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Spatial Heterogeneity and Irreversible Vegetation Change in Semiarid Grazing Systems

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ABSTRACT: Recent theoretical studies have shown that spatial redistribution of surface water may explain the occurrence of patterns of alternating vegetated and degraded patches in semiarid grasslands. These results implied, however, that spatial redistribution processes cannot explain the collapse of production on coarser scales observed in these systems. We present a spatially explicit vegetation model to investigate possible mechanisms explaining irreversible vegetation collapse on coarse spatial scales. The model results indicate that the dynamics of vegetation on coarse scales are determined by the interaction of two spatial feedback processes. Loss of plant cover in a certain area results in increased availability of water in remaining vegetated patches through run-on of surface water, promoting within-patch plant production. Hence, spatial redistribution of surface water creates negative feedback between reduced plant cover and increased plant growth in remaining vegetation. Reduced plant cover, however, results in focusing of herbivore grazing in the remaining vegetation. Hence, redistribution of herbivores creates positive feedback between reduced plant cover and increased losses due to grazing in remaining vegetated patches, leading to collapse of the entire vegetation. This may explain irreversible vegetation shifts in semiarid grasslands on coarse spatial scales.

Keywords: grazing, herbivory, positive feedback, spatially explicit model, vegetation collapse, vegetation patterns.

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A typical characteristic of many semiarid grazing systems is their sensitivity to degradation of the soil (Sinclair and Fryxell 1985; Graetz 1991). Despite the low absolute amount of rain, rainfall typically occurs in intense showers. The capacity of the soil to absorb water is, however, relatively low, especially in more clayey soils (Rietkerk et al. 2000). Vegetation, however, promotes the infiltration of water, which is an important limiting factor for plant growth in semiarid systems (Elwell and Stocking 1976; Kelly and Walker 1976; Breman and De Wit 1983). Theoretical models predict that feedback between infiltration of water and plant growth leads to alternate stable states in the vegetation, one state with a high plant standing crop, and one without vegetation that is considered to be

degraded (van de Koppel et al. 1997; Rietkerk and van de Koppel 1997). Once the vegetation has reached the bare state, it is not easily restored (Le Houerou 1989; Walker et al. 1981). This may explain the occurrence of alternating patches of vegetation and bare soil that is characteristic of many rangelands (Wilson and Agnew 1992; van de Koppel et al. 1997).

Degradation occurs in many semiarid regions all over the world (van de Koppel et al. 1997). The scale at which degradation occurs, however, varies among sites (Ludwig and Tongway 1995). In many systems, the degradation feedback results in the formation of fine-scale patterns (1 m^2 – 100 m^2 ; Belsky 1986; Montana 1992; Ludwig and Tongway 1995; Rietkerk et al. 2000). Run-off of water from bare patches leads to increased water availability in vegetated patches (Montana 1992; Bromley et al. 1997), which may allow vegetated patches to cope with increased grazing. Hence, spatial redistribution of water appears to compensate for the detrimental effects of grazing. In other systems, degradation is a phenomenon occurring over large areas and may result in a dramatic collapse of production at scales of hectare to square kilometers (Oldeman et al. 1991). In these systems, local redistribution of water seems to have little effect, and plant production is lost.

Recent theoretical studies investigate the consequences of spatial redistribution of water in semiarid systems (Klausmeier 1999; HilleRisLambers et al. 2001). These studies show that spatial interaction, in particular run-on and run-off of water, can induce regular patterns of vegetation alternating with bare soil. Their results imply that spatial redistribution of water cannot explain the collapse of primary production that is observed in many semiarid grazing systems (Sinclair and Fryxell 1985; Friedel 1991; Laycock 1991; van de Koppel et al. 1997), as plant growth is maintained at coarse scales. Moreover, simplifying assumptions that underlie their models, such as a spatially homogeneous herbivore presence, preclude analysis of this aspect of semiarid grazing systems. Hence, the implications of spatial heterogeneity for concepts explaining irreversible vegetation shifts remain unexplored.

In this article we investigate the consequences of spatial interactions among patches for the dynamics of semiarid plant-herbivore systems. We base our analysis on a water-plant-herbivore model in which spatial interactions are explicitly included using partial differential equations. We first analyze a simplified, conceptual version of the model in which complexity is strongly reduced. This model allows us to gain basic insight into the functioning of spatial interaction using graphical techniques. Then, we assess the robustness of the results by analyzing a more complex simulation model. Our analysis specifically addresses the question whether spatial interactions induce positive feed-

back to vegetation degradation and hence induce coarse-scale and irreversible vegetation change.

