Oecologia (2001) 128:465–479
DOI 10.1007/s004420100737

P.B. Adler · D.A. Raff · W.K. Lauenroth

The effect of grazing on the spatial heterogeneity of vegetation

Received: 18 November 2000 / Accepted: 19 April 2001 / Published online: 3 July 2001

Abstract Grazing can alter the spatial heterogeneity of vegetation, influencing ecosystem processes and biodiversity. Our objective was to identify why grazing causes increases in the spatial heterogeneity of vegetation in some cases, but decreases in others. The immediate effect of grazing on heterogeneity depends on the interaction between the spatial pattern of grazing and the preexisting spatial pattern of vegetation. Depending on the scale of observation and on the factors that determine animal distribution, grazing patterns may be stronger or weaker than vegetation patterns, or may mirror the spatial structure of vegetation. For each possible interaction between these patterns, we make a prediction about resulting changes in the spatial heterogeneity of vegetation. Case studies from the literature support our predictions, although ecosystems characterized by strong plant-soil interactions present important exceptions. While the processes by which grazing causes increases in heterogeneity are clear, how grazing leads to decreases in heterogeneity is less so. To explore how grazing can consistently dampen the fine-scale spatial patterns of competing plant species, we built a cell-based simulation model that features two competing plant species, different grazing patterns, and different sources of vegetation pattern. Only the simulations that included neighborhood interactions as a source of vegetation pattern produced results consistent with the predictions we derived from the literature review.

Keywords Spatial heterogeneity · Spatial dependence · Herbivory · Competition · Disturbance

P.B. Adler (✉) · W.K. Lauenroth
Graduate Degree Program in Ecology and
Department of Rangeland Ecosystem Science,
Colorado State University, Fort Collins, CO 80523, USA
e-mail: petera@lamar.colostate.edu

D.A. Raff
Department of Civil Engineering,
Colorado State University, Fort Collins, CO 80523, USA

Introduction

The potential for grazing to alter the spatial heterogeneity of vegetation has both theoretical and practical importance. Its theoretical significance stems from our increasing appreciation of the influence of pattern on process. Although Watt (1947) recognized how vegetation pattern can control microclimate and soil factors, as well as biotic interactions in neighboring patches, only relatively contemporary researchers have extended his work. We now have evidence that pattern influences the spread of disturbance, the movement and persistence of organisms, and the redistribution of matter and nutrients (reviewed by Turner 1989; Pickett and Cadenasso 1995). Especially in semi-arid terrestrial ecosystems, patchiness may play a critical role in maintaining ecosystem productivity by concentrating limiting resources (Ludwig and Tongway 1995; Aguiar and Sala 1999). If grazing alters the spatial structure of an ecosystem, it will have potentially important consequences for a wide variety of ecosystem functions.

From a practical or management perspective, an important issue is the relationship between spatial heterogeneity and biodiversity. Changes in spatial heterogeneity caused by grazing imply changes in habitat diversity, and influence the diversity of consumers ranging from insects to birds and mammals (Smith 1940; England and DeVos 1969; Grant et al. 1982; Bock et al. 1984; Dennis et al.1998). Grazing also influences plant diversity in many ecosystems (Milchunas and Lauenroth 1993), but it is not clear whether changes in spatial pattern drive this effect. When grazing increases plant diversity primarily by reducing competition (Collins et al 1998), the spatial distribution of grazing may not matter. But grazing can also affect plant diversity by creating environmental heterogeneity at different spatial scales (McNaughton 1983; Sommer 2000).

Grazing offers a potentially important tool for conservation management because of its influence on habitat structure and biodiversity (Collins et al. 1998). Weber et al. (1998) concluded that grazing impacts on vegetation dynamics depended in large part on heterogeneity in grazing pressure, and “consequently, management...should account for spatial grazing aspects” (p 687). To use grazing as a management tool, however, we must be able to predict when grazing will increase rather than decrease spatial heterogeneity. Previous reviews have focused on how large herbivores respond to environmental heterogeneity (Bailey et al. 1996; Pastor et al. 1997; Hobbs 1999). While these reviews recognized that grazing influences spatial heterogeneity, they do not explain why grazing increases heterogeneity in some cases, but decreases it in others.

In this review, we focus on two basic questions. The first, with relevance to management issues, asks *when* does grazing increase the spatial heterogeneity of vegetation? Initially, we attempted to answer this question by focusing on the influence of ecosystem productivity, ecosystem type, and grazer selectivity. However, none of these factors successfully revealed general trends among case studies in the literature. Only after isolating the interaction between the spatial pattern of grazing and the pre-existing spatial pattern of vegetation at a specific scale, ignoring the biological details of each case, were we able to generate useful predictions. The observation that grazing can consistently dampen the fine-scale patterns of competing plant species in very different ecosystems led us to ask a second, and more theoretical question, *how* does grazing decrease spatial heterogeneity? To address this question, we built a simulation model to explore the consequences of alternative explanations.

We begin our analysis by defining spatial heterogeneity. Next we discuss influences on the spatial distribution of grazing pressure, frequently overlooked in studies of grazing and vegetation. In the following section we explain our predictions, then show that they are largely consistent with the results of published case studies from a wide variety of ecosystems. Finally, we use the simulation model to test how grazing can have consistent effects on the spatial heterogeneity of competing plants species despite contrasting effects on their relative abundance.

What is spatial heterogeneity?

Because the term *spatial heterogeneity* has been used in such diverse ways (Kolasa and Rollo 1991), it is especially important to define it clearly. When spatial heterogeneity is measured using non-spatial statistics, it corresponds to spatial variability; when it is measured using spatially explicit metrics, it corresponds to spatial pattern. We followed the latter approach, operationally defining spatial heterogeneity in terms of spatial dependence: the relationship between the values of one variable observed at different locations. When spatial dependence is strong, given the value of a variable at one location we can make reasonable predictions of the value of that variable at another location. In the absence of spatial dependence, we find no relationship between the values of the variable, even if the observations are very close together. Significant spatial dependence implies non-randomness or pattern, while spatial independence implies a random pattern. Likewise, we associate strong spatial dependence with spatial heterogeneity, and weak spatial dependence with spatial homogeneity. This definition equates spatial homogeneity with spatially random data, not with perfectly uniform, invariant data.

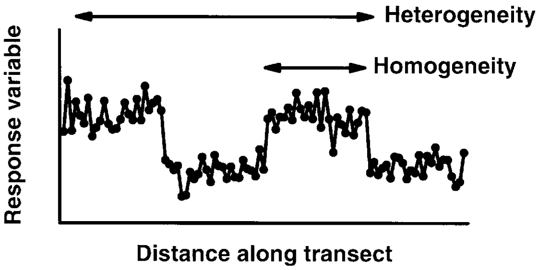

Fig. 1 Conceptual representation of “patchy” data: within each patch, the cover data is distributed randomly, creating low spatial dependence, equivalent to spatial homogeneity. At a larger scale spanning the distinct patches, the cover data is spatially dependent, and displays spatial heterogeneity

Spatial heterogeneity as we have defined it varies with scale. In field studies, the scale of observation is defined at the lower end by the frame size (the unit of sampling, such as a quadrat or pixel) and at the upper end by the overall extent of the study area (Atkinson 1997). Measures of spatial heterogeneity are sensitive to both quantities. Consider a landscape composed of two patch types. The patch types are distinguished by a difference in the mean of a randomly distributed variable. If we sample the variable only within one patch type, we find no spatial heterogeneity. However, if we move up in scale by increasing the extent of our sampling to include both patch types, we will find strong spatial heterogeneity (Fig. 1).

Previous authors have quantified spatial heterogeneity using measures of spatial dependence such as variograms (Sarnelle et al. 1993; Pastor et al. 1998) and autocorrelation indices (Riera et al. 1998). Spatial dependence can also be described by fractal dimension (Palmer 1988; Milne 1991; Ritchie 1998). Throughout this paper we will refer only to spatial heterogeneity, and not to spatial dependence, hoping to make the discussion more accessible to readers unfamiliar with the more technical term.

Factors influencing the spatial distribution of grazing

Although research on sources of spatial pattern in vegetation is central to ecology, factors controlling the spatial distribution of grazing pressure may be less familiar to some ecologists. In the wildlife and rangeland management literature, controls on grazing distribution have been extensively reviewed (Coughenour 1991; Bailey et al. 1996; Hobbs 1996, 1999). Here we summarize the influence of resources, predators and social behavior, plant quality feedbacks, and human management on spatial patterns of grazing.

The most obvious controls on grazing distribution are resources, primarily food, but also water and minerals in terrestrial systems. Senft et al. (1987) presented a hierarchical foraging model: grazers often select the landscape unit richest in resources, then the most productive communities within the landscape, and so on, down to the most palatable species within a feeding station (defined as the area an ungulate can graze without moving its feet). In both wild and domestic terrestrial grazing systems, grazing pressure typically decreases, even exponentially (Valentine 1947), with distance from water (Andrew 1988; Pickup et al. 1998; Turner 1999; Nash et al. 1999). Physical constraints such as steep slopes may limit access to high resource areas (Coughenour 1991; Bailey et al. 1996). The grazer's habitat is structured by the interaction of resources and such constraints.

