d + \delta P)P. \qquad (3)$$

Here g_{max} is the maximal growth rate of the vegetation, d depicts specific plant losses, and δP represents the density-dependent part of plant losses due to, for instance, self-shading. We assumed net plant growth to be density dependent to prevent unlimited growth resulting from spatial concentration of water in the spatial model described below.

The model above can be analyzed for changes in the equilibrium plant standing crop with changing rainfall. Figure 1*A* illustrates the relation between equilibrium standing crop and rainfall rates. At low rainfall rates, the line depicting equilibrium plant standing crop is folded (fig. 1*A*, between T_1 and T_2; Rietkerk et al. 1997). The folded shape has important implications. Rather than finding gradual changes in equilibrium plant standing crop with decreasing rainfall, we find that plant standing crop suddenly collapses if rainfall is reduced below a threshold value T_1. The vegetation only recovers when rainfall is increased above T_2. Consequently, the vegetation can be in two alternative states at rainfall rates between T_1 and T_2, depending on prior rainfall levels. Switches between these two states are predicted to occur only after sufficiently large disturbances or when rainfall levels cross the threshold levels of T_1 or T_2.

The model provides a possible explanation for the collapse of vegetation on fine spatial scales (e.g., of about 1 m^2) and for the occurrence of patchy vegetation often observed in semiarid regions (Montana 1992; Ludwig and Tongway 1995; van de Koppel et al. 1997; Aguiar and Sala 1999; Ludwig et al. 1999*a*; Rietkerk et al. 2000). The concept of alternate stable states is much less clear when applied on coarser scales (e.g., ha to km^2 scales), as the assumption of homogeneous vegetation, intrinsic to the above model, is clearly violated. Below, we investigate a spatial model to consider the implications of heterogeneity within the vegetation on ecosystem functioning.

Spatial Interactions through Lateral Exchange of Water

In a prior article, we developed a spatially implicit formulation of local water infiltration that includes spatial exchanges of surface water between patches of vegetation within a particular area (van de Koppel et al. 2002). No interactions occur beyond the boundaries of this area, which behaves as a watershed. The model describes infiltration W_{in} at a particular location as a function of local plant standing crop P and average standing crop in the entire area P_{avg}:

$$W_{in} = PPT \frac{P + k \cdot W_0}{P_{avg} + k}. \qquad (4)$$

This formulation assumes that, within this area, lateral exchange of water between patches is sufficiently high relative to the growth rate of the vegetation to consider it instantaneous. As a consequence, a patch of vegetation exerts a negative effect equally over the entire area under consideration in the model by promoting local infiltration and, hence, reducing resource availability. The benefits of this infiltration remain localized, as only local plant growth

is promoted. The model above can be used to predict local, within-patch plant standing crop as a function of the average standing crop in the area under consideration. In our earlier article, we established that, when lateral exchange is high, the predictions of the above model are in close agreement with that of a more detailed spatially explicit formulation. Note that the model does not include any description of vegetation spread. Instead, spread of vegetation is implicitly considered in terms of the local
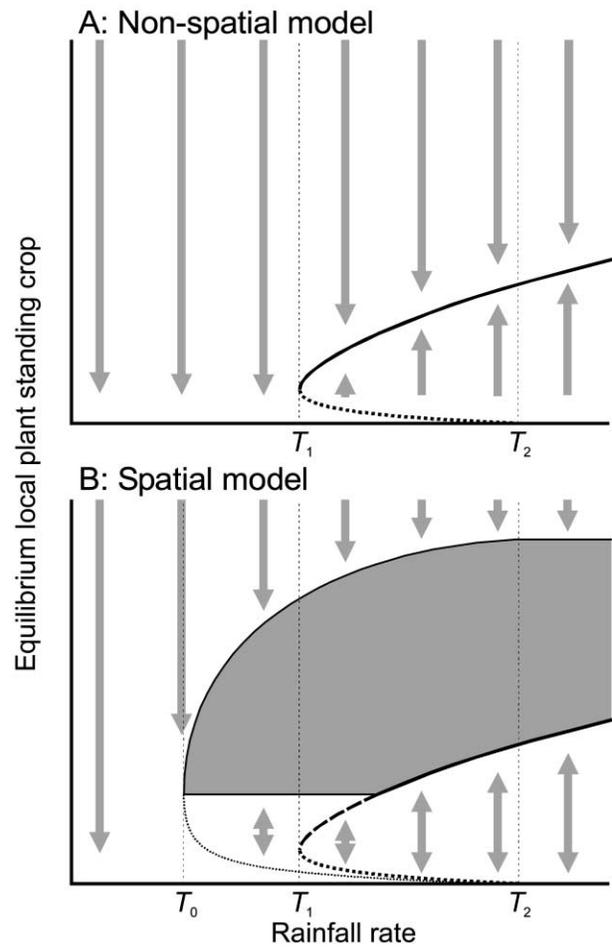