A General Spatially Explicit Model of a Semiarid Grazing System

The dominant cause of patch formation in semiarid grasslands is, trivially, spatial differences in abiotic characteristics such as soil type or elevation. Vegetation patterning, however, also occurs on soils that are relatively homogeneous and flat (Belsky 1986; Rietkerk et al. 2000). These patterns do not relate to variation in the soil but instead reflect interactions between vegetation and the abiotic environment (Belsky 1986; Montana 1992; Wilson and Agnew 1992; Ludwig and Tongway 1995; Klausmeier 1999). Surface water that accumulates during rain showers is subject to rapid lateral exchange between patches (Anderson and Hodgkinson 1997; Bromley et al. 1997). Surface flow quickly compensates for local differences in the infiltration of surface water between patches, for instance, induced by differences in plant standing crop. Hence, vegetation patches interact by influencing water redistribution. Patches may furthermore interact via the herbivores. An important determinant of the grazing pressure within a patch of vegetation is the availability of alternative forage in surrounding patches (Charnov 1976; WallisdeVries 1996). In other words, patches affect the grazing pressure in other patches by influencing the distribution of herbivores within the area. Finally, patches may influence other patches by the spread of seeds and tillers. Hence, a model that describes the spatial interactions between patches of vegetation should consider the spatial and temporal dynamics of surface water, soil water, vegetation, and within-patch herbivore abundance.

We formulate a spatially explicit model of a bounded flat area of grassland of size A square meters (e.g., a hectare), in which the dynamics of surface water, water in the top centimeters of the soil, plant standing crop, and herbivore abundance are described at the fine scale of a square meter. Lateral exchange of surface water is determined by differences in the amount of accumulated water on top of the soil, which in turn depends on the balance between rainfall and losses such as infiltration. If we assume that rainfall is constant and homogeneous, ignoring seasonal aspects (following HilleRisLambers et al. 2001), the rate of change of surface water at Cartesian coordinates x and y can be described by the following differential equation:

$$\frac{\partial O}{\partial t} = R - F(O, P) - r_o O + D_o \left(\frac{\partial^2 O}{\partial x^2} + \frac{\partial^2 O}{\partial y^2} \right). \quad (1a)$$

Here, O is the amount of surface water at a given location and R is the rainfall rate; $F(O, P)$ describes the rate of infiltration of surface water, which is an increasing function of both surface water O and plant density P ; r_w describes the specific (e.g., per unit of water) loss of surface water to evaporation or drainage. The last term in the equation describes the net exchange of water with the surroundings as a function of the local gradient in surface water level, where the “diffusion coefficient” D_o (Edelstein-Keshet 1988) relates the net flow rate of water to spatial differences in surface water level. For an explanation of the use of partial differential equations for surface water flow, see HilleRisLambers et al. (2001). In this analysis we assume a simple linear relation between infiltration, surface water, and plant density: $F(O, P) = (a + bP)O$, where a is the specific rate of infiltration of water in the absence of plants and b is a constant relating plant density to infiltration rate.

Soil water changes are determined by infiltration, uptake by plants, losses through evaporation and percolation, and lateral exchange with the surroundings through diffusion through the soil. Changes in the amount of soil water W over time can be modeled by

$$\frac{\partial W}{\partial t} = F(O, P) - r_w W - U(W, P) + D_w \left(\frac{\partial^2 W}{\partial x^2} + \frac{\partial^2 W}{\partial y^2} \right), \quad (1b)$$

where r_w is the specific rate of water loss through evaporation and percolation, and $U(W, P)$ describes uptake by plants, which is a monotonically increasing function of both soil water content and plant density. In our analysis, we adopt a linear uptake function: $U(W, P) = uWP$, where u is an uptake constant. Finally, D_w is the diffusion coefficient of soil water.

The rate of change of plant biomass is determined by plant production, senescence, consumption by herbivores, and spatial propagation of plants due to seed fall or spreading out of tillers:

$$\frac{\partial P}{\partial t} = G(W, P) - D(P) - C(P, H) + D_p \left(\frac{\partial^2 P}{\partial x^2} + \frac{\partial^2 P}{\partial y^2} \right). \quad (1c)$$

Here $G(W, P)$ describes plant growth, which is assumed to be an increasing function of both soil water and plant density, $D(P)$ describes plant senescence, $C(P, H)$ describes herbivore consumption rate as an increasing function of

plant density and local herbivore abundance H , and the last term of equation (1c) describes propagation of plants to the neighborhood. Since we assume water-limited plant growth, $G(W, P)$ is assumed to be proportional to $U(W, P)$: $G(W, P) = gWP$, where g is a plant growth constant. Senescence is assumed to be a density-dependent factor due to, for instance, self-shading at high plant density: $D(P) = d(1 + \delta P)P$, where d is the specific mortality rate when plant density is low and δP represents the increase of specific mortality due to density-dependent effects. Finally, consumption by herbivores is modeled as $C(P, H) = cPH$, where H is local herbivore abundance and c is a consumption constant.