Predators can exert considerable influence on the distribution of grazing. Studies from marine and aquatic systems clearly show that the threat of predation excludes herbivores from otherwise suitable habitat (Hay 1981a, 1981b; Hay et al. 1983; Andrew 1993; McConk 1997). Social behavior such as herding, which may be related to predation risk (reviewed in McNaughton 1984), can increase the probability of concentrated grazing pressure.

Feedbacks between grazing and plant quality may be important sources of spatial pattern in grazing, especially in terrestrial systems. Secondary production depends on both the quantity and quality of available forage (Hobbs and Swift 1985). While grazing reduces the quantity of available forage, in many systems it increases forage quality, typically measured as nitrogen or crude protein content (Coppock et al. 1983b; McNaughton 1984; du Toit et al. 1990; Jefferies et al. 1994), although other essential minerals such as sodium may respond similarly (McNaughton et al. 1997). Possible mechanisms for the increases in nutrient concentrations following grazing may include a reduction in senescent material, maintenance of leaves in an early phenological state (Richards et al. 1962; Hobbs 1999), or increases in belowground available nitrogen (Holland and Detling 1990). Such positive feedbacks promote the continued use of previously grazed patches. However, for animals to continue re-grazing a previously grazed patch, a minimum quantity of forage will also be necessary. Hobbs and Swift (1988) showed that patch grazing is more likely to occur in productive systems than dry systems: although forage quality may increase in both cases, only in more productive ecosystems is regrowth rapid enough to provide the minimum required quantity of forage.

While patch grazing may produce short-term positive feedbacks, changes in composition may eventually cause negative feedbacks (Coppock et al. 1983a; Pastor et al. 1998). When the short-term increases in forage quality caused by grazing are outweighed by compositional shifts towards unpalatable or low-nitrogen plant species, patch grazing cannot persist (Jefferies et al. 1994; Pastor et al. 1997). Such shifts in composition are more likely to occur in ecosystems where very distinct plant functional groups compete, such as grass-shrub steppe or tundra or mixed hardwood-coniferous forests, and where the abundance of the dominant species declines with grazing.

Most management activities in domestic grazing systems promote uniform grazing distribution. At the landscape scale, herding, water development, and fencing are used to manipulate animal distribution, and may play a larger role in transforming native grazing systems than the substitution of domestic grazers for wild ones (Hartnett et al. 1997). Within fenced pastures, increases in the intensity and/or duration of grazing causes an increase in the proportion of habitat in grazed patches (Berg et al. 1997; Cid and Brizuela 1998).

Although foraging theory assumes that consumers constantly select at all scales, experimental evidence suggests that at scales which are fine relative to the grazer, spatially random, or homogeneous grazing may occur, meaning that the spatial heterogeneity of grazing will be low if we measure biomass removed per area at many locations. A recent field trial using artificial vegetation mosaics showed that cattle were more selective when choosing among large patches compared to small ones (WallisDeVries et al. 1999). Wallace et al. (1995) found that bison in Yellowstone National Park clearly chose feeding areas non-randomly based on forage availability and topography, but feeding stations within feeding areas were randomly located. Because of variability in the behavior and selectivity of individual animals, and foraging constraints imposed by herds, it seems reasonable that gregarious behavior would increase the likelihood of unselective grazing within grazed areas (Augustine and McNaughton 1998). Relatively random grazing should be most likely to occur at scales which are small relative to the herbivore, among strong generalist rather than selective grazers, in communities where differences in plant quality among species or patches is small (grasslands rather than grass-shrub steppes), and perhaps with herding rather than solitary herbivores.

Interactions between spatial patterns of grazing and vegetation

We hypothesize that the effect of grazing on the spatial heterogeneity of vegetation depends on the interaction between the spatial distribution of grazing and the pre-existing spatial heterogeneity in vegetation. Factors such as environmental heterogeneity, ecosystem productivity, ecosystem type, and grazer selectivity may be the ultimate determinants of patterns in grazing and vegetation, but do not control the immediate effect of grazing on spatial heterogeneity. When the spatial patterns of grazing and vegetation are generated independently, then changes in the spatial heterogeneity of vegetation depend on the relative strength of spatial heterogeneity in graz-

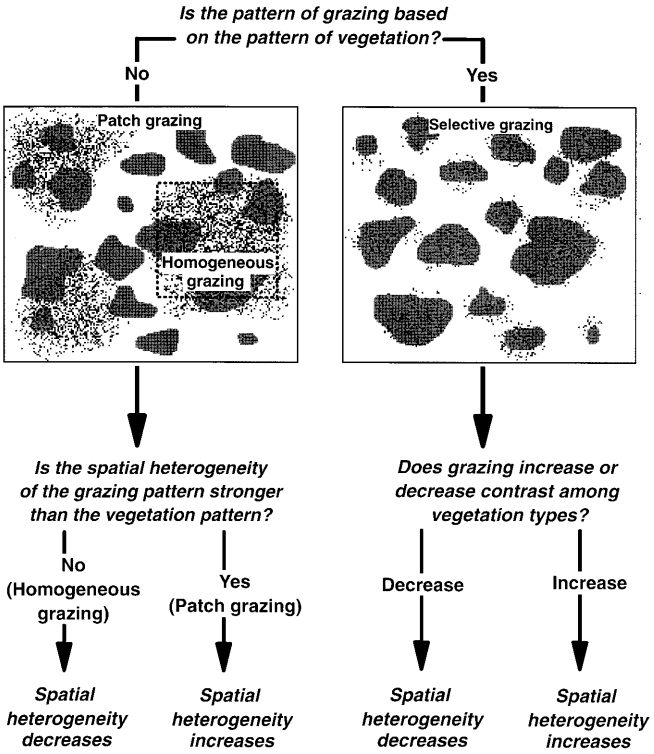

Fig. 2 Flow chart showing predictions for the effects of grazing on the spatial heterogeneity of vegetation. In the schematic drawings, *different shades of gray* represent vegetation pattern, while *black dots* show the distribution of grazing. The *drawing on the left,* in which grazing distribution is generated independently of vegetation pattern, demonstrates how the pattern of grazing depends on the scale of observation: spatially extensive sampling would reveal "patch grazing," while sampling confined within a grazed area (indicated by the *dashed box*) would observe "homogeneous grazing." Spatial heterogeneity is measured by spatial dependence

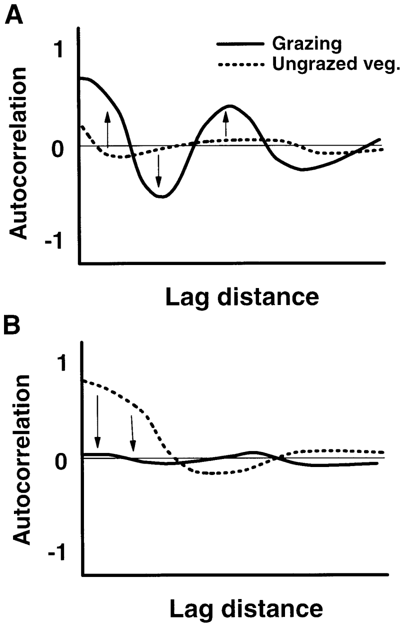

Fig. 3A, B Hypothetical autocorrelograms demonstrating interactions between spatial patterns of grazing and vegetation. *Arrows* indicate how the vegetation pattern will change as a result of grazing. *Lag distance* refers to the geometric distance separating pairs of sampling points. **A** Interaction 1: strong spatial heterogeneity in grazing pressure introduces pattern into a randomly distributed vegetation variable. **B** Interaction 2: randomly distributed grazing pressure reduces the spatial heterogeneity of a patchy-distributed vegetation variable. Both interactions can occur simultaneously at nested spatial scales

ing and vegetation at a given scale of observation, defined by the frame size and extent of sampling (Fig. 2). If the spatial heterogeneity of grazing is stronger than the spatial heterogeneity of vegetation, then the spatial heterogeneity of vegetation will increase following grazing. We refer to this scenario as "patch grazing." If the spatial heterogeneity of grazing is weak relative to the spatial heterogeneity of vegetation, then the spatial heterogeneity of vegetation will decrease. We call this scenario "homogeneous grazing."

