

Herbivore regulation and irreversible vegetation change in semi-arid grazing systems

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Models made to explain sudden and irreversible vegetation shifts in semi-arid grasslands typically assume that herbivore density is independent of the state of the vegetation, e.g., under the control of humans. We relax this assumption and investigate the mathematical implications of vegetation-regulated herbivore population dynamics. We show that irreversible vegetation change may also occur in systems where herbivore population dynamics are affected by changes in plant standing crop. Our analysis furthermore shows that irreversible vegetation change may occur for a larger set of soil and climatic conditions when herbivore numbers are independent of the vegetation, as compared to systems where vegetation density determines herbivore population size. Hence, our analysis suggests that irreversible vegetation change is less likely to occur in systems with natural herbivore population dynamics than in systems where humans control herbivore density.

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Models explaining the irreversible effects of drought or overgrazing on vegetation cover in semi-arid grasslands point at the existence of alternate stable vegetation states (Noy-Meir 1975, May 1977, Rietkerk and Van de Koppel 1997). In one state, the vegetation is dense, whereas the other state is characterised by bare soil or a sparse vegetation. Changes in herbivore numbers cause one of these states to disappear, and hence result in a dramatic and irreversible change in plant standing crop. Traditionally, theoretical studies focused on foraging constraints in herbivores as a potential mechanism for the observed phenomena (Noy-Meir 1975, May 1977). Recent studies, however, indicate that soil degradation is responsible for the special properties of semi-arid grasslands (Rietkerk et al. 1996, Rietkerk and Van de Koppel 1997, Van de Koppel et al. 1997, Rietkerk 1998).

A typical characteristic of the models addressed above is that the dynamics of the herbivore population are assumed to be uncoupled from the dynamics of the

vegetation: herbivore population size is considered to remain constant despite dramatic changes in vegetation density. This assumption may be reasonable for managed herbivore systems where herbivore numbers are kept constant by human intervention, for instance by supplying additional food or water to herbivores when natural resources are scarce. It is obvious, however, that the assumption does not hold in more natural systems where human interference is minimal, or in systems where management responds to climatic variability in primary production. In these systems, deterioration of the vegetation is likely to lead to a decrease of the herbivore population size (Drent and Prins 1987). As a result, grazing pressure is relaxed, allowing the vegetation to recover after a period of overgrazing. Hence, it is conceivable that soil degradation does not invoke multiple stable states in systems with more natural herbivore population dynamics.

Despite the sensitivity of most theoretical studies explaining irreversible vegetation shifts to the assump-

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tion of constant herbivore numbers, the consequences of vegetation-determined herbivore population change in semi-arid grazing systems have not been studied so far (but see Rietkerk 1998). In this paper, we investigate the implications of vegetation-regulated herbivore population dynamics in systems sensitive to soil degradation. First, we present a graphical analysis of general plant-herbivore models in which we investigate the conditions for multiple stable states to occur as a consequence of soil degradation. Second, we compare more explicit models of the dynamics of semi-arid grasslands, in which the conditions for multiple stable states are related to well-known ecosystem parameters.

Herbivore dynamics: a general approach

A diverse collection of models has been used to study discontinuous dynamics in herbivore-dominated systems (Noy-Meir 1975, May 1977, Yodzis 1989, Rietkerk and Van de Koppel 1997, Rietkerk et al. 1997, Van de Koppel et al. 1997, Augustine et al. 1998). These models differ in specific details, but all share a similar structure. The rate of change of plant standing crop P is represented by a differential equation, such as:

$$dP/dt = f(P)P - c(P)H \quad (1A)$$

where the function $f(P)$ represents per capita plant growth as a function of plant standing crop, $c(P)$ the rate of grazing per herbivore, and H the density of herbivores. In most plant-herbivore models, per capita plant growth $f(P)$ is assumed to be maximal at low plant standing crop, and to decrease with plant standing crop due to density dependent regulation (Fig. 1a). In semi-arid systems, however, plants may facilitate their own growth by decreasing runoff of water, pro-