Lateral exchange of water and plant propagules is modeled assuming simple passive diffusive motion (Holmes et al. 1994). In principle, herbivore movement could be modeled in a similar way, assuming that herbivores move in a direction depending on the local gradient of plant standing crop. However, this ignores the fact that herbivore behavior may be influenced by vegetation at distances beyond that of their direct surroundings. For this sort of behavior, partial differential equations are inappropriate (McLaughlin and Roughgarden 1992). We used an alternative and more simple approach to describe herbivore movement. We assume that the rate at which herbivores emigrate from a particular location is a function of local plant density and decreases as plant density increases (following Nisbet et al. 1997). We furthermore assume that herbivores that move away from a particular location redistribute evenly over the area. Hence, herbivore immigration is determined by the total numbers of emigrants from the total area. The rate of change of local herbivore density H , therefore, is

$$\frac{\partial H}{\partial t} = \frac{1}{A} \iint_{x, y \in D} E(P(x, y)) H(x, y) dx dy - E(P) H, \quad (1d)$$

where the left term describes the rate of immigration of herbivores to that location, A is the size of the area under consideration, $E(P)$ is the per capita rate of emigration from that location, and D defines the computational area. Herbivore immigration is determined by the total number of animals that start to move over the entire area. In this analysis, we adopt that the rate of herbivore emigration from a certain location is inversely proportional to the local plant density: $E(P) = e/P$, where e is the rate of emigration when P is equal to 1. Note that growth and mortality of herbivores are not considered in our model.

Models that follow the general structure as described above allow us to simulate the dynamics of semiarid grassland as a system of grid cells. Their complexity, however, precludes mathematical analysis aimed at gaining a con-

ceptual understanding of its dynamics, as it is technically a multidimensional nonlinear system. In the following section, we will make a series of simplifying assumptions that will allow us to reduce the complexity and analyze equations (1) graphically. Finally, we will assess the robustness of our graphical results by comparing the predictions of the simplified analytical model with the result of simulations of a spatially explicit model as described by equations (1).

A Simplified Model

Although there are strong interactions between the components of the model presented above, there are distinct differences in the time scale at which the rate of change of water, plants, and herbivores occurs. Growth of plants occurs at time scales of days to weeks. Processes that relate to the dynamics of surface or soil water or to the movement of herbivores occur at time scales that range from seconds to hours. We could argue, therefore, that surface water, soil water, and herbivore numbers react virtually instantaneously to vegetation change when viewed on the time scale at which vegetation changes occur. Hence, for surface water, soil water, and herbivore numbers, we can adopt the quasi-steady state assumption (Edelstein-Keshet 1988) that allows the amount of O , W , and H to be represented by their equilibrium values. Moreover, the rate of lateral exchange of surface water far exceeds other processes such as infiltration. Consequently, on a flat surface, we can assume that surface water levels are approximately equal for all patches. On the scale of meters or above, lateral exchange of soil water through diffusion through the soil is minimal, and hence we will ignore it in our simplified model. We will, moreover, not explicitly consider diffusion of plant propagules and seeds. These assumptions are relaxed in the simulation analysis in the second part of this article.

Surface Water

Assuming that $dO/dt \cong 0$, we can formulate the balance of surface water in the total area. Rainfall in the area will equal the sum of infiltration in the soil and losses to drainage and evaporation:

$$\iint_{x,y \in D} R(x,y) dx dy = \iint_{x,y \in D} [F(O(x,y), P(x,y)) + r_o O(x,y)] dx dy, \tag{2}$$

which implies that, on the scale of the area that is considered, the rain either infiltrates depending on local stand-

ing crop or is lost to drainage and evaporation. Amount O is equal for the entire area D , so for a particular location, the fraction $f(P)$ of the rainfall that infiltrates can be expressed as

$$f(P) = \frac{a + bP}{a + \frac{b}{A} \iint_{x,y \in D} P(x,y) dx dy + r_o}, \tag{3}$$

where $(1/A) \iint_{x,y \in D} P(x,y) dx dy$ represents the average biomass of the vegetation in the entire area under consideration. After some rearranging, and adopting that $k = (a + r_o)/b$ and $W_0 = a/(a + r_o)$, we can express infiltration F in equation (1a) as

$$F(P, P_{avg}) = R \frac{P + kW_0}{P_{avg} + k}, \tag{4}$$

where $P_{avg} = (1/A) \iint_{x,y \in D} P(x,y) dx dy$, k is a half-saturation constant, and W_0 is the proportion of the rainfall that infiltrates in bare soil (Rietkerk and van de Koppel 1997).