Figure 1: Relation between rainfall rate and equilibrium local plant standing crop for the nonspatial (*A*) and the spatial (*B*) models. The bold line depicts equilibrium plant standing crop in the homogeneous vegetation. The gray area in *B* represents the range of possible stable local plant standing crop values (*P*). Solid lines denote stable equilibria, whereas dotted lines are unstable equilibria. The dashed line in *B* depicts the unstable homogenous equilibria that occur at low rainfall rates. Threshold rainfall rates T_1 and T_2 indicate a bifurcation in model behavior. The gray arrows indicate the direction of change of plant standing crop. Double arrows indicate that the direction of change depends on vegetation cover. Parameter values are PPT = $0 - 3$ mm/d, $W_0 = 0.15$, $k = 5$, $r_W = 0.2$, $c_{max} = 1$, $g_{max} = 0.05$, $k_1 = 5$, $d = 0.05$, $\delta = 0.01$.

stability of bare patches to small increments in plant standing crop due, for instance, to seed dispersal.

Our model differs from other models that address spatial aspects of arid systems in that it does not explicitly describe lateral exchange of water or plants between patches of vegetation. As a consequence, it does not produce regular, self-organizing patterns, as are predicted by a number of recent studies (Von Hardenberg et al. 2001; Rietkerk et al. 2002*b*). Vegetation in human-influenced arid grassland is most often characterized by irregular patterns and shapes of varying cover. Therefore, we adopted a spatially implicit approach that ignores self-organizing properties of vegetation. Our approach focuses on analyzing the equilibrium standing crop and stability properties of vegetation patches in a given spatial setting and investigates possible emergent properties of spatial interactions for ecosystem functioning, avoiding the complexity of pattern-forming processes.

Resistance to Drought

In contrast with the nonspatial model, the spatial model derived above does not predict distinct equilibria to occur at course spatial scale. In a prior article, we showed that spatial interactions, in combination with the low infiltration in bare soil, lead to bimodal vegetation patterns in which bare patches alternate with vegetated patches with a particular standing crop (van de Koppel et al. 2002). The stability of bimodal vegetation patterns is determined by coarse-scale properties such as the cover of the vegetation. As a consequence, for each rainfall rate, a range of equilibria is predicted, each having a different cover and equilibrium standing crop. This range of equilibria is represented by a gray area in figure 1*B*. Note that within this range, the model adopts any spatial pattern that is imposed

upon it. At high rainfall rates, the range is bounded by the homogenous vegetation curve, which we depicted as a bold curve in figure 1*B*. This curve is similar to that of the nonspatial model, apart from its stability properties.