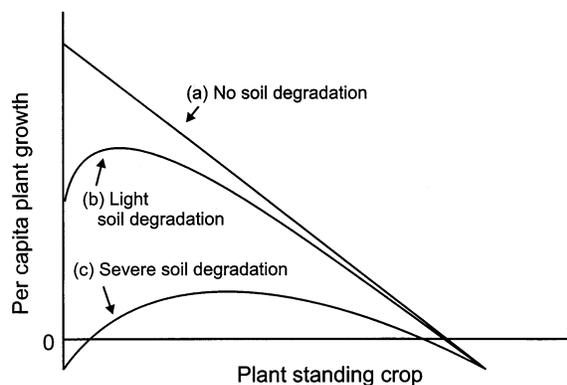


Fig. 1. The relation between per capita plant growth and plant standing crop in a system without soil degradation, a system with light soil degradation, and a system with severe soil degradation.

moting infiltration of water into the soil, and preventing nutrient losses due to erosion of the top soil (see, e.g., Snyman and Fouche 1991). Decrease of plant cover due to herbivore grazing may have indirect adverse effects on plant growth, because resources essential to growth are lost from the system (Elwell and Stocking 1976). This phenomenon is generally referred to as soil degradation. The net effect of soil degradation on plant growth is that per capita plant growth rate is decreased at low plant standing crop (Fig. 1a versus 1b), a phenomenon which is referred to as an Allee effect in ecological literature (see, e.g., Begon et al. 1996). Consequently, $f(P)$ is low at low plant standing crop, maximal at intermediate plant standing crop, and low again at high plant standing crop. If soil degradation is severe, per capita plant growth may become negative, as is shown in Fig. 1c.

Herbivore consumption $c(P)$ is generally assumed to increase with plant standing crop. Several functions are in use, however. The simplest function is a linear relation between herbivore consumption and plant standing crop. Most models, however, use more realistic functions in which herbivore consumption saturates and reaches a maximum at high plant standing crop (type II functional response, Holling 1959), or a sigmoid function which includes herbivore switching behaviour (type III functional response, Holling 1959). Theoretical studies have shown that both herbivore saturation at high plant standing crop, and soil degradation at low standing crop may induce threshold behaviour in plant-herbivore systems. Net plant growth may become negative at low plant density ($dP/dt < 0$), whereas it is positive at high plant density ($dP/dt > 0$). In such conditions, a small change in herbivore numbers may lead to large and irreversible changes in plant standing crop (Noy-Meir 1975, May 1977, Rietkerk and Van de Koppel 1997, Van de Koppel et al. 1997). These models assume a constant herbivore density H , and therefore apply exclusively to systems where herbivore population dynamics are uncoupled from forage availability.

In models of systems with natural herbivore population dynamics, the rate of change of the herbivore population has to be considered explicitly. In most plant-herbivore models, this rate of change is represented as

$$dH/dt = (g(P) - d) \cdot H \quad (1B)$$

where $g(P)$ represents per capita herbivore population growth as a function of plant standing crop, and d represents the mortality rate. Often, but not necessarily, $g(P)$ is linearly related to $c(P)$: $g(P) = e c(P)$, where e is the 'efficiency of growth' of the herbivore.

Analyses of the behaviour of system 1A and B without soil degradation (e.g., $f(P)$ decreases monotonically with increasing P) can be found in many textbooks on mathematical ecology (e.g., Yodzis 1989, DeAngelis

1992). In case of a linear herbivore functional response, a single stable equilibrium is found, which is always stable. In case of a saturating or sigmoid functional response, the plant-herbivore equilibrium may be unstable when herbivore grazing is very efficient (Rosenzweig 1971). No multiple stable states or irreversible changes are found in these models, independent of the type of functional response used. This result depends, however, on the assumption that herbivore growth and mortality are density independent. Density dependent mortality (other than food limitation), caused by for instance territoriality in herbivores, may induce multiple stable states. Such behaviour, however, is uncommon among most ungulate herbivores.

The effects of soil degradation on the dynamic behaviour of system 1 can be investigated graphically using phase-plane analysis (Yodzis 1989). Fig. 2A depicts a graphical presentation of a plant-herbivore system with a linear herbivore functional response, but without soil degradation. We have depicted the plant isocline, given by $dP/dt = 0$ (dashed line), and the herbivore isocline, given by $dH/dt = 0$ (solid line) in the plant-herbivore plane. Below the plant isocline, plant density increases. Above, plant density decreases. Since net per capita herbivore growth is determined by plant density only (see eq. 1B), the herbivore isocline is represented by a vertical line. To the left of the isocline, plant density is insufficient to sustain herbivore population growth, and herbivore density decreases. To the right of the isocline, herbivore density increases. At the intersections of both isoclines, both P and H are constant, and the plant-herbivore system is in equilibrium. In this specific model this equilibrium is always stable (see, e.g., Edelstein-Keshet 1988), meaning that the system will return to this equilibrium after a small disturbance. Two boundary equilibria exist in this system: one at which herbivores are absent, and plants reach their maximum standing crop, and one at which both plants and herbivores are absent. Both boundary equilibria are unstable, meaning that both populations can invade if they are absent.