Soil Water

Considering equation (4), and assuming that diffusion of soil water through the soil can be ignored, equation (1b) simplifies to

$$\frac{\partial W}{\partial t} = R \frac{P + kW_0}{P_{avg} + k} - r_w W - uWP = 0. \tag{5}$$

At the time scale of plant growth, soil water content can be expressed algebraically as

$$W(P, P_{avg}) = R \frac{P + kW_0}{P_{avg} + k} \frac{1}{r_w + uP}. \tag{6}$$

Herbivore Grazing

Considering that herbivore numbers are close to equilibrium, local fine-scale herbivore density can be approximated as a function of plant density:

$$H(P) = \frac{\iint_{x,y \in D} E(P(x,y)) H(x,y) dx dy}{AE(P)}. \tag{7}$$

Given that $E(P) = e/P$, equation (7) can be reduced to

$$H(P) = \iint_{x,y \in D} \frac{H(x,y)}{P(x,y)} dx dy \frac{P}{A}. \tag{8}$$

The immigration rate is equal for the entire area, as migrating herbivores are assumed to redistribute randomly. Hence, $H = CP$, where $C = \iint (H(x, y)/P(x, y)) dx dy / A$. (For conciseness, we left out the notation under the integral.) The total density of herbivores in the area is $\iint H(x, y) dx dy = \iint (CP(x, y)) dx dy = C \iint P(x, y) dx dy$. Hence, C can be expressed as $C = \iint H(x, y) dx dy / \iint P(x, y) dx dy$. We assumed a fixed number of herbivores in the total area. The local, fine-scale number of herbivores can now be expressed as a function of local plant density:

$$H(P, P_{\text{avg}}) = \frac{P}{P_{\text{avg}}} H_{\text{avg}}, \quad (9)$$

where H_{avg} is the density of herbivores averaged over the area.

Plant Growth

We have now expressed surface water, soil water, and herbivore numbers as functions of local or fine-scale plant standing crop P , average plant standing crop P_{avg} , and average herbivore density H_{avg} in the area. Hence, equation (1c) can be expressed as

$$\begin{aligned} \frac{\partial P}{\partial t} &= gW(P, P_{\text{avg}})P - d(P) - cPH(P, P_{\text{avg}}) \\ &= g \left(R \frac{P + kW_0}{P_{\text{avg}} + k} \frac{1}{r_w + uP} \right) P \\ &\quad - d(1 + \delta P)P - cP \left(\frac{P}{P_{\text{avg}}} H_{\text{avg}} \right). \end{aligned} \quad (10)$$

This equation allows us to use graphical techniques to study the behavior of vegetation on a fine scale as a function of the local standing crop and the average standing crop in the area. It has, however, an implicit assumption. The model assumes that the surrounding vegetation can be represented by the average over the whole area. This implies that there are no effects of distance: locations that are close to each other influence each other as much as those far apart.

As a reference, we start with analyzing a system with no fine-scale herbivore redistribution, similar to the models of Klausmeier (1999) and HilleRisLambers et al. (2001). We then analyze a system where herbivore redistribute on a small scale but the number of herbivores in the entire area under consideration ($H_{\text{avg}} \times A$) is constant. Since most semiarid region systems are under human management, this assumption is applicable to current-day grazing systems (Noy-Meir 1975). Finally, we will relax this as-

sumption and consider coarse-scale movements of herbivores to other areas in response to changes in the forage availability in the area. This last model is typical for semi-natural or natural grazing systems.

Constant Herbivore Distribution

The consequences of changes in the average plant standing crop of the entire area for plant growth on a fine scale can easily be visualized if we plot the isocline at which $dP/dt = 0$ in a P - P_{avg} plane (fig. 1). To the left of the $dP/dt = 0$ isocline, net local plant growth is positive. To the right, local plant growth is negative. If average plant standing crop in the entire area (P_{avg}) is low, local plant growth is zero at only a single value of local plant standing crop (fig. 1, $P_{\text{avg}} < T_{\text{avg}}$). Under this condition, losses of water to the surrounding vegetation are low, and there may even be run-on of water. Consequently, plants can invade bare patches, and no patterning is expected. When average plant standing crop in the entire area increases ($P_{\text{avg}} > T_{\text{avg}}$), however, the zero-growth isocline is folded. Locations with a very low plant standing crop are prone to loss of water to the surrounding vegetation. Bare spots receive insufficient water, and as a result, plant growth is negative (as indicated by the arrows in fig. 1). Above a threshold plant standing crop, as given by the lower part of the fold, infiltration is sufficient and plants can grow. This indicates that there are two stable states, one without vegetation and one with a high plant standing crop, as represented by the upper part of the isocline. Depending