Examples of patch grazing (see next section) typically involve the repeated grazing of small areas within otherwise homogeneous grasslands promoted by the positive feedback between grazing and forage quality, or, in marine and aquatic systems, the confinement of herbivores to areas offering shelter from predators (Fig. 3A). Examples of homogeneous grazing often occur at smaller spatial scales, where (relatively) randomly distributed grazing overrides fine-scale spatial heterogeneity in vegetation created by environmental heterogeneity or neighborhood interactions (Fig. 3B). Both patchy and homogeneous grazing can occur simultaneously, but at different spatial scales (illustrated in Fig. 2). Under both patch grazing and homogeneous grazing, the changes in spatial heterogeneity will occur whether grazing has a positive or negative effect on the vegetation variable of interest; all that matters is that grazing alters the spatial pattern of variability.

A different interaction occurs when grazing patterns closely track vegetation patterns, or when both grazing and vegetation respond to the same patterning agent, such as topography. We refer to this scenario as "selective grazing," following Senft et al.'s (1987) model that extends to landscape scales the concept of selection, typically defined as the consumption of plant species out of proportion with their abundance. At broader scales, animals may respond more directly to environmental factors than to differences in forage quality, but the process is sufficiently analogous to warrant use of the same term. In the case of selective grazing, the effect of grazing on spatial heterogeneity does depend on the qualitative effect of grazing on the vegetation (Fig. 2). Spatial heterogeneity will decrease if grazing reduces the contrast between vegetation patches by negatively affecting abundance of the selected resource, but will increase if grazing heightens the contrast in vegetation by positively affecting resource abundance. We ignore the trivial case in which both grazing and vegetation are homogeneous, and the extremely unlikely case in which the spatial heterogeneity of grazing and vegetation are equal, but respond to independent patterning agents (theoretically, no change in spatial heterogeneity would occur).

An example of selective grazing negatively affecting the selected resource occurs in the shortgrass steppe of Colorado, where concentration of grazing pressure in productive swales causes a shift towards the species composition typical of uplands (Milchunas et al. 1989), reducing spatial heterogeneity at the landscape level. Although we found examples of selective grazing positively influencing resource levels, none of the case studies measured vegetation spatial patterns. Jefferies et al. (1994) reviewed studies from tundra ecosystems in which herbivores selected for high nutrient content, early successional vegetation, and maintained the vegetation in that state, at least over ecological time scales. These studies are distinct from examples of patch grazing, in which grazing imposes heterogeneity in forage quality on otherwise homogeneous vegetation. Unfortunately, without direct measurements of pattern, we can only speculate that selective grazing can increase spatial heterogeneity.

Results: evidence from the literature

If our predictions are correct, case studies reporting increases in spatial heterogeneity following grazing should represent patch grazing (since we found no examples of selective grazing having a positive effect on resource levels), while papers reporting decreases in spatial heterogeneity should represent homogeneous grazing or selective grazing. In order to assign each case study to one of these categories, ideally we would have quantitative information on the spatial heterogeneity of grazing and on the change in the spatial heterogeneity of vegetation. However, few of the studies quantified spatial heterogeneity as we have defined it, and those measuring pattern in both grazing and vegetation were even more rare. Thus, our classifications are subjective, but we indicate the strength of the evidence for each classification (Tables 1, 2). “Strong” evidence was offered only by case studies that used spatially explicit measures to quantify the spatial heterogeneity of both grazing and vegetation. Quantitative, but non-spatially explicit data, and qualitative description provided evidence of “moderate” strength. Many of the studies focused on vegetation pattern, including our own, offered no information on grazing pattern. Our classification of these papers is based on “incomplete” evidence. In the total absence of information on grazing distribution, we assumed homogeneous grazing. These levels of evidence apply to the use of the case studies for our purpose, and do not reflect the strength of the papers with respect to their original objectives.

Increases in spatial heterogeneity following grazing

To support our predictions, case studies reporting increases in spatial heterogeneity following grazing should contain evidence of patch grazing (Table 1). Increases in spatial heterogeneity reported by papers studying homogeneous or selective grazing would provide evidence against our predictions. Pastor et al. (1998) quantified the spatial heterogeneity of both grazing and vegetation, and demonstrated that spatial heterogeneity in consumption by moose created similar spatial heterogeneity in vegetation. Eight studies (Bakker et al. 1983; Coppock et al. 1983b; McNaughton 1984; Ring et al. 1985; Kellner and Bosch 1992; Lutge et al. 1996; Cid and Brizuela 1998; Posse et al. 2000), representing seven different ecosystems, documented patch grazing by domestic or wild ungulates. Presumably because of positive feedbacks with forage quality (Hobbs and Swift 1988), the grazers foraged in previously grazed areas, producing dramatic changes in vegetation structure and sometimes composition. The landscape-level contrasts between the grazed patches and adjacent ungrazed or lightly grazed vegetation caused an increase in spatial heterogeneity relative to ungrazed landscapes. Both Ring et al. (1985) and Cid and Brizuela (1998) documented changes in spatial heterogeneity over time, as small grazed patches formed, grew, and sometimes coalesced. Poff and Nelson-Baker (1997) showed similar patterns in model simulations of grazing in streams. Studies from three aquatic systems (Hay et al. 1981a, 1981b; Hay et al. 1983; Andrew 1993; McConk 1997) found that the presence or absence of herbivores, often controlled by the availability of shelter from predators, created areas of low and high plant or algal biomass. The resulting mosaic in biomass implies an increase in spatial heterogeneity relative to entirely ungrazed habitat. In a laboratory experiment, Sommer (2000) found that the spatial heterogeneity of benthic microalgal assemblages was increased by the patchy grazing of one insect herbivore, but was not affected by the relatively random grazing of a second herbivore. Studies of piospheres, the zones surrounding livestock watering points, generally show that strong grazing intensity gradients produce corresponding gradients in vegetation (reviewed in Andrew 1988; recent case studies include Pickup et al. 1998; Turner 1999; Nash et al. 1999). The results from all of these case studies are consistent with our prediction.

Three studies in this group, however, contained evidence of homogeneous grazing, and should have shown decreases not increases in the spatial heterogeneity of vegetation. Hartnett et al. (1996), working in the tallgrass prairie of Kansas, found that grazing increased species richness and fine-scale spatial heterogeneity. However, their descriptor of spatial heterogeneity, percent dissimilarity in pairwise quadrat comparisons, is not spatially explicit. Furthermore, Glenn et al. (1992) (Table 2) used the same descriptor in nearby sites but reached the opposite conclusion: grazing reduced heterogeneity at fine scales.

Results in Belsky (1986) and Rietkerk et al. (2000) present a stronger challenge to our hypothesis. Belsky demonstrated that heavy, apparently unselective grazing created a small-scale two-phase vegetation mosaic in a

Table 1 Case studies reporting increases in the spatial heterogeneity (*SH*) of vegetation following grazing. In order to be consistent with our predictions, these papers should represent “patch” grazing, and not “homogeneous” (*Homog.*) or “selective” grazing (indicated under *Distribution*). Under *Evidence* we indicate the strength of evidence for our classification of the interaction. Strong evidence required quantitative, spatially explicit description of both grazing and vegetation patterns. Moderate (*Mod.*) evidence required non-spatial data or qualitative information on both grazing and vegetation pattern. Incomplete (*Incmplt.*) evidence occurred when no information on grazing distribution was given, which in no way reflects the strength of the paper for its original purpose

Author	System	Grazer	Distribution	Evidence	Description
Pastor et al. (1998)	Boreal forest (Isle Royale, USA)	Moose	Patch	Strong	Patterns of moose-browsing introduced parallel pattern in vegetation
Bakker et al. (1983)	Grassland (N. Europe)	Sheep	Patch	Mod.	Patch-grazing led to areas with contrasting structure and composition
Berg et al. (1997)	Salt-marsh (N. Europe)	Sheep	Patch	Mod.	Patch grazing led to areas with contrasting structure and composition
Cid and Brizuela (1998)	Grassland (Pampas, Argentina)	Cattle	Patch	Mod.	SH first increased then decreased following introduction of cattle to pasture
Coppock et al. (1983b)	Grassland (mixed-grass prairie USA)	Bison and prairie dogs	Patch	Mod.	Bison preferentially grazed on prairie dog towns, creating contrasts with less-grazed areas
Kellner and Bosch (1992)) Lutge et al. 1996	Grassland (S. Africa)	Cattle	Patch	Mod.	Patch grazing led to areas with contrasting structure and composition
McNaughton (1983, 1984)	Grassland (Serengeti)	Wild ungulates	Patch	Mod.	Grazing lawns contrasted with adjacent, less-grazed areas
Posse et al. (2000)	Grassland (Tierra del Fuego)	Sheep	Patch	Mod.	Grazing created and maintained “lawn” physiognomy within tussock grassland
Ring et al. (1985)	Grassland (mixed-grass prairie USA)	Cattle	Patch	Mod.	Patch grazing led to areas with contrasting structure and composition
Piosphere studies (various)	Mostly arid and semi-arid systems	Livestock	Patch	Mod.	Grazing intensity gradients extending from water sources create parallel vegetation gradients
Andrew (1993)	Temperate reef	Sea urchins	Patch	Mod.	Sea urchins maintained barren habitat, but only near shelter
Hay (1981a, 1981b), Hay et al. (1983)	Coral reef	Fish and (Caribbean)	Patch sea urchins	Mod.	Heavy grazing near shelter altered vegetation relative to nearby ungrazed areas
McConk (1997)	Coral reef (Australia)	Fish	Patch	Mod.	Distribution of algal spp. determined by presence/absence of herbivores
Sommer (2000)	Artificial marine littoral	Gastropod	Patch	Mod.	Spatially heterogeneous grazing increased the heterogeneity of microalgal assemblages
Belsky (1986)	Grassland (Serengeti)	Wild ungulates	Homog.	Mod.	Grazing maintained a two-phase vegetation mosaic
Hartnett et al. (1996)	Grassland (tallgrass prairie USA)	Bison	Homog.	Incmplt.	Bison grazing increased species richness and “spatial diversity (heterogeneity)"
Rietkerk et al. (2000)	Savanna (West Africa)	Cattle	Homog.	Incmplt.	Patch size in areas grazed moderately was larger than in areas grazed at low intensity