If we include the effects of soil degradation (as given by Fig. 1b) in system 1, the plant isocline becomes a bent curve which has a maximum at intermediate plant standing crop (Fig. 2B). The general behaviour of this model is similar to that of many plant-herbivore models with saturating herbivore responses (Rosenzweig and McArthur 1963, Rosenzweig 1969, Yodzis 1989). Equilibria located to the right of the hump in the plant isocline are stable. Equilibria to the left of the hump, however, are unstable: the system moves away from this equilibrium following a small disturbance (Fig. 2B). In the configuration presented in Fig. 2B, soil degradation induces cyclic behaviour. Severe grazing pressure at high herbivore density leads to deteriorating soil conditions and collapse of the vegetation. Herbivore density now decreases dramatically due to starvation.

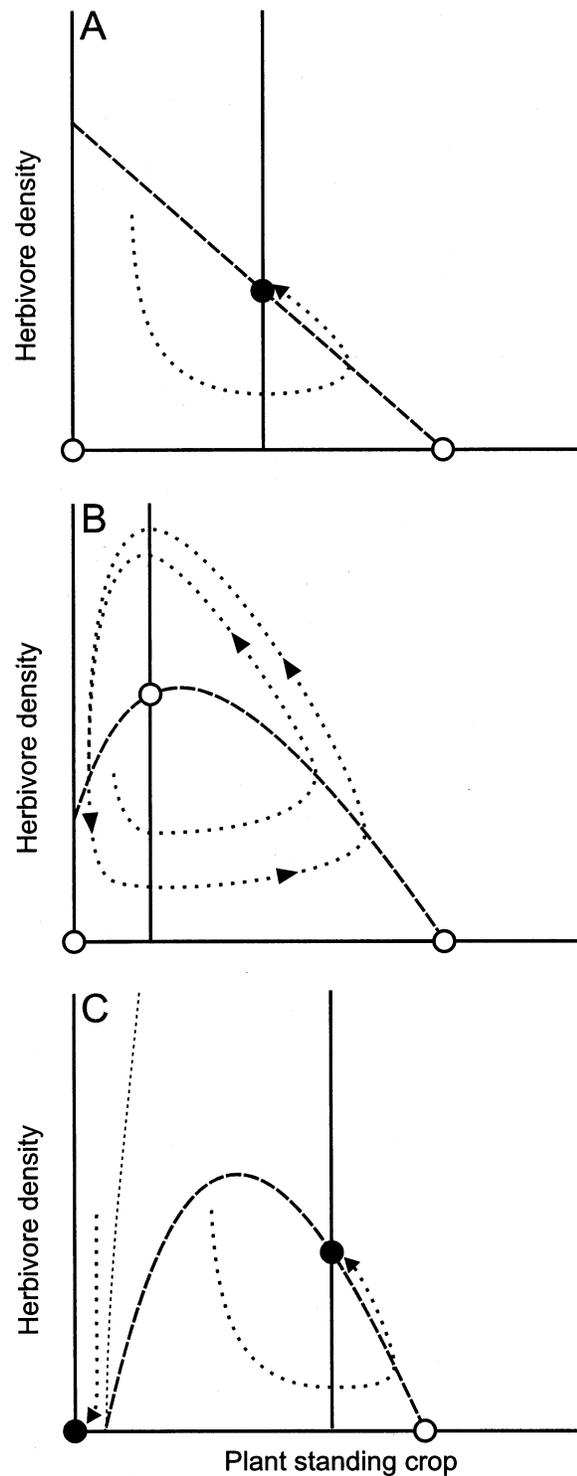


Fig. 2. Phase plane representations of the dynamics of a plant-herbivore system with linear functional response of the herbivore and (A) no soil degradation, (B) intermediate soil degradation, and (C) severe soil degradation. The solid line represents the herbivore isocline, the dashed line represents the plant isocline, and the dotted arrows represent the direction of change of the system in time. Solid circles represent stable equilibria, whereas open circles represent unstable equilibria.