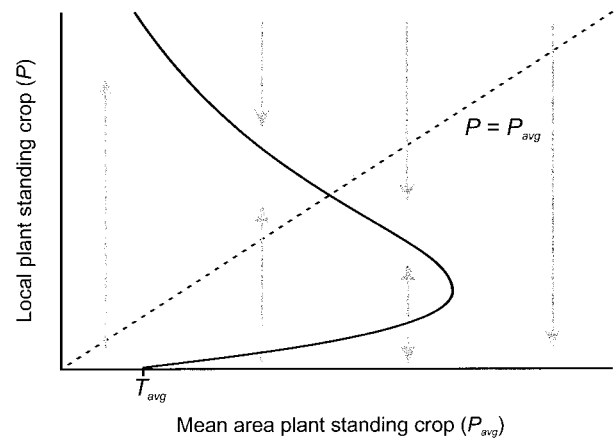


Figure 1: Plane in which local plant standing crop P is expressed along the horizontal axis, and the average plant standing crop of the entire area under consideration (P_{avg}) is expressed along the vertical axis. The solid line, called zero-growth isocline, represents all combinations of P and P_{avg} at which net plant growth is zero. The dashed line represents a homogeneous vegetation, where $P = P_{\text{avg}}$. The arrows show the direction of change of local plant standing crop.

on initial plant standing crop, patches either develop a dense vegetation or become bare. Hence, at $P_{avg} > T_{avg}$, pattern formation is expected.

An interesting property emerges if we compare the growth of homogeneous ($P = P_{avg}$ for the entire area) and heterogeneous vegetation. In figure 1, the $P = P_{avg}$ line intersects only once with the zero-growth isocline, and plant growth is positive when the entire area is bare (at $P = 0, P_{avg} = 0$). Consequently, no alternative stable states occur if the system is disturbed homogeneously. If $P_{avg} > T_{avg}$, however, a stable pattern may develop after a significantly large spatially heterogeneous disturbance. Hence, in this simple model with constant local herbivore numbers, the development of stable patterns can only be explained because of spatial interactions.

Fine-Scale Herbivore Redistribution

If we include herbivore redistribution, the zero-growth isocline changes in shape (fig. 2). If the average density of the vegetation in the total area (P_{avg}) drops to low values, herbivore redistribution results in high grazing pressure in remaining vegetated patches. Consequently, equilibrium plant standing crop is low at low P_{avg} . The $dP/dt = 0$ curve drops at low P_{avg} values as a result of enhanced losses due to grazing. If the proportion of rainfall that infiltrates in bare soil, W_0 , is relatively high, then plant growth remains positive at low P_{avg} , despite the high rate of herbivory (fig. 2). The shape of the $dP/dt = 0$ curve changes fundamentally if W_0 is very low. In this situation, the $dP/dt = 0$ curve may close at low P_{avg} , as is shown in figure 3. A decrease of P_{avg} does not lead to restoration of growth on

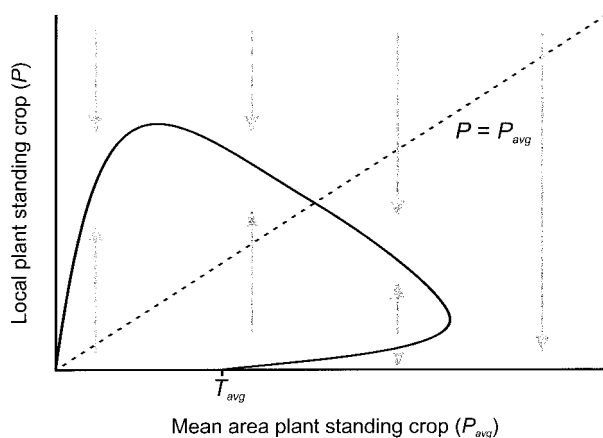


Figure 2: Shape of the zero-growth isocline in the P - P_{avg} plane for systems with redistributing herbivores. Note the change at low P_{avg} as compared with systems with constant local herbivore numbers, given in figure 1. See figure 1 for further explanation.

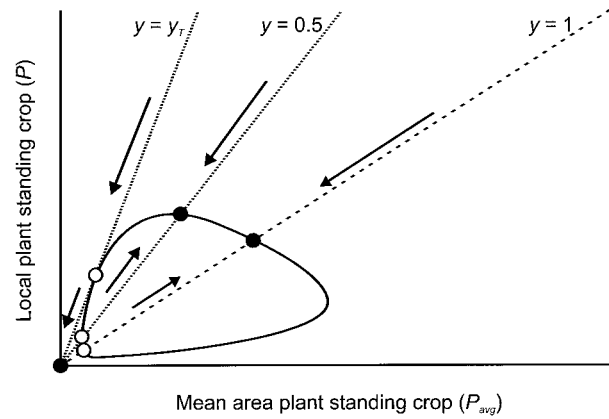


Figure 3: Consequences of partial loss of vegetation cover for the stability of the remaining vegetation. The solid line depicts the zero-growth isocline, the dashed line depicts the path of change of homogeneous vegetation, and the dotted lines depict the path of change of vegetation with a partial cover. Line $y = y_T$ represents the threshold vegetation cover below which the vegetation will collapse. The arrows depict the direction of change for each cover, for the situation where the remaining vegetation has equal plant standing crop per patch.

bare soil, as was the case when infiltration in bare soil, W_0 , was higher (fig. 2). At low P_{avg} , growth cannot compensate for enhanced grazing at low P_{avg} , which may result in a collapse of plant standing crop in the entire area. Hence, such systems may have homogeneous vegetation, may have a stable pattern with bare patches in response to a mild spatially heterogeneous disturbance, or may collapse to a state in which the total area lacks vegetation, in response to a severe disturbance.