Figure 1*B* indicates a number of important properties of the spatial model. In the spatial model, vegetation (*gray area*) is predicted to occur at rainfall levels below the extinction threshold T_1 predicted by the nonspatial model. This implies that, as a consequence of spatial interactions, vegetation can persist at rainfall rates that would cause a total collapse of plant standing crop in the nonspatial model. Decline of rainfall leads to a partial loss of vegetation cover instead of a collapse of the entire vegetation. Hence, spatial exchange of water increases the adaptive capacity of arid ecosystems by buffering catastrophic vegetation shifts that may result from changed rainfall. On the other hand, the range of rainfall levels at which disturbances may lead to fine-scale vegetation collapse, and patchy vegetation is much larger (the entire length of fig. 1*B*) compared to the nonspatial model (only levels between T_1 and T_2). Hence, at high rainfall rates, spatial interactions may invoke patchiness and loss of productivity.

Resistance to Loss of Cover

The above model can be applied to situations where, for instance, human interference or grazing causes a partial collapse of the vegetation. In figure 2 we depicted for a high and a low rainfall rate average plant growth and standing crop in equilibrium, averaged over the entire area, as a function of vegetation cover. The model analysis indicates that for an extensive range of vegetation cover (0.5–1), decrease of cover hardly causes a decrease of productivity and causes only a minor decline in standing crop. Moreover, at low rainfall rates, both productivity and
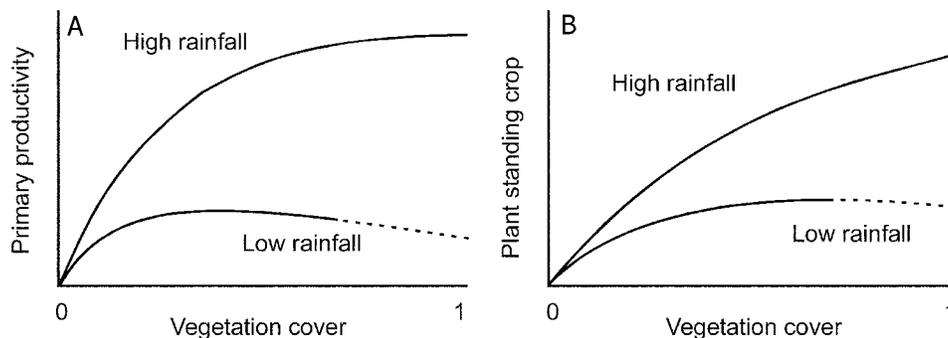

Figure 2: Relation between vegetation cover and (*A*) the growth rate of the vegetation (given by $g_{max}W/[W + k_1]P$) and (*B*) average plant standing crop. The upper and lower lines represent model predictions at rainfall rates of 2 and 0.9 mm/d, respectively. Other parameters as in figure 1. Solid lines denote stable equilibria, whereas dotted lines depict vegetation that is unstable, as small, fine-scale disturbances may lead to the development of (more) bare patches.
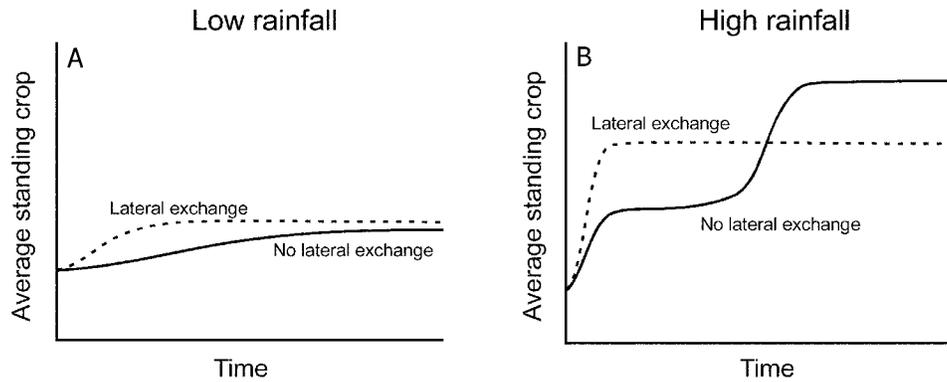
Low rainfall

High rainfall

Figure 3: Simulation runs of the nonspatial (*solid lines*) and the spatial (*dashed lines*) models for rainfall rates of (*A*) 0.9 mm/d and (*B*) 1.5 mm/d. Fifty percent of the vegetation started with a standing crop of 5 g/m² in both models. The other 50% had an initial standing crop of 2 g/m² in the low rainfall simulation and 0.5 g/m² in the high rainfall simulation. See text for a more detailed explanation.

standing crop are increased by a partial loss of cover, as compared to homogeneous vegetation. This indicates that the water-use efficiency is higher when water is concentrated in a part of the vegetation. Hence, our spatial model suggests that production in arid vegetation is more resistant to vegetation collapse than is predicted by nonspatial models.