Low grazing intensity allows for recovery of the vegetation, followed by an increase of herbivore density, and the cycle restarts.

The model behaves qualitatively different from traditional plant-herbivore models when the effects of soil degradation are severe, as in Fig. 1c. At low plant standing crop, per capita plant growth $f(P)$ becomes negative. As a result, the plant isocline intercepts with the herbivore axis at $H < 0$ (Fig. 2C). Plant growth is negative at $P = 0$, even in the absence of herbivores. Consequently, two stable states occur in the system: one at $P = H = 0$, and one at the intercept of the plant and herbivore isocline. Dependent of starting conditions, the system evolves to one of both stable equilibria. From eq. 1A can be inferred that the plant isocline has a negative intercept with the H -axis if and only if $f(P)$ is negative. Hence, the condition for multiple stable states to occur in systems with a dynamic herbivore population is independent of the type of herbivore functional response. See the Appendix for a formal derivation of stability conditions.

Our model analysis suggests that multiple stable vegetation states may also occur in semi-arid systems with natural herbivore population dynamics. The conditions for multiple stable states to occur are obvious from our graphical analysis: the plant isocline should intersect with the herbivore axis at $H < 0$, and hence net per capita plant growth should be negative at $P = 0$. Net plant growth should remain positive at intermediate plant density, however, allowing for an internal plant-herbivore equilibrium. Finally, the slope of the plant isocline should be negative at the intercept of the plant and herbivore isocline for the plant-herbivore equilibrium to be stable.

Herbivore dynamics in semi-arid grazing systems

The analysis above indicates that multiple stable states may both occur in systems with a constant or a dynamic herbivore population. This does not imply, however, that they are equally likely to occur in each model. In order to compare the potential for multiple stable states in relation to soil or climatic conditions, we perform a sensitivity analysis of two models where plant growth $f(P)$ is explicitly related to properties of semi-arid grazing systems (as given in Rietkerk et al. 1997). An important determinant of plant growth is the availability of water. In the extreme case where plant growth is limited by water availability only, per capita plant growth f can be expressed as a function of water availability:

$$f(W) = hW - l \quad (2)$$

where h is a coefficient relating specific plant growth to water availability, W is the water availability in the soil, and l is the loss rate of plant tissue due to senescence. Water availability is determined by rainfall infiltration, uptake by plants, and evaporation and drainage:

$$dW/dt = W_{in}(P) - uWP - r_w W \quad (3)$$

where $W_{in}(P)$ is the infiltration rate of water as a function of plant standing crop, u is a coefficient relating specific uptake rate of water by plants to water availability, and r_w is the rate of water loss due to evaporation and drainage. Water infiltration is minimal when vegetative cover is absent, and increases with plant standing crop (Elwell and Stocking 1976). The relation between water infiltration and plant standing crop can be described using the following equation (Walker et al. 1981):

$$W_{in}(P) = PPT(P + kW_0)/(P + k). \quad (4)$$

Here PPT stands for the rainfall, W_0 is the minimum water infiltration in the absence of plants, and k is a half saturation constant.

Since the dynamics of soil water act on a much faster time-scale than plant growth, we can assume that water availability is near equilibrium when considering the growth of plants: $dW/dt = 0$. This assumption allows us to express water availability as a function of plant standing crop (Van de Koppel et al. 1997):

$$W^*(P) = PPT \frac{P + kW_0}{P + k} \frac{1}{uP + r_w} \quad (5)$$

Insertion of eqs 2 and 5 into eq. 1A yields the plant growth differential equation for this system:

$$dP/dt = (hW^*(P) - l - bH)P, \quad (6)$$

where b is a coefficient relating per capita consumption to herbivore density. For this model, we can assess the potential for multiple stable states in systems with constant herbivore populations. Rietkerk and Van de Koppel (1997) show that the above model has a potential for multiple stable states when the following criterion is met:

$$dW_{in}(0)/dP < uW^*(0) \quad (7)$$

With eq. 7, we can investigate under which site-specific properties multiple stable states are to be expected.