Figure 3 allows for prediction of changes in the stability of vegetated patches if part of the vegetation has degraded to bare soil. The equilibrium plant standing crop of homogeneous vegetation is given by the intersection of the upper part of the zero-growth isocline with the $P = P_{avg}$ line (denoted as $y = 1$ line in fig. 3). If plant cover is reduced, the equilibrium point is shifted to the left. The line that connects this point with the origin allows us to predict the behavior of the system if all vegetated patches would change as one. This line is given by $P = P_{avg}/y$, where y is the proportion of the area that is vegetated. A homogeneous decrease in the standing crop of all vegetated patches would move the system along this line. In the case of 50% vegetation cover, as in figure 3, a slight decrease of the standing crop of all vegetated patches would result in an increase of plant growth, and the system would return to the former state. Hence, the system is resistant to a small homogeneous disturbance. If the proportion of the area that is vegetated decreases, the $P = P_{avg}/y$ line moves to the left (fig. 3). Below a threshold (y_T in fig. 3),

no intersections with the zero-growth isocline occur. This threshold is given by line y_T in figure 4 ($y = \pm 20\%$). If the cover of the vegetation drops below this critical value of y , the vegetation collapses, causing the total area to become bare. Hence, a threshold vegetation cover exists, below which the vegetation in the entire area collapses.

Coarse-Scale Herbivore Redistribution

In the model used above, it is assumed that herbivores are confined to the area under consideration. This assumption may be realistic for modern-day pastoral systems, where the availability of land that can be used for grazing is limited due to competition with arable farmers (De Bruijn and Van Dijk 1995). In ecosystems where competition for land is less stringent or in systems with wild grazers, herbivores may have the opportunity to leave the area in response to local depletion of forage. In this section, we extend the model to include migration out of the area when local forage availability becomes low.

Changes in the number of herbivores due to movement in and out of the area can be described in a similar fashion as changes in fine-scale herbivore numbers. The model describes immigration and emigration, but this time on a coarse scale (in part following Nisbet et al. 1997):

$$\frac{dH_T}{dt} = I_a - E_a(P_{\text{avg}})H_T, \quad (11)$$

where H_T is the total amount of herbivores in the area under consideration ($= \iint H(x, y) dx dy$), I_a is the immigration of herbivores in the area, and $E_a(P_{\text{avg}})$ is a function describing the specific rate of emigration of herbivores from the area as a function of average plant standing crop. Obviously, this model crudely simplifies the true complexity of immigration and emigration behavior of herbivores, as it does not consider the availability of alternative food sources in the landscape and assumes a constant immigration. It is nevertheless sufficient in our analysis since we only want to study the interactive effects between herbivore numbers and forage availability in the area.

In the previous section we used a local emigration function $E(P)$ that decreased proportionally with local plant standing crop. We thereby implicitly assumed that herbivore movements are unrestricted, as is the case on fine spatial scales. For coarse scales we do not want to make this assumption. Therefore, we use a slightly more complicated function for between-area emigration, allowing for movement restrictions that would cause between-area emigration to decrease less than proportionally with increasing plant standing crop: $E_a(P) = ek_a/(k_a + P_{\text{avg}} - c)$, where e and c are arbitrary emigration constants and k_a

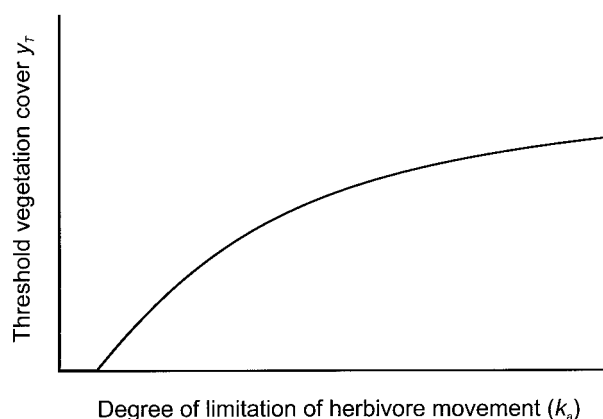


Figure 4: Relation between the threshold vegetation cover and the degree of limitation of movement of the herbivores (k_a). The vegetation collapses if the cover is reduced to a level below the solid line, while a stable pattern is predicted above.

reflects the effect of movement restriction on emigration rate. This equation predicts that in areas with unlimited herbivore movement ($k_a = c$), herbivore numbers will change in proportion to the availability of forage, assuming that only forage availability determines herbivore distribution. If herbivore movement is restricted ($k_a \gg c$), herbivore numbers react less than proportionally to changes in mean area plant standing crop.