Rate of Recovery after a Disturbance

We performed a number of simulations to study the consequences of spatial interactions on the return time of the vegetation to equilibrium, which reflects the capacity of the vegetation to recover after a disturbance. We investigated differences in the time needed for either the nonspatial model or the spatially implicit model to return to equilibrium after a spatially heterogeneous disturbance. The nonspatial simulations considered 20 unlinked vegetation patches of equal size; the spatial model considered 20 similar patches that exchanged surface water. In 50% of the area (50% of the cells), the standing crop was reduced to 50% of the equilibrium standing crop of homogeneous vegetation. The standing crop of the other half of the vegetation was decreased to about 5% in the high rainfall simulation and 20% for the low rainfall simulations. The latter high value was chosen to avoid permanent degradation in the nonspatial simulation, which would lead to trivial results.

Our simulations show that for both high and low rainfall, there was a partial loss of cover in the spatial model, as those patches where plant standing crop was severely reduced collapsed to bare soil. In the nonspatial model, this did not occur. Hence, vegetation in the spatial model has low engineering resilience relative to the nonspatial model. However, the average standing crop in the spatial

model recovered faster then in the nonspatial model (fig. 3). Hence, in our simulations, spatial interactions increase the ecosystem resilience of arid vegetation with regard to standing crop on coarse scales. At high rainfall levels, this comes at a cost, as the loss of cover finally reduces total standing crop. At low rainfall rates, standing crop is enhanced in the spatial model despite the partial collapse of the vegetation. As in figure 2, water-use efficiency is higher in vegetation with only a partial cover, and hence a higher average standing crop is obtained in an area where vegetation is partly degraded.

Extent of Recovery after a Disturbance

We investigated the interactive effects of rainfall level and reduction of cover during the disturbance on the extent to which the vegetation was able to recover to the standing crop that it maintained before the disturbance. We used 100 unlinked vegetation patches of equal size in the nonspatial model. The spatial model considered 100 similar patches that exchanged surface water. We investigated the effect of disturbances in which plant standing crop in a specific fraction of the cells was reduced to near-zero values. The fraction of cells was varied, because this is one of the parameters of the sensitivity analysis. We compared the equilibrium standing crop that was reached after recovery in the spatial model with that of the nonspatial model, to assess the implications of spatial exchange of water on ecosystem resilience. The analysis revealed that four regions can be recognized where the effects of spatial interactions on coarse-scale standing crop are principally different. At high rainfall levels, spatial interactions have a negative effect on standing crop after the vegetation recovered from perturbation (fig. 4, region *D*). In the spatial model, loss of cover due to a disturbance is irreversible,
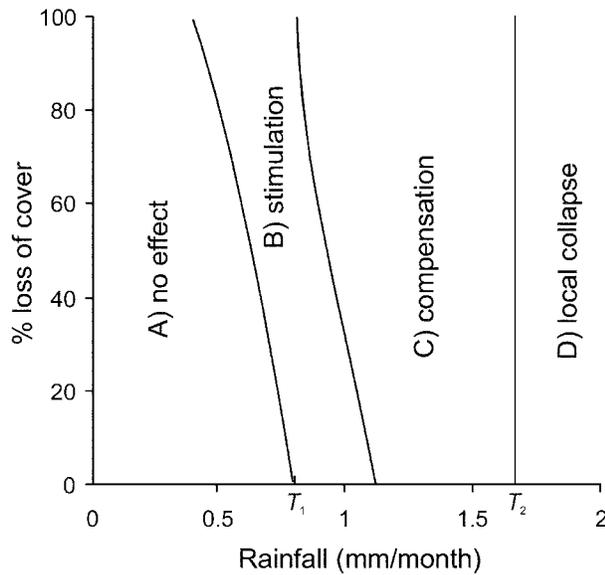
Figure 4: Effects of spatial exchange of water within the vegetation on the production of the vegetation, in terms of realized standing crop, as a function of rainfall (*X*-axis) and reduction of vegetation cover following a disturbance (*Y*-axis). In region *A*, spatial interactions have no effects. In region *B*, spatial exchange of water stimulates production when vegetation cover is reduced, even beyond the production of undisturbed vegetation. In region *C*, spatial exchange of water compensates for loss of cover. In region *D*, spatial exchange stimulates vegetation collapse. See text for further explanation.