The two most important abiotic parameters determining water availability into the soil are the rainfall rate PPT , and the proportion of the rainfall that infiltrates into the soil in the absence of plants W_0 . PPT is determined by the climate, whereas W_0 is determined by soil properties: infiltration rates are higher in sandy

soils than in clayey soils. Fig. 3A shows for which combinations of PPT and W_0 multiple states are predicted. The W_0 - PPT plane is divided into three sections based on the type of dynamics that is expected. At high PPT and W_0 (section I), only one stable state is found independent of herbivore densities. Changes in vegetation densities after for instance a drought or overgrazing are reversible, and hence no threshold effects are expected. In section II, the amount of rainfall infiltrating into bare soil is reduced, and hence alternate stable states may occur when herbivore densities are sufficiently high. In such systems, drought may result in a switch to a degraded state. Section II is subdivided in two parts. In the upper part, vegetation changes may be reversed if herbivore numbers are decreased significantly. In the lower section, soil degradation is severe. As a consequence, changes are irreversible, even when all herbivores are removed. In section III, the amount of water infiltrating is too low to support vegetation. Consequently, no vegetation can develop. The shape of the curves in the parameter plane is not dependent on herbivore density. This allows us to make a comparison with systems that have a dynamic herbivore population.

To assess the potential for multiple stable states in systems with dynamic herbivore populations, we need to include the population dynamics of the herbivore in our model. In its most simple form, herbivore growth is modelled by a linear numerical response:

$$dH/dt = (ebP - d)H \quad (8)$$

where e is the consumption-to-growth conversion coefficient and d is the natural mortality rate of the herbivore. Fig. 3B shows for which combinations of PPT and W_0 multiple states can be expected in a

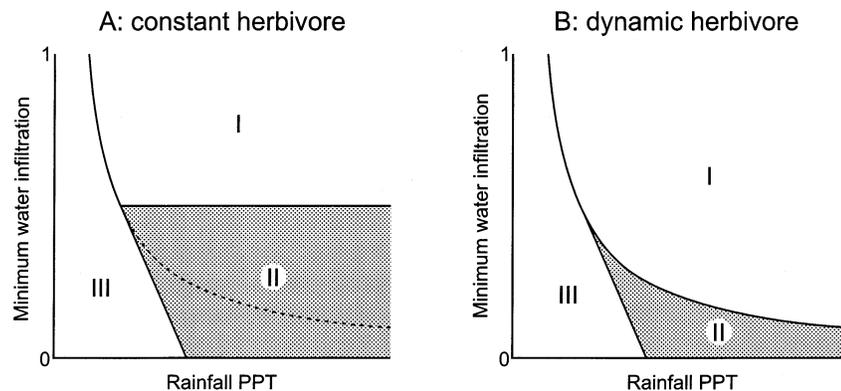
system with a dynamic herbivore population (eqs 6 and 8). In section I, no multiple stable states exist. A single vegetation state is found, which is always stable for the parameter ranges used. In section II, the system has two stable states. Hence, a disturbance, such as for instance a period of drought may lead to the irreversible loss of both plants and herbivores from the system. In section III, water infiltration is always insufficient to support vegetation, as in Fig. 3A.

It is clear from Fig. 3 that the parameter range in which multiple stable states occur is considerably smaller for systems with a dynamic herbivore population compared to systems with a constant herbivore population size. Early theoretical studies showed that a saturating or sigmoid functional response may induce multiple stable states even in systems without soil degradation (Noy-Meir 1975). Consequently, these functional responses will increase the potential for multiple stable states in systems with constant herbivore numbers. Functional responses, however, do not affect the conditions for multiple stable states in systems with natural herbivore population dynamics, as was shown in the former section. Hence, our models predict that systems with dynamic herbivore populations are less vulnerable to the effects of soil degradation than systems with constant herbivore numbers.

Discussion

Theoretical studies on irreversible vegetation shifts in semi-arid grazing systems typically assume that the dynamics of herbivore populations are independent from changes in vegetation density (Noy-Meir 1975, May 1977, Walker et al. 1981, Rietkerk and Van de

Fig. 3. Parameter planes depicting the qualitative behaviour of the models in case of (A) a constant herbivore population and (B) a dynamic herbivore population. In range I, only a vegetated state is possible, and vegetation changes are always reversible. In range II, multiple stable states may occur, and irreversible vegetation shifts can be expected. Underneath the dashed line in plane A, vegetation changes are irreversible even when herbivore numbers are decreased. In range III, only bare soil is found, because rainfall is too low to support plant growth. See text for further explanation. Parameter values used: $PPT = 0-10$, $W_0 = 0-1$, $k = 5$, $u = 0.02$, $r_w = 0.1$, $h = 0.01$, $l = 0.1$, $b = 0.01$ (both planes); $e = 0.2$, $d = 0.03$ (dynamic herbivore plane).