Figure 4 depicts the effect of increase in herbivore movement restriction (increase in k_a) on the threshold vegetation cover. This threshold has been obtained by inserting $P = P_{\text{avg}} \times y$ in equation (10) and then deriving for which values of y below 1 equation (10) has a single solution. At low k_a , herbivores can move freely, which allows herbivores to migrate in case of low forage availability (low P_{avg}), and hence prevents overgrazing. As a result, the critical vegetation cover is found to be low or nonexistent. This situation is similar to figure 1. The critical vegetation cover is found to increase as movement limitations (k_a) increase (fig. 4). The critical cover levels off to a maximum value at high k_a , where severe movement restrictions effectively keep herbivores locked in the area. This situation is similar to figure 3. Summarizing, the potential for coarse-scale vegetation degradation is lowest in systems where herbivores can range freely on coarse scales. The potential for vegetation degradation increases when movements on coarse scales are restricted.

The Robustness of the Graphical Analysis

We investigated whether the predictions made by the simplified analytical model depend on the assumptions that allowed for the graphic approach, using a spatially explicit

version of system 1. In this model, the dynamics of surface water, soil water, plants, and herbivores are simulated without quasi-steady state assumptions. Furthermore, this model more accurately considers local spatial interactions by using partial differential equations. The analytical model predicts that the vegetation tends to develop to a two-phase mosaic, in which patches either are bare or tend to a much higher standing crop, while only a few patches have a stable intermediate standing crop. This implies that the simulation model should develop a bimodal distribution of plant standing crop values (van de Koppel et al. 2001). We tested this prediction by simulating the dynamics of surface water, soil water, plants, and herbivores in a 25×25 spatial grid in which 75% of the cells were given a high positive initial value, randomly distributed over the area, and 25% were given an initial density close to (but not exactly) zero. Figure 5 shows the frequency distribution of plant standing crop in the cells after the total biomass in the grid had reached equilibrium, resulting from a simulation of the spatially explicit model. We also depicted the within-cell plant growth curve for the average plant standing crop in equilibrium as predicted by the analytical model. The analysis confirms that models with local spatial interactions develop a bimodal biomass distribution, as was predicted by the analysis of the analytical model. Moreover, we found that the plant growth curve derived from the analytical model gave an accurate prediction of the average within-cluster equilibrium standing crop of the simulation model. Repetitions of the simulations with slightly different initial cover gave qualitatively similar results.

Our simulations confirmed that a threshold vegetation cover could exist below which the vegetation in the entire area would inevitably collapse. Furthermore, our simulations showed that, as in the analytical model, the threshold vegetation cover becomes higher as the herbivores are more restricted in their coarse-scale movements (higher k_n). The exact position of the threshold in the simulation model was found to be close to but slightly above that of the value predicted by the analytical model. This is most probably due to the effects of localized interactions.

Discussion

Recent theoretical investigations indicate that a positive feedback between plant standing crop and local water infiltration, together with spatial redistribution of water, can induce pattern formation in semiarid grasslands (Klausmeier 1999; HilleRisLambers et al. 2001). The results of HilleRisLambers et al. 2001 implied that although collapse of vegetation is possible on a scale of patches (square meters), spatial redistribution of surface water prevents irreversible vegetation collapse on coarser scales (hectares).