Table 2 Cases studies reporting decreases in the SH of vegetation following grazing. We predicted that papers in this class would contain evidence of "Homog." or "selective" grazing (indicated under *Distribution*). Under *Evidence* we indicate the strength of evidence for our classification of the grazing distribution. Strong evidence required quantitative, spatially explicit description of both grazing and vegetation patterns. Mod. evidence required non-spatial or qualitative information on both grazing and vegetation pattern. Incmplt. evidence occurred when no information on grazing distribution was given, which in no way reflects the strength of the paper for its original purpose. For abbreviations, see Table 1

Author	System	Grazer	Distribution	Evidence	Description
Sarnelle et al. (1993)	Artificial streams	Snails	Homog.	Strong	Grazing reduced SH of algal spp. cover
Sala et al. (1986)	Grassland (Argentine pampas)	Cattle	Homog.	Mod.	Grazing reduced compositional differences between flooded and dry sites
Fuhlendorf and Smeins (1998)	Grassland (semiarid savanna USA)	Cattle	Homog.	Incmplt.	Grazing reduced patterning of vegetation caused by soil variability
Glenn et al. (1992)	Grassland (tallgrass prairie USA)	Cattle	Homog.	Incmplt.	At small scales, grazing reduced plot dissimilarity
Mabbutt and Fanning (1985)	Semi-arid woodland (Australia)	Sheep and cattle	Homog.	Incmplt.	Grazing initially heightened grove-intergrove contrasts, then fragmented groves
Matus and Tóthmérész (1990)	Grassland (central Europe)	Cattle	Homog.	Incmplt.	Grazing reduced the number of significant plant spp. associations
Milchunas and Lauenroth (1989); Adler and Lauenroth (2000)	Grassland (shortgrass steppe USA)	Cattle	Homog.	Incmplt.	Grazing "smoothed" above and belowground biomass at very small scales; grazing reduced SH of dominant plant spp. cover
Tracy et al. (1998)	Grassland (Chihuahan desert)	Cattle	Homog.	Incmplt.	Grazing reduced SH of termite activity and litter cover
Bergelson (1990)	Artificial grassland	Slugs	Selective	Mod.	Heavy grazing on *Senecio* patches reduced their aggregation
Dale and Zbigniewicz (1997)	Boreal forest (Canada)	Hares	Selective	Mod.	Artificially heavy, selective browsing reduced intensity of shrub spatial patterns
Gibson (1988)	Grassland (Wales)	Sheep	Selective	Mod.	Selective grazing caused break-up of hummock-hollow pattern
Milchunas et al. (1989)	Grassland (shortgrass steppe USA)	Cattle	Selective	Mod.	Heavy grazing in swales reduced ridge-swale differences in vegetation
Bisigato and Bertiller (1997)	Shrub-steppe (Argentina)	Sheep	Selective?	Incmplt.	Grazing caused fragmentation of vegetation patches

Serengeti grassland. The removal of grazing changed patterns in water infiltration (see Aguiar and Sala 1999; Klausmeier 1999) and led to the disintegration of the two-phase mosaic. The paper makes no mention of the patch grazing phenomenon typical of other grassland studies in this group, so we felt that this case represented homogeneous grazing, for which we predicted the opposite response: decreases in spatial heterogeneity following grazing. Rietkerk et al. (2000) measured the scale dependence of vegetation along a gradient of livestock grazing intensity. Patchiness was fine scale in the lightly grazed site, more coarse scale in a moderately grazed area, and intermediate in scale in a very heavily grazed site. Like the Belsky paper, apparently homogeneous grazing increased heterogeneity through a strong positive feedback between vegetation and infiltration.

The response observed by Rietkerk et al. appears characteristic of systems in which spatial patterns of vegetation are generated by plant-soil feedbacks and the redistribution of nutrients. In desert grasslands of southwestern North America, grazing plays a role in the conversion of fine-grained grassland vegetation to more coarse-grained shrub-dominated vegetation (Schlesinger et al. 1990). Tongway and Ludwig (1994) suggested that the fine-scale resource regulation exercised by perennial grasses is very sensitive to degradation by grazing. Mabbut and Fanning (1985), working in semiarid Australian woodland, described a broader scale two-phase vegetation mosaic created by similar plant-soil interactions. However, they found that after a transient increase in grove-intergrove contrasts, grazing eventually fragmented the groves. In all these examples, grazing caused a change in the distribution of soil water and nutrients, which in turn altered vegetation distribution.

Why do our predictions fail for this group of case studies? One possibility is that we have misclassified these papers as examples of homogeneous grazing. Grazing in the two-phase mosaics of Australia is typically very selective (J. A. Ludwig, personal communication). But even if we classified these cases as selective grazing our predictions would still fail, since we predict no change in the scale of pattern in selective-grazing situations. More likely, these systems are unique in the strength of their plant-soil interactions, and the fact that resource redistribution is a primary source of vegetation spatial pattern. In these ecosystems, plant mortality caused by grazing leads to the redistribution and concentration of resources in fewer, larger patches, unless severe degradation results in the export of resources and the disintegration of patches.

Decreases in spatial heterogeneity following grazing

Based on our predictions, studies reporting decreases in spatial heterogeneity following grazing should correspond to homogeneous grazing or selective grazing (Table 2). We identified eight case studies representing homogeneous grazing. Sarnelle et al. (1993) provided the strongest evidence, using a geostatistical approach to show that grazing by randomly distributed snails in artificial streams reduced the small-scale spatial heterogeneity of overstory algae. Sala et al. (1986) found that a fine-scale vegetation pattern was erased by a “coarse-grained” grazing distribution. Fuhlendorf and Smeins (1998, 1999) showed that soil variability created clear vegetation patterns in ungrazed but not in grazed grasslands. Two studies from the shortgrass steppe of eastern Colorado, described “smoothing” of vegetation (Milchunas and Lauenroth 1989) and decreases in fine-scale spatial heterogeneity under livestock grazing (Adler and Lauenroth 2000). Tracy et al. (1998) reported decreases in fine-scale spatial heterogeneity of termite mounds and litter in grazed compared to ungrazed desert grassland. In a central European pasture, grazing reduced the number of significant plant species’ associations, indirect evidence for a decrease in spatial heterogeneity (Matus and Tóthmérész 1990). Although these case studies provide support for our prediction, we recognize that none of these studies, except for Sarnelle et al. (1993), measured grazing distribution quantitatively, and many offered no information on the spatial pattern of grazing. However, the majority of these studies were conducted at fine spatial scales, where typically broad-scale influences on animal distribution should be minor. Patch grazing of the kind described in the previous section theoretically could occur at fine scales, but none of the papers mentioned the phenomenon.

Five studies reporting decreases in spatial heterogeneity following grazing contained evidence of selective grazing. Bergelson (1990) showed that slugs grazed preferentially on high-density patches of *Senecio* in an artificial vegetation mosaic, and had a randomizing effect on the spatial pattern of *Senecio* seedlings. Grazing reduced spatial heterogeneity of shrubs in a boreal forest community under artificially high levels of herbivory (Dale and Zbigniewicz 1997). Gibson (1988) found that selective grazing of a dominant tussock grass caused homogenization of a hummock-hollow vegetation mosaic. Grazing reduced differences in plant composition between swales and uplands in shortgrass steppe (Milchunas et al. 1989). Prior work demonstrated much heavier grazing in swales than uplands (Senft et al. 1985), suggesting that grazing distribution responded primarily to vegetation pattern. Finally, selective grazing caused the fragmentation of shrub patches in Patagonian steppe, which we interpreted as a loss of spatial heterogeneity at the landscape scale (Bisigato and Bertiller 1997). The results of these studies are consistent with our predictions.