Koppel 1997). In this study, we relax this assumption and show that multiple stable states and hence irreversible vegetation shifts may also occur in systems where herbivore numbers are affected by changes in plant standing crop. Severe soil degradation at low plant standing crop may prevent recovery of the vegetation after disturbances, even after food shortage has caused herbivore numbers to collapse. Our models indicate, however, that multiple stable states occur for a much larger set of soil and climatic conditions when herbivore density remains constant compared to systems where herbivore populations respond to vegetation changes. This supports the notion that, in general, irreversible vegetation changes are less likely to occur in systems with dynamic herbivore populations compared to systems with constant herbivore numbers.

The analysis of the general model predicts that there is a potential for irreversible vegetation change in semi-arid systems with dynamic herbivore populations when plant growth is positive at high plant density, but negative at low plant density, even in the absence of herbivores. The water limitation model furthermore predicts that alternate stable states are most likely in systems where water infiltration in the absence of vegetation is minimal, for instance on clayey soils. Although this condition has been predicted by other theoretical studies (Rietkerk et al. 1997), we are unaware of any study in support of these predictions. Empirical studies that focus on the relation between the resilience of overgrazed pastures and soil properties would strongly enhance our insight into the dynamics of semi-arid grasslands.

Our analysis indicates that soil degradation may destabilise plant-herbivore equilibria and induce cyclic dynamics (Rietkerk 1998). Similar dynamic behaviour has frequently been found in predator-prey models in which the predator has a saturating functional response (e.g., Rosenzweig and McArthur 1963). Rosenzweig (1971) showed that exploiter-victim systems with a saturating functional response of the exploiter, such as most plant-herbivore systems, are vulnerable to enrichment: increase in the input rates of limiting resources may lead to system instability and collapse of the predator population. The model presented in this paper, with a linear functional response of the herbivore, predicts the opposite: Increase in rainfall reduces water limitation to plants in overgrazed areas and promotes recovery of the vegetation. This prediction is in agreement with the general finding that catastrophic vegetation dynamics occur most frequently in systems with low plant productivity such as semi-arid savannas or arctic tundras (Van de Koppel et al. 1997).

Our analyses are based on extreme cases where herbivore dynamics are either fully independent, or determined completely by forage availability. For many semi-managed rangeland systems, the assumption that herbivore production is completely uncoupled from

vegetation dynamics cannot be maintained (Illius and O'Conner 1999). Although domestic herbivore populations in semi-arid regions in Africa are managed by humans, large-scale and long-term disturbances such as the droughts of the early 1980s will inevitably lead to a decline of herbivore density. On the other hand, in Lake Manyara National Park, a system with wild herbivore populations, the total grazing pressure was found to remain constant despite fluctuations in rainfall (Prins and Douglas-Hamilton 1990). It is obvious that herbivore growth and mortality are determined by a multitude of factors including water availability, vegetation composition, and predation, and hence vegetation biomass per se may be a poor predictor of the numerical response of herbivores to vegetation change. Furthermore, recent insights suggest that there may be seasonal and spatial differentiation in the degree of coupling between vegetation density and herbivore growth (Illius and O'Conner 1999). Herbivore numbers may be determined by forage availability in key resource areas during the dry season, and hence herbivore dynamics would be uncoupled from vegetation conditions elsewhere in the system.

Recent developments in rangeland management proposed that stocking rates should track climatic variation (Toulmin 1994). Such "dynamic management" would buffer temporal changes in forage availability, optimise resource-use, and prevent irreversible loss of primary production (Illius et al. 1998). Our analysis, however, suggests that such management strategies do not preclude the possibility of vegetation degradation. The effectiveness of these management strategies may depend on the rate at which stocking rate changes are implemented. If management response is sufficiently quick as to preclude soil degradation, dynamic management could potentially prevent loss of secondary production. If, however, changes in stocking rate are implemented in response to loss of productive vegetation, our model suggests that destocking will not necessarily yield the expected recovery of vegetation.