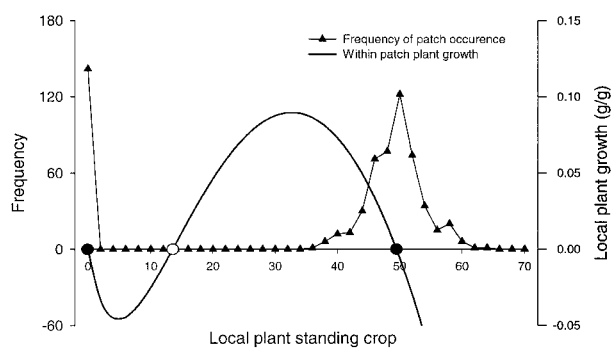


Figure 5: Frequency distribution of plant standing crop within patches (triangles) of vegetation, as is predicted by the spatially explicit simulation model. The solid line depicts the growth rate as predicted by the analytical model. Parameters used: $R = 50 \text{ mm mo}^{-1}$; $a = 0.02 \text{ mo}^{-1}$; $b = 0.02 \text{ g}^{-1} \text{ mo}^{-1}$; $r_o = 1 \text{ mo}^{-1}$; $r_w = 0.1 \text{ mo}^{-1}$; $u = 0.01 \text{ mm g}^{-2} \text{ mo}^{-1}$; $g = 0.001 \text{ g}^{-1} \text{ mo}^{-1}$; $d = 0.03 \text{ mo}^{-1}$; $\delta = 0.005 \text{ g}^{-1} \text{ mo}^{-1}$; $c = 0.01 \text{ g}^{-1} \text{ mo}^{-1}$; $e = 0.01 \text{ g}^{-1} \text{ mo}^{-1}$; $H_{\text{avg}} = 0.8 \text{ g m}^{-2}$; $D_o = 20,000 \text{ m}^2 \text{ mo}^{-1}$; $D_w = 1 \text{ m}^2 \text{ mo}^{-1}$; $D_p = 0.01 \text{ m}^2 \text{ mo}^{-1}$.

Contrary to the results of Klausmeier (1999) and HilleRisLambers et al. (2001), we found that coarse-scale degradation and collapse of vegetation can be explained if both redistribution of herbivores as well as redistribution of surface water are taken into account. Disturbances that only affect a small proportion of the vegetation will result in the formation of a two-phase pattern of alternating bare soil and vegetated patches, as predicted by Klausmeier (1999) and HilleRisLambers et al. (2001). Severe disturbances that reduce vegetation cover beyond a threshold level, however, will result in a positive feedback between reduced cover, on the one hand, and increased herbivore grazing, on the other hand. This will eventually lead to the collapse of vegetation on a scale of hectares.

The discrepancy between our results and the results of the models of Klausmeier (1999) and HilleRisLambers et al. (2001) can be explained by the differences in the assumptions that underlie the models. The models ignored losses of surface water due to drainage and assumed that within-patch herbivore abundance does not change with changing within-patch standing crop (HilleRisLambers et al. 2001) or is absent altogether (Klausmeier 1999). In other words, losses due to herbivore grazing remain constant despite changes in forage availability. This may hold for herbivore redistribution on scales of hectares to square kilometers but it is unlikely to be valid on the scale of square meters. Although these assumptions are not critical when explaining pattern formation, they severely limit the ability of ecological models to assess the potential for degradation on coarse spatial scales.

Our analysis shows that spatial interactions invoke feedback in response to a spatially heterogeneous disturbance.

Reduced plant cover in an area results in increased availability of water in remaining vegetated patches, thereby increasing local plant growth. Hence, spatial interaction through lateral exchange of water acts as a negative feedback to decreases in plant cover. Reduction of vegetation cover, however, also results in focusing of herbivore grazing in remaining vegetated patches. This may lead to overgrazing in the remaining vegetated patches. Hence, herbivore redistribution creates a positive feedback between reduced cover and increased within-patch herbivore grazing, which may lead to a collapse of the vegetation. The interplay of these two feedback mechanisms determines the dynamic response of the vegetation to changes in vegetation cover. If water redistributes quickly and herbivore density only responds weakly to changes in within-patch plant standing crop, then the effect of enhanced water availability exceeds that of increased grazing, and the system compensates for the disturbance. If herbivores redistribute quickly and in an ideal free manner to local changes in plant standing crop, then the effects of enhanced grazing may dominate that of enhanced water availability. Reduced cover will lead to reduced production and finally to collapse of the vegetation on scales exceeding that of patches.

The model shows that the sensitivity of semiarid vegetation is strongly dependent on the ability of herbivores to respond to changes in plant density, both on fine and on coarse scales. The potential for coarse-scale vegetation degradation is lowest in systems where herbivore numbers only react weakly to fine-scale differences in plant standing crop, while they can range freely on a coarse scale. The potential for vegetation degradation is highest when fine-scale movements of herbivores are unlimited, but movements are restricted on coarser scales. Pastoral systems in many semiarid regions have become a striking example of the latter type. In the Sahel region in Africa, expansion of agricultural fields in what was formerly an entirely pastoral landscape has severely reduced and fragmented the area available to grazers (De Bruijn and Van Dijk 1995). Movements of herbivores have been severely limited both because of blocked migration routes and, in cases of domestic herbivores, because of the obligations of herders to remain close to their agricultural fields (De Bruijn and Van Dijk 1995). Hence, in such systems, fine-scale movements, on the scale of square meters, are unlimited, while coarse-scale movements between fields are severely restricted. Our model predicts that in such cases the potential for coarse-scale vegetation degradation is large. In more natural systems where herbivores can move unrestricted, pattern formation may occur, but negative feedback to loss of vegetation cover will prevent coarse-scale degradation and loss of production.

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