Changes in spatial heterogeneity at nested spatial scales

Multi-scale studies provide clear evidence that the effects of grazing on spatial heterogeneity can be scale-dependent. Pringle (1996) described the effect of grazing by Atyid shrimp on algal communities in Puerto Rican streams. In pools grazed by shrimp, two distinct communities were present: a “low-growing understory turf dominated by sessile diatoms” in the deeper, grazed portion of the pool, and a band of algae in the shallow margins of the pool where predation risk prevented grazing. At the scale of the whole pool, grazing increased spatial heterogeneity by creating depth zonation of the communities. Within the grazed portion of the pool, however, spatial heterogeneity decreased relative to the structural complexity of the ungrazed community. Gelwick and Matthews (1997) found very similar patterns in artificial streams. In Yellowstone National Park grasslands grazed by wild ungulates, Augustine and Frank (in press) showed that grazing reduced spatial heterogeneity in soil nitrogen and nitrogen mineralization at fine scales (m^2) but increased patchiness in soil nitrogen at a broader, slope scale (5–30 m). In all three cases grazing appears to have been distributed homogeneously at the finer scale, but in patches at the broader scale. These studies indicate the importance of specifying a particular spatial scale before asking how grazing will alter spatial heterogeneity.

Theoretical implications

We found no cases in which grazing clearly increased the spatial heterogeneity of some vegetation components, while decreasing the heterogeneity of others. The consistency of the heterogeneity response is particularly interesting in cases of selective and homogeneous grazing: how can grazing have positive effects on the abundance of some individual plant species, negative effects on others, but decrease the heterogeneity of all species (Adler and Lauenroth 2000)? The implication is that the effect of grazing on the size of each population in a community is independent of its effect on each population’s spatial structure. We built a simulation model to explore how this could occur.

Modeling decreases in spatial heterogeneity

The objective of our modeling exercise was not to simulate a natural ecosystem, but simply to construct an analytical tool to help us formulate hypotheses. This tool contains a vegetation component, in the form of two plant species, a competitive dominant and an opportunist; a grazing component, in the form of selective grazing with a negative effect on the grazed species or unselective (homogeneous) grazing on both species; and an independent source of vegetation pattern. We modeled three common sources of pattern in vegetation that are likely to interact with grazing:

1. Disturbance: grazing can influence succession in disturbed patches (Coffin et al. 1998), altering patch mosaics at a broader scale.
2. Environmental heterogeneity: the selection pressures exerted by grazing can mask the effects of factors such as soil texture that create pattern in the absence of grazing (Fuhlendorf and Smeins 1998).
3. Neighborhood interactions: grazing may override the fine-scale patterns formed by plant-level processes such as local seed rain (Coffin and Lauenroth 1989; Pastor et al. 1999), clonal growth (Klimes 1999), or local resource depletion (Whittaker 1975; Tilman 1982).

The model is an adaptation of Tilman’s (1994) two species competition model that demonstrates coexistence between a competitive dominant (species 1) and a superior disperser (species 2). Species 1 can invade areas occupied by species 2 as well as unoccupied sites, but species 2 can only invade unoccupied sites. Population dynamics in the model are determined by four parameters, a mortality rate and colonization rate for each species. Tilman’s model is neither spatially explicit, nor does it contain pattern-generating mechanisms. We made the model spatially explicit by running it on a grid of 40×40 square cells. Each cell corresponds to the area of an individual mature plant and can be in only one of three states: species 1, species 2, or empty. At each time step, mortality precedes colonization. The number of cells of each species to be killed or colonized is determined by the mortality or colonization rate multiplied by the population size, but the location of the affected cells is chosen at random. Once a cell is colonized, establishment depends on the state of the target cell (species 2 cannot establish in a cell occupied by species 1).

At this point, the model is spatially explicit and produces results consistent with Tilman’s (1994) analytical solutions (stochastic colonization causes minor departures), but still creates no spatial heterogeneity. We introduced heterogeneity in three ways:

1. Disturbance was simulated at each time step by killing all cells in a randomly chosen patch of variable size.
2. We simulated environmental heterogeneity, such as differences in soils, by splitting the grid, and increasing the mortality rate of species 1 on one half of the grid (the colonization routines are unchanged).
3. To simulate neighborhood interactions, once a cell is colonized we made the probability of establishment conditional on the states of the eight neighboring cells. The probability of establishment decreases linearly with the number of neighboring cells occupied by the competing species. Thus, if species 1 colonizes a cell completely surrounded by species 2, it has zero probability of establishment; if species 2 occupies none of the neighboring cells, the probability of establishment is one. This is the only form of the model in which species 1 can be prevented from invading a cell. Also, it is the only model that replaces uniform dispersal with more realistic patterns of dispersal mimicking local seed rain or clonal growth, a difference that can heavily influence model results (reviewed in Pacala and Levin 1997).

Grazing is modeled by increasing the mortality rates of the grazed plant species, as observed in some field studies (Williams 1970; Moloney 1988). Therefore, in the neighborhood interactions model, grazing should increase the proportion of cells occupied by bare ground during the colonization phase, reducing the likelihood of negative neighborhood interactions and weakening spatial heterogeneity, whether the competitive dominant (species 1) or the disperser (species 2) is grazed.

Parameter selection and statistical analysis

The parameters in our model are aggregates of biological processes. Colonization rate represents individual processes such as seed production, dispersal, germination, and, in the neighborhood interactions model, clonal growth. Providing empirical support for the chosen parameters would be misleading. Therefore, we chose sets of parameters that would best reproduce patterns observed in the literature, and later discuss under what conditions the chosen values would be reasonable. Based on the average time to population equilibrium in our stochastic version of the Tilman model, we arbitrarily chose to end all runs at 20 time steps. Because spatial heterogeneity, and not abundance, was the variable of interest, we controlled for large differences in abundances among the disturbance, environmental heterogeneity, and neighborhood models by adjusting colonization rates (parameter values shown in Table 3).

We used Moran's *I*, a coefficient of autocorrelation, to measure the strength of spatial heterogeneity in the distribution of each species after each 20 time step run. Values of Moran's *I* near zero indicate randomness, or spatial homogeneity, while values significantly greater than zero (positive spatial autocorrelation) or less than zero (negative spatial autocorrelation), indicate spatial heterogeneity. To construct autocorrelograms, we plotted Moran's *I* across increasing discrete lag distance classes. For comparison of grazing treatments, we analyzed values of Moran's *I* from a short lag distance class (spanning 2–4 cells), the scale demonstrating the strongest spatial heterogeneity in most of the model runs. We used S-Plus 4.5 with a library of spatial functions written by Reich and Davis (1998) to calculate Moran's *I*.

Model results and discussion

Each model generated characteristic spatial patterns (Fig. 4). The disturbance model generated significant spatial heterogeneity, as measured by autocorrelation, at small and moderate scales for species 1, but no significant spatial heterogeneity for species 2. The environmental heterogeneity model produced significant spatial heterogeneity in both species, even at broad spatial scales. In the neighborhood interactions model, spatial heterogeneity was significant for both species, but only at very fine scales. The scales of pattern simply reflected our arbitrary choices for the patch size of disturbance, the structure of environmental heterogeneity, and the range of neighborhood interactions.

To produce results consistent with our predictions based on the literature review, the spatial heterogeneity of both species, as measured by Moran's *I*, must be lower in each of the three grazed scenarios compared to the ungrazed scenario. Neither the disturbance model nor the environmental heterogeneity model produced such re-

Table 3 Parameter values for species 1 and 2 and abundance (% cover) of both species after 20 time steps for the four grazing treatments in each model (*n*=10). *G1* Species 1 grazed; *G2* species 2 grazed; *G1,2* both species grazed

Source of pattern	Treatment	Mortality		Colonization		Cover (%)	
		1	2	1	2	1	2
Disturbance	Ungrazed	3.0	3.0	0.11	2.5	42.1	36.9
	G1	5.0	3.0	0.11	2.5	33.5	49.7
	G2	3.0	6.0	0.13	2.5	51.0	23.5
	G1,2	4.5	4.5	0.11	2.5	35.4	41.4
Environmental heterogeneity	Ungrazed	3.0	3.0	0.12	2.5	41.1	40.2
	G1	5.0	3.0	0.12	2.5	27.4	60.6
	G2	3.0	6.0	0.14	2.5	47.5	26.6
	G1,2	4.5	4.5	0.12	2.5	47.5	26.6
Neighborhood	Ungrazed	3.0	3.0	0.13	2.0	44.4	39.5
	G1	5.0	3.0	0.13	2.0	29.1	57.4
	G2	3.0	6.0	0.15	2.0	51.0	25.2
	G1,2	4.5	4.5	0.13	2.0	34.4	46.5
Disturbance×neighborhood	Ungrazed	3.0	3.0	0.20	2.5	43.6	34.0
	G1	5.0	3.0	0.20	2.5	30.0	53.4
	G2	3.0	6.0	0.22	2.5	53.4	17.5
	G1,2	4.5	4.5	0.20	2.5	35.4	41.4
Environmental heterogeneity×neighborhood	Ungrazed	3.0	3.0	0.20	2.5	41.0	39.7
	G1	5.0	3.0	0.20	2.5	18.8	73.1
	G2	3.0	6.0	0.22	2.5	48.7	26.9
	G1,2	4.5	4.5	0.20	2.5	24.6	62.6