In many natural grazing systems, herbivores react to seasonal vegetation change by migrating to other regions. Annual movements were typically found throughout African and North American grasslands before human influence became dominant in these systems (see Fryxell et al. 1988 for a review). Until this century, domestic livestock herders followed the natural annual movements of wild herbivores. In the last decades, however, pastoral herdsmen were encouraged to settle permanently in more arid regions, for example around man-made water holes. As a result, the vegetation around these human settlements was severely overgrazed during seasons unfavourable to plant growth (Sinclair and Fryxell 1985). Vegetation has proven to be more resilient in rangelands with traditional management allowing for seasonal movements of herbivores (Wade 1974). The effect of migration on the dynamics

of herbivore-dominated systems may be two-fold. Annual migration may prevent local overgrazing during unfavourable seasons. On the other hand, migration may increase the total number of herbivores that can be maintained within the region (Fryxell et al. 1988), and hence increase the overall grazing pressure. Hence, migration may lead to an enhanced herbivore grazing in low-productive areas because more productive parts of the landscape maintain a large population density (Holt 1984, 1985, Oksanen 1990).

In order to successfully predict the potential for sudden and irreversible vegetation change in herbivore dominated systems, we need a more thorough understanding of the numerical response of herbivore populations to changes in the vegetation. The impact of vegetation change on herbivore numbers may depend on biological factors such as forage availability, on abiotic factors such as water availability or human management, and on the availability of alternative sources of food or water within the landscape. Hence, adequate prediction of degradation potential in semi-arid grazing systems requires understanding of how geographical, economic and social influences interact with the ecological determinants of herbivore dynamics.

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Appendix

To derive the stability conditions for equilibria, we investigate the Jacobian matrix of the model described by eq. 1:

$$\mathbf{J} = \begin{bmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{bmatrix}$$

$$= \begin{bmatrix} f(P) + \frac{\partial f(P)}{\partial P} P - \frac{\partial c(P)}{\partial P} H & -c(P) \\ \frac{\partial g(P)}{\partial P} H & g(P) - d \end{bmatrix}$$

The stability conditions for system 1 read:

$$\text{Trace}(\mathbf{J}) = A_{11} + A_{22} < 0, \quad \text{and} \quad (\text{A1})$$

$$\text{Det}(\mathbf{J}) = A_{11}A_{22} - A_{12}A_{21} > 0. \quad (\text{A2})$$

For the boundary equilibrium ($P = 0, H = 0$), the stability criteria reduce to $f(P) + (g(P) - d) < 0$, and $f(P)(g(P) - d) > 0$. ($g(P) - d$) is negative at $P = 0$, and hence the last criterion is the most restrictive. Thus, the boundary equilibrium ($P = 0, H = 0$) is stable if $f(P) < 0$. Note that the stability of the ($P = 0, H = 0$) equilibrium is independent of the shape of the functional or numerical response of the herbivore, and solely determined by $f(P)$.

Two boundary equilibria exist where the plant isocline intersects the P -axis, which we denote with ($P = P_1^*, H = 0$) and ($P = P_2^*, H = 0$). At both equilibria, $H = 0$, and hence $f(P) = 0$. Thus, the stability criteria reduce to $(\partial f(P)/\partial P)P + (g(P) - d) < 0$, and $((\partial f(P)/\partial P)P)(g(P) - d) > 0$. At ($P = P_1^*, H = 0$), $(\partial f(P)/\partial P)P$ is positive. In this case, A1 and A2 cannot be satisfied simultaneously, and hence ($P = P_1^*, H = 0$) is always unstable. At ($P = P_2^*, H = 0$), $\partial f(P)/\partial P$ is negative. In this case, criteria A2 is most restrictive, and reduces to $g(P_2^*) < d$. Hence, ($P = P_2^*, H = 0$) is stable whenever plant density is insufficient for positive net herbivore population growth.

At the internal equilibrium ($P = P^*, H = H^*$), $g(P^*) = d$ and $f(P^*) = c(P^*)H^*$. Hence, the criteria for stability reduce to $f(P^*) + (\partial f(P)/\partial P)P^* - \partial c(P)/\partial P H^* < 0$ and $\partial g(P)/\partial P H^* c(P^*) > 0$. $\text{Det}(\mathbf{J})$ is always positive, and hence the stability of the internal equilibrium is determined by $\text{Trace}(\mathbf{J})$. The sign of $\text{Trace}(\mathbf{J})$ is always negative when the slope of the plant isocline is negative, and vice versa. Hence, internal equilibria are stable when the slope of the isocline is negative. Else, they are unstable, and limit cycles occur (Van de Koppel et al. 1996).