as water essential to plant growth is lost to surrounding patches. In the nonspatial model, however, vegetation fully recovers. Consequently, spatial interaction stimulates local vegetation collapse at high rainfall rates, despite a fast return to equilibrium. When rainfall is reduced below the critical threshold T_2, reduction of cover is irreversible and vegetation remains patchy in both model systems. Lateral exchange of water in the spatial model, however, in part compensates for reduced cover by stimulating plant growth in the remaining patches. Hence, at coarse scales, spatial interaction in part compensates for loss of cover (fig. 4, region *C*), as was found in figure 2 (high rainfall). In region *B*, spatial interactions not only compensate for reduced vegetation cover but even stimulate production, as in figure 2 (low rainfall). At rainfall levels below T_1, this stimulation is absolute, as no vegetation can survive in the nonspatial model. In region *A*, spatial interactions have no effect on vegetation production, as the vegetation cannot maintain itself in either of the models at those combinations of rainfall and cover. Our sensitivity analysis indicates that the degree to which spatial interactions compensate for loss of cover depends on the rainfall level. The prediction of our model system that recovery time is reduced, however, seems to be quite robust.

Robustness of Predictions

The validity of the predictions derived above depends strongly on the assumption that rainwater redistributes within the areas in proportion to local plant standing crop. Our model overestimates redistribution of water in cases where the rate of overland flow is low relative to the size of the area under consideration. Moreover, predictions of models with a spatially explicit formulation would be more sensitive to the shape of the pattern that is imposed on the system, as water losses to drainage are likely to be higher in large bare patches relative to small ones. We furthermore ignore the effects of vegetation spread on the stability of the vegetation. Vegetation spread, in combination with local redistribution of water, may create self-organizing patterns in the vegetation, as are found in undisturbed, flat, or smoothly sloping landscapes (Klausmeier 1999; Von Hardenberg et al. 2001; Rietkerk et al. 2002b). Spatial spread of vegetation strongly increases the engineering resilience, as the vegetation reorganizes to a particular pattern after a disturbance. We performed simulations with a spatially explicit model of arid vegetation (HilleRisLambers et al. 2001; Rietkerk et al. 2002b). These confirmed the general predictions derived in this article, although the prediction may differ quantitatively.

Discussion

The study presented in this article indicates that spatial interactions between patches of vegetation affect the resilience (in broad terms) of arid ecosystems. Our analysis shows that spatial exchange of water among vegetation patches allows vegetation to persist at rainfall rates that result in vegetation collapse in models that do not consider spatial interactions. Furthermore, vegetation proved to be resistant to loss of vegetation cover in the model, in that productivity and standing crop were maintained on coarse scales (e.g., ha) despite a partial collapse of vegetation on finer scales (e.g., m²). Hence, spatial interactions through lateral exchange of water may improve the adaptive capacity of arid ecosystems.