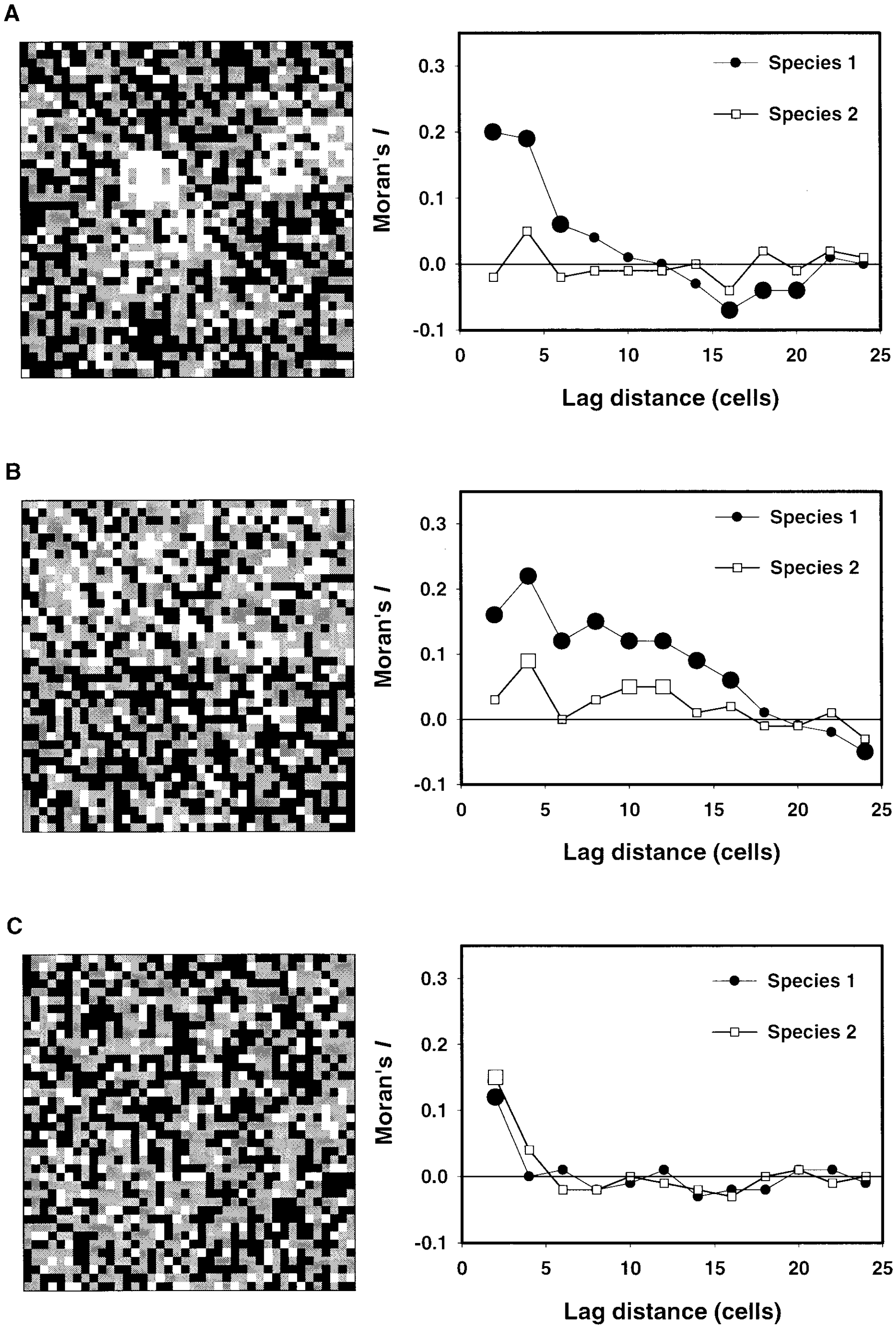

Fig. 4 Spatial patterns created by models simulating **A** disturbance, **B** environmental heterogeneity, and **C** neighborhood interactions. Each example comes from one simulation of the ungrazed scenario, producing abundances for both species of 40–45%. *On the left* are maps of cells occupied by species 1 (*in black*) and species 2 (*in gray*) after 20 time steps (empty cells are left *white*). *On the right* are autocorrelograms for both species. *Large symbols* indicate significant values of Moran's *I* (Bonferroni corrected α=0.0042)

sults (Fig. 5A, B). In the disturbance model, while homogeneous grazing reduced the heterogeneity of both plant species, the effect of selective grazing on population size and spatial structure was correlated: Spatial heterogeneity decreased for the selected species, but increased for the ungrazed species. Apparently, the species not selected for by grazing was most successful in colonizing disturbed patches. In the environmental heterogeneity model, the spatial heterogeneity of species 1 appeared unaffected by selective grazing on either species, but increased in response to homogeneous grazing. The spatial heterogeneity of species 2 increased following grazing on species 1, decreased following grazing on species 2, and showed a slight increasing following homogeneous grazing.

The neighborhood interactions model, in contrast, did produce results consistent with our predictions (Fig. 5C). The spatial heterogeneity of both species decreased under grazing of either species 1 or 2, and also under homogeneous grazing. By combining the neighborhood interaction model with the disturbance model, we produced results almost identical to those from the neighborhood interactions model alone, except that spatial heterogeneity was much stronger in all three scenarios (Fig. 5D). Adding neighborhood interactions to the environmental heterogeneity model, however, failed to "cor-

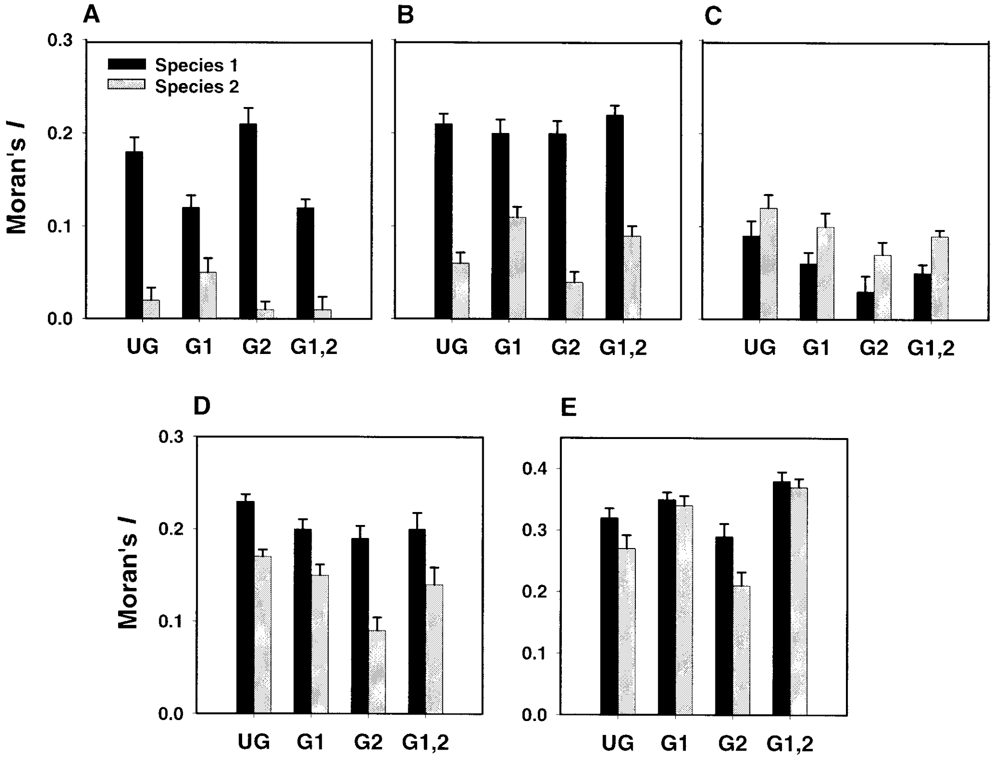

Fig. 5 Mean Moran's *I* for species 1 (competitive dominant) and species 2 (dispersal specialist) under four simulated grazing scenarios using five sources of vegetation pattern: **A** disturbance, **B** environmental heterogeneity, **C** neighborhood interactions, **D** disturbance and neighborhood interactions, and **E** environmental heterogeneity and neighborhood interactions. *Error bars* show SE (n=10). *UG* Ungrazed; *G1* species 1 grazed; *G2* species 2 grazed; *G1,2* both species grazed

rect" the results (Fig. 5E), probably because of the large difference in the scale of environmental heterogeneity and the scale of neighborhood interactions. If the environmental heterogeneity were smaller scale, or the neighborhoods more extensive, the model might produce results consistent with our predictions.

In all the models, the effects on spatial heterogeneity were subtle simply because grazing (increased mortality) has a much stronger effect on abundance than on pattern. Large increases in mortality quickly drive the grazed species to extinction, making tests of spatial heterogeneity trivial. Therefore, we could only simulate "light grazing" (small increases in mortality). Increasing the low baseline mortality rate (3%), which is more consistent with the mortality rates observed among cohorts of mature perennial plants than with the high rates of mortality common among seedlings (Harper and White 1974; West 1979), had little effect on the model results. Although the absolute strength of spatial heterogeneity changed, the relative strength of spatial heterogeneity among the grazing scenarios appeared robust.

Only models incorporating neighborhood interactions produced results consistent with the predictions we derived from the literature review. Based on these model results, neighborhood interactions offer the best explanation for the consistency in the spatial effects of grazing despite variable effects on relative abundance. Replacing uniform, long-distance dispersal with spatially explicit, local dispersal was an important advance in modeling competition and coexistence in plant communities (Pacala and Levin 1997; Bolker and Pacala 1999). Our analysis supports previous work showing that neighborhood interactions may be equally important in modeling the spatial response of communities to disturbance (Coffin and Lauenroth 1989; Pastor et al 1999).

Conclusions

We began this review with two questions. The first, more relevant to management applications, asked when does grazing increase the spatial heterogeneity of vegetation? We found that for different interactions between the spatial patterns of grazing and vegetation we can make useful predictions for changes in heterogeneity. This approach extends work by previous authors on grazing (Sala 1988), predation (Schneider 1992), and disturbance in general (Kolasa and Rollo 1991). These predictions should enable conservation planners to use grazing as a conservation tool. By managing the distribution of grazing in relation to existing patterns of vegetation, we can maintain or increase spatial heterogeneity at appropriate scales. Just as grazing can be patchy, homogeneous, or selective relative to vegetation, so can fire or windstorms. Therefore, our predictions should be useful not only to grazing management but to the management of disturbance in general. The second question, more theoretical in nature, asked how does homogeneous grazing dampen fine-scale spatial heterogeneity? Implicit in this question is an assumption that for homogeneous grazing to have similar effects in quite different ecosystems, a common mechanism must be operating. Our model results suggest that neighborhood interactions at the individual plant scale, rather than disturbance events or underlying environmental heterogeneity, may form the basis of this common mechanism.

By addressing pattern and scale, research on the interaction between spatial patterns of vegetation and grazing tackles "the central problem in ecology" (Levin 1992). So where to next? Our review identified many studies that examined spatial patterns of vegetation in different grazing treatments, some that discussed the spatial distribution of grazing, but very few that measured both. In order to properly test our predictions, both types of patterns must be described. A more ambitious research agenda is to expand our predictions, which forecast immediate effects at one specified spatial scale, to broader temporal and spatial dimensions using a combination of modeling and field experiments. How will feedbacks between vegetation and grazing influence heterogeneity over time? Can we predict the outcome of the interaction between patterns of grazing and vegetation for the continuum of spatial scales, rather than for an isolated scale? Solutions to these problems will provide a conceptual framework on which to hang the initial pieces of understanding we have developed.

Acknowledgements Special thanks to Dan Milchunas for invaluable discussions and comments on previous versions of the manuscript. Comments by J. Ellis, K. Metzger, J. Bradford, A. Ellingson, R. Monson, one anonymous reviewer, and members of the Burke-Lauenroth laboratory greatly improved the clarity of this material. Support was provided by an NSF Graduate Fellowship to P. B. A., the Shortgrass Steppe LTER Project (DEB-9632852), and the Colorado Experiment Station (1-57661).

References

Adler PB, Lauenroth WK (2000) Livestock exclusion increases the spatial heterogeneity of vegetation in the shortgrass steppe, Colorado. Appl Veg Sci 3:213–222

Aguiar MR, Sala OE (1999) Patch structure, dynamics, and implications for the functioning of arid ecosystems. Trees 14:273–277

Andrew MH (1988) Grazing impact in relation to livestock watering points. Trees 3:7–11

Andrew NL (1993) Spatial heterogeneity, sea urchin grazing, and habitat structure in reefs in temperate Australia. Ecology 74: 292–302

Atkinson PM (1997) Scale and spatial dependence. In: Gardingen PR van, Foody GM, Curran PJ (eds) Scaling-up: from cell to landscape. Cambridge University Press, Cambridge, pp 35–60

Augustine DJ, Frank DA (in press) Effects of migratory ungulates on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. Ecology

Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J Wildl Manage 62:1165–1183

Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL (1996) Mechanisms that result in large herbivore grazing distribution patterns. J Range Manage 49:386–400

Bakker JP, Leeuw J de, Wieren SE van (1983) Micro-patterns in grassland vegetation created and sustained by sheep-grazing. Vegetatio 55:153–161

Belsky AJ (1986) Population and community processes in a mosaic grassland in the Serengeti, Tanzania. J Ecol 74:841–856

Berg G, Esselink P, Groenewg M, Kiehl K (1997) Micropatterns in *Festuca rubra*-dominated vegetation induced by sheep grazing. Plant Ecol 132:1–14

Bergelson J (1990) Spatial patterning in plants: opposing effects of herbivory and competition. J Ecol 78:937–948

Bisigato AJ, Bertiller MB (1997) Grazing effects on patchy dryland vegetation in northern Patagonia. JArid Environ 36:639–653

Bock CE, Bock JH, Kenney WR, Hawthorne VM (1984) Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. J Range Manage 37:239–242

Bolker BM, Pacala SW (1999) Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. Am Nat 153:575–602

Cid MS, Brizuela MA (1998) Heterogeneity in tall fescue pastures created and sustained by cattle grazing. J Range Manage 51: 644–649

Coffin DP, Lauenroth WK (1989) Disturbances and gap dynamics in a semiarid grassland: a landscape level approach. Landscape Ecol 3:19–27

Coffin DP, Laycock WA, Lauenroth WK (1998) Disturbance intensity and above- and belowground herbivory effects on long-term (14 year) recovery of a semiarid grassland. Plant Ecol 139:221–233

Collins SL, Knapp AK, Briggs JM, Blair JM, Steinauer EM (1998) Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747

Coppock DL, Detling JK, Ellis JE, Dyer MI (1983a) Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant-species diversity. Oecologia 56:1–9

Coppock DL, Ellis JE, Detling JK, Dyer MI (1983b) Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. Oecologia 56:10–15

Coughenour MB (1991) Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. J Range Manage 44:530–542

Dale MRT, Zbigniewicz MW (1997) Spatial pattern in boreal shrub communities: effects of a peak in herbivore density. Can J Bot 75:1342–1348

Dennis P, Young MR, Gordon IJ (1998) Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. Ecol Entomol 3:253–264

England RE, DeVos A (1969) Influence of animals on pristine conditions on the Canadian grasslands. J Range Manage 22: 87–94

Fuhlendorf SD, Smeins FE (1998) The influence of soil depth on plant species response to grazing within a semi-arid savanna. Plant Ecol 1:89–96

Fuhlendorf SD, Smeins FE (1999) Scaling effects of grazing in a semi-arid grassland. J Veg Sci 10:731–738

Gelwick FP, Matthews WJ (1997) Effects of algivorous minnows (*Campostoma*) on spatial and temporal heterogeneity of stream periphyton. Oecologia 112:386–392

Gibson DJ (1988) The relationship of sheep grazing and soil heterogeneity to plant spatial patterns in dune grassland. J Ecol 76:233–252

Glenn SM, Collins SL, Gibson DJ (1992) Disturbances in tallgrass prairie: local and regional effects on community heterogeneity. Landscape Ecol 7:243–251

Grant WE, Birney EC, French NR, Swift DM (1982) Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. J Mammal 63:248–260

Harper JL, White J (1974) The demography of plants. Annu Rev Ecol Syst 5:419–463

Hartnett DC, Hickman KR, Fischer-Walter LF (1996) Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. J Range Manage 49:413–420

Hartnett DC, Steuter AA, Hickman KR (1997) Comparative ecology of native and introduced ungulates. In: Samson FB, Knopf FL (eds) Ecology and conservation of Great Plains vertebrates. Springer, Berlin Heidelberg New York, pp 72–101

Hay ME (1981a) Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. Am Nat 118:520–540

Hay ME (1981b) Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. Aquat Bot 11:97–409

Hay ME, Colburn T, Downing D (1983) Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. Oecologia 58:299–308

Hobbs NT (1996) Modification of ecosystems by ungulates. J Wildl Manage 60:695–713

Hobbs NT (1999) Responses of large herbivores to spatial heterogeneity in ecosystems. In: Jung HG, Fahey GC (eds) Nutritional ecology of herbivores: Proceedings of the Vth International Symposium on the Nutrition of Herbivores. American Society of Animal Science, Savory, Ill., pp 97–129