Our study suggests that spatial interactions are important for the resilience of arid ecosystems. For a large range of rainfall levels, disturbances lead to loss of cover, as the system adopts the spatial structure that is imposed on it by the disturbance. Consequently, engineering resilience is absent. However, despite the partial loss of cover, spatial exchange of water increases the rate of recovery of plant standing crop at coarse spatial scales, following a disturbance, as remaining patches quickly compensate for loss of production in bare patches. Hence, spatial exchange of water is predicted to improve ecosystem resilience, as production quickly recovers after the disturbance. The im-

portance of spatial processes for the resilience of ecosystems has recently been stressed for coral reefs (Nystrom and Folke 2001) and forest ecosystems (Peterson 2002). Similar to our model, these systems are able to absorb and adjust to spatially heterogeneous disturbances (e.g., they do not return to the exact state that existed before the disturbance). The resulting spatial heterogeneity was argued to strongly increase ecosystem resilience.

Our model results are in line with recent detailed studies on the functioning of patterned vegetation in semiarid regions all over the world. Banded "tiger bush" landscapes in Niger were found to act as a natural water harvesting system and to be more resilient to climate change (Valentin and d'Herbes 1999; Valentin et al. 1999). Model studies of banded or spotted woodland vegetation in Australia suggest that patterned vegetation was about 40% more productive than vegetation without patterning (Ludwig et al. 1999b). Moreover, the degree of enhancement of productivity appeared to be influenced by the shape of the vegetation patches. This points at the importance of self-organizing processes, as analyzed in the articles by Von Hardenberg et al. (2001) and Rietkerk et al. (2002b).

Our model analysis predicts that switches of vegetation to an alternate state, and hence variation in plant standing crop, occur more frequently on fine than on coarse spatial scales. This concurs with findings by Holm et al. (2002), who reported that variance in primary productivity was better explained by landscape indicators on coarse scales (patch-mosaic to landscape scale) than on finer patch scales. The conclusion from our model that spatial interactions increase productivity and resilience is compatible with the notion that many arid lands are source-sink systems (Noy-Meir 1973; Ludwig and Tongway 1995; Aguiar and Sala 1999; Ludwig et al. 1999b), where plant productivity is determined by spatial concentration of rainfall from bare areas into vegetated patches. Spatial concentration of water within vegetated patches invokes a strong local positive feedback to plant growth, while negative feedback due to depletion of water is spread over a larger surface. Similar dynamical behavior can be expected from other ecosystems if the growth of organisms is uncoupled from fine-scale negative feedback and becomes regulated by the spatial arrangement of the ecosystem at coarser scales.

Our model results provide a potential mechanism for the notion in literature that coarse-scale switches between ecosystem states or biomes are buffered by ecological mechanisms (Levin 1998; Jeltsch et al. 2000; Lenton and van Oijen 2002). Most ecosystems are intrinsically heterogeneous in space and would therefore have ample potential to buffer positive feedback. Moreover, our model analysis invokes the hypothesis that coarse-scale catastrophic shifts between ecosystem states are more likely in systems that have little spatial heterogeneity or have no spatial feedback mechanisms to compensate for positive feedback. Shallow lakes may provide such an example. A large number of studies report on sudden shifts between states dominated by submerged plants and pelagic microalgae, respectively (see Scheffer et al. 1993; Scheffer et al. 2001 for reviews). Microalgae that currently characterize many nutrient-rich lakes dominate the upper layer of the water column. They thereby exert a strongly homogenizing effect on the remainder of the lake, blocking potential spatial feedbacks that may occur via patches of submerged vegetation.

Our analysis emphasizes the importance of considering scale effects in ecological thinking. Most theory in ecology is developed without reference to spatial scale and is typically based on measurements obtained on scales of at most square meters to tens of square meters. Current developments in ecology, however, are pressing the study of ecological interactions to an ever coarser scale (see, e.g., Levin 1992; Lenton and van Oijen 2002; Rietkerk et al. 2002a). Taking into account scale-dependent characteristics and spatial aspects of ecological interactions, both within and between populations, is essential if ecosystem dynamics are to be predicted on landscape, regional, or even global scales.

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