Hobbs NT, Swift DM (1985) Estimates of habitat carrying capacity incorporating explicit nutritional constraints. J Wildl Manage 49:814–822

Hobbs NT, Swift DM (1988) Grazing in herds: when are nutritional benefits realized? Am Nat 131:760–764

Holland EA, Detling JK (1990) Plant response to herbivory and belowground nitrogen cycling. Ecology 71:1040–1049

Jefferies RL, Klein DR, Shaver GR (1994) Vertebrate herbivores and northern plant communities: reciprocal influences and responses. Oikos 71:193–206

Kellner K, Bosch OJH (1992) Influence of patch formation in determining the stocking rate for southern African grasslands. J Arid Environ 22:99–105

Klausmeier CA (1999) Regular and irregular patterns in semiarid vegetation. Science 284:1826–1828

Klimes L (1999) Small-scale plant mobility in a species-rich grassland. J Veg Sci 10:209–218

Kolasa J, Rollo CD (1991) Introduction: the heterogeneity of heterogeneity, a glossary. In: Kolasa J, Pickett STA (eds) Ecological heterogeneity. Springer, Berlin Heidelberg New York, pp 1–21

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Ludwig JA, Tongway DJ (1995) Spatial organisation of landscapes and its function in semi-arid woodlands, Australia. Landscape Ecol 10:51–63

Lutge BU, Hardy MB, Hatch GP (1996) Plant and sward response to patch grazing in the Highland Sourveld. Afr J Range Forage Sci 13:94–99

Mabbutt JA, Fanning PC (1985) Vegetation banding in arid Western Australia. J Arid Environ 12:41–59

Matus G, Tóthmérész B (1990) The effect of grazing on the structure of a sandy grassland. In: Krahulec F, Agnew ADQ, Agnew S, Willems JH (eds) Spatial processes in plant communities. SPB, The Hague, pp 23–30

McConk LJ (1997) Effects of herbivory on zonation of *Sargassum* spp. within fringing reefs of the central Great Barrier Reef. Mar Biol 129:713–722

McNaughton SJ (1983) Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecol Monogr 53:291–320

McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. Am Nat 124:863–886

McNaughton SJ, Banyikwa FF, McNaughton MM (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278:1798–2000

Milchunas DG, Lauenroth WK (1989) Three dimensional distribution of plant biomass in relation to grazing and topography in the Shortgrass Steppe. Oikos 55:82–86

Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol Monogr 63:327–366

Milchunas DG, Lauenroth WK, Chapman PL, Kazempour MK (1989) Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. Vegetatio 80:11–23

Milne BT (1991) Lessons from applying fractal models to landscape patterns. In: Kolasa J, Pickett STA (eds) Ecological heterogeneity. Springer, Berlin Heidelberg New York, pp 199–235

Moloney KA (1988) Fine-scale spatial pattern and temporal variation in the demography of a perennial bunchgrass. Ecology 69:1588–1598

Nash MS, Whitford WG, Soyza AG de, Van Zee JW, Havstad KM (1999) Livestock activity and Chihuahuan Desert annual-plant communities: boundary analysis of disturbance gradients. Ecol Appl 9:814–823

Pacala SW, Levin SA (1997) Biologically generated spatial pattern and the coexistence of competing species. In: Tilman D, Kareiva P (eds) Spatial ecology. Princeton University Press, Princeton, N.J., pp 233–249

Palmer MW (1988) Fractal geometry: a tool for describing spatial patterns of plant communities. Vegetatio 75:91–102

Pastor J, Moen R, Cohen Y (1997) Spatial heterogeneities, carrying capacity, and feedbacks in animal-landscape interactions. J Mammal 78:1040–1052

Pastor J, Dewey B, Moen R, Mladenoff DJ, White M, Cohen Y (1998) Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan, USA. Ecol Appl 8:411–424

Pastor J, Cohen Y, Moen R (1999) Generation of spatial patterns in boreal forest landscapes. Ecosystems 2:439–450

Pickett STA, Cadenasso ML (1995) Landscape ecology: spatial heterogeneity in ecological systems. Science 269: 331–334

Pickup G, Bastin GN, Chewings VH (1998) Identifying trends in land degradation in non-equilibrium rangelands. J Appl Ecol 35:365–377

Poff NL, Nelson-Baker K (1997) Habitat heterogeneity and algal-grazer interactions in streams: explorations with a spatially explicit model. J N Am Benthol Soc 16:263–276

Posse G, Anchorena J, Collantes MB (2000) Spatial micro-patterns in the steppe of Tierra del Fuego induced by sheep grazing. J Veg Sci 11:43–50

Pringle CM (1996) Atyid shrimps' (Decapoda: *Atyidae*) influence over the spatial heterogeneity of algal communities over different scales in tropical montane streams, Puerto Rico. Freshwater Biol 35:125–140

Reich R, Davis R (1998) Quantitative spatial analysis. Colorado State University, Fort Collins, Colo.

Richards CR, Haenlein GFW, Calhoun MC, Connolly JD, Weaver HG (1962) Date of cut vs. the combination of crude fiber and crude protein as estimators of forage quality. J Anim Sci 21: 844–847

Riera JL, Magnuson JJ, Vande Castle JR, MacKenzie MD (1998) Analysis of large scale spatial heterogeneity in vegetation indices among North American landscapes. Ecosystems 1:268–282

Rietkerk M, Ketner P, Burger J, Hoorens B, Olff H (2000) Multi-scale soil and vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system in West Africa. Plant Ecol 148:207–224

Ring CB, Nicholson RA, Launchbaugh JL (1985) Vegetational traits of patch grazed rangeland in west-central Kansas. J Range Manage 38:51–55

Ritchie ME (1998) Scale-dependent foraging and patch choice in fractal environments. Evol Ecol 12:309–330

Sala OE (1988) The effect of herbivory on vegetation structure. In: Werger MJA, Art PJM van der, During HJ, Verhoeven JTA (eds) Plant form and vegetation structure. SPB, The Hague, pp 317–330

Sala OE, Oesterheld M, Leon RJC, Soriano A (1986) Grazing effects upon plant community structure in subhumid grasslands of Argentina. Vegetatio 67:27–32

Sarnelle O, Kratz KW, Cooper SD (1993) Effects of an invertebrate grazer on the spatial arrangement of a benthic microhabitat. Oecologia 96:208–218

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. Science 247:1043–1048

Schneider DC (1992) Thinning and clearing of prey by predators. Am Nat 139:148–160

Senft RL, Rittenhouse LR, Woodmansee RG (1985) Factors influencing patterns of cattle grazing behavior on shortgrass steppe. J Range Manage 38:82–87

Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological hierarchies. BioScience 37:789–799

Smith CC (1940) The effect of overgrazing and erosion upon the biota of the mixed-grass prairie of Oklahoma. Ecology 21: 381–397

Sommer U (2000) Benthic microalgal diversity enhanced by spatial heterogeneity of grazing. Oecologia 122:284–287

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton, N.J.

Tilman D (1994) Competition and biodiversity in spatially structured habitats. Ecology 75:2–16

Toit JT du, Bryant JP, Frisby K (1990) Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. Ecology 71:149–154

Tongway DJ, Ludwig JA (1994) Small-scale resource heterogeneity in semi-arid landscapes. Pac Conserv Biol 1:201–208

Tracy KN, Golden DM, Crist TO (1998) The spatial distribution of termite activity in grazed and ungrazed Chihuahuan Desert grassland. J Arid Environ 40:77–89

Turner MG (1989) Landscape ecology: the effect of pattern on process. Annu Rev Ecol Syst 20:171–197

Turner MD (1999) Spatial and temporal scaling of grazing impact on the species composition and productivity of Sahelian annual grasslands. J Arid Environ 41:277–297

Valentine KA (1947) Distance from water as a factor in grazing capacity of rangeland. J For 45:749–754

Wallace LL, Turner MG, Romme WH, O'Neill RV (1995) Scale of heterogeneity of forage production and winter foraging by elk and bison. Landscape Ecol 10:75–83

WallisDeVries MF, Laca EA, Demment MW (1999) The importance of scale of patchiness for selectivity in grazing herbivores. Oecologia 121:355–363

Watt AS (1947) Pattern and process in the plant community. J Ecol 35:1–22

Weber GE, Jeltsch F, Van Rooyen N, Milton SJ (1998) Simulated long-term vegetation response to grazing heterogeneity in semi-arid rangelands. J Appl Ecol 35:687–699

West N (1979) Survival patterns of major perennials in Salt Desert shrub communities of southwestern Utah. J Range Manage 32: 442–445

Whittaker RH (1975) The design and stability of plant communities. In: Doblen WH van, Lowe-McConnell RH (eds) Unity in concepts in ecology. Junk, The Hague, pp 169–181

Williams OB (1970) Population dynamics of two perennial grasses in Australian semi-arid grassland. J Ecol 58:869–875