Impact of grazing on species composition: Adding complexity to a generalized model

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Abstract The impact of grazing widely differs among plant communities. A generalized model published in 1988 proposed that this variation could be accounted for by the interaction between primary productivity and the evolutionary history of grazing. As productivity increased, the model predicted larger changes of species composition. Evolutionary history of grazing interacted with productivity: the changes in low-production systems were smaller if evolutionary history was long, whereas the changes in high-production systems were independent of evolutionary history. In this paper, we focus on: (i) the difficulties of determining the evolutionary history of grazing of a community, and (ii) additional mechanisms, which, as a sequence of filters in the process of community assembly, could be operating across the gradient of primary production. Assigning a given evolutionary history of grazing to a site has been difficult due to the lack of information on the historical population and distribution of herbivores with an adequate spatial and temporal resolution, and the lack of agreement on the size of the relevant evolutionary time window. Regarding the variation through a gradient of primary production, we propose three additional mechanisms coherent with the prediction of the model. First, the regional pool of available species increases with primary production. Second, grazing intensity (consumption as a proportion of above-ground production) also increases with primary production. Third, the strength of interspecific positive biotic interactions that protect plants from herbivores decreases with primary production. We highlight an additional potential mechanism, seed dispersal, whose variation across the gradient of productivity is not yet sufficiently understood. By connecting the logic of environmental filters to explain community assemblage with the original proposition of the generalized model, we suggest a series of research lines that can lead to a better understanding of why different communities respond differently to grazing.

Key words: community assembly, disturbance, evolutionary history, primary productivity, succession.

INTRODUCTION

The impact of grazing on the species composition and diversity of grasslands and savannas is highly relevant to both ecosystem management and disturbance ecology. For management, the central issue is which species will be promoted or diminished by grazing. Disturbance ecology provided the conceptual framework to understand the effect of herbivores on the structure of plant communities (e.g. McNaughton 1983; Wilson 1999). In fact, range management and disturbance ecology have been closely intertwined over the last century.

Milchunas *et al.* (1988) proposed a model to address why species composition is more affected in certain plant communities than in others by grazing by large generalist herbivores. With some modifications (Cingolani *et al.* 2005), this model is now the standard reference for any work on the effect of grazing on species composition. In this article, we (i) describe the

major developments previous to the formulation of that generalized model; (ii) describe the model; (iii) address some problems that arise when the model is used to predict or explain specific grazing effects, and propose some additions; and (iv) provide a synthesis and future lines of research.

PREVIOUS MODELS

The changes of species composition triggered by grazing were initially explained on the basis of classical succession theory (Clements 1916). Accordingly, all plant communities in the absence of disturbance were at a climax or steady state, which was only disrupted by disturbance. Therefore, disturbance reset the plant community to a more immature stage, after which succession led to a single, gradual pathway of recovery toward the climax through various intermediate seral stages.

Clements' ideas were applied to range management immediately by Sampson (1917), and later by Dyksterhuis (1949) who developed a model to classify the

different rangeland conditions of communities with similar climax according to grazing intensity (the range succession model sensu Westoby *et al*. 1989). At each condition, determined by a particular stocking rate, vegetation composition reached a temporary equilibrium resulting from two opposite forces, disturbance (i.e. grazing) and system change (i.e. succession). The range succession model also accounted for climatic variability: a season with above-average rainfall would act like succession and push the plant community toward its climax condition, while a season with below-average rainfall would push it toward a younger seral condition, as grazing does. Hence, management could increase stocking rate in wet years and reduce it in dry years. During rangeland succession, younger, heavily grazed seral stages were considered to be in a poorer condition as a forage resource than older, ungrazed or lightly grazed seral stages. The early stages were dominated by ruderal species, often exotics, with high dispersal ability, fecundity and growth rate. Throughout the succession, later seral stages were enriched in perennial species with higher forage value, until the climax stage was reached and communities were considered to be in an excellent condition as a forage resource.

These ideas were modified by the state-and-transition model (Westoby *et al*. 1989), which developed in agreement with parallel developments in basic ecology, such as the idea of alternative climax conditions, the importance of chance events, or the different mechanisms for species replacement (Drury & Nisbet 1973; Connell & Slatyer 1977). The model introduced a management tool based on communities not at equilibrium and not responsive to disturbance with predictable successional trajectories. Rangelands alternated among a spectrum of discrete states with the transitions among states triggered by a combination of grazing and other environmental factors (e.g. fire, rainfall). The model constituted a conceptual framework for developing a catalogue of state and transitions for different rangelands, and allowed a more versatile management (named opportunistic management) that helped range managers to seize opportunities for desirable transitions and avoid undesirable ones.

Both the range succession and the state and transition models, however, were not able to explain the variable impact of grazing on community composition across different communities, the issue that we address in this article. For instance, the semiarid shortgrass steppe in the North American Great Plains is relatively little affected by grazing (Milchunas *et al*. 1989; Milchunas *et al*. 2008). The steppe, dominated by two perennial grasses and a number of accompanying forbs, undergoes subtle changes in species composition under heavy grazing. In contrast, the subhumid Flooding Pampa grasslands, in Argentina, drastically change even at moderate grazing intensity (Sala *et al*.

1986). In this case, a few cool and warm season grasses, mostly native, are replaced by a number of exotic annual forbs and grasses (Sala *et al*. 1986). Milchunas *et al*. (1988) attempted to explain variations of this sort.

A GENERALIZED MODEL

Milchunas *et al*.'s (1988) generalized model proposed that the position of a community across gradients of moisture and evolutionary history of grazing determined its response to grazing (see in Appendix S1 a commentary by Milchunas, Lauenroth and Sala with some clarifications). The evolutionary history of grazing is a combined measure of the length of time and the intensity of grazing by large generalist herbivores (Milchunas & Lauenroth 1993). The generalized model was largely based on the intermediate disturbance hypothesis. Although the best known graphical representation of this model (fig. 3 in Milchunas *et al*. 1988) depicted species diversity as the response variable, the model focused on species composition as well as diversity (fig. 2 in Milchunas *et al*. 1988). Diversity and changes in species composition are related; disturbance may change species composition while diversity remains constant. Thus, we will limit our analysis to why species composition varies between contrasting grazing regimes. Because mean annual precipitation accounts for most regional variation of primary productivity in grasslands (Sala *et al*. 1988), the moisture axis of the model also reflects a gradient of productivity. Thus, the generalized model stated that the moisture axis was exchangeable with above-ground primary productivity (Milchunas *et al*. 1988), an issue that was later stressed and formalized further by Cingolani *et al*. (2005). The model proposed four basic situations that resulted from the interaction between two trends: subhumid grasslands experienced a remarkably greater response to grazing than semiarid ones, and semiarid grasslands with short evolutionary history of grazing had a greater response than those with a long history (Fig. 1).

The mechanisms for the different amount of change in species composition in response to productivity and evolutionary history of grazing were as follows. A central mechanism was the convergent selection for traits that confer resistance to grazing and drought, and the divergent selection for traits that confer resistance to grazing and ability to compete for light (Fig. 1; Coughenour 1985). Grasses from arid and semiarid habitats have small stature, basal meristems, high shoot density, deciduous shoots and high silica concentration, which enhance both the ability to tolerate drought and to avoid grazing. On the contrary, grasses from subhumid to humid habitats are taller and allocate more resources above-ground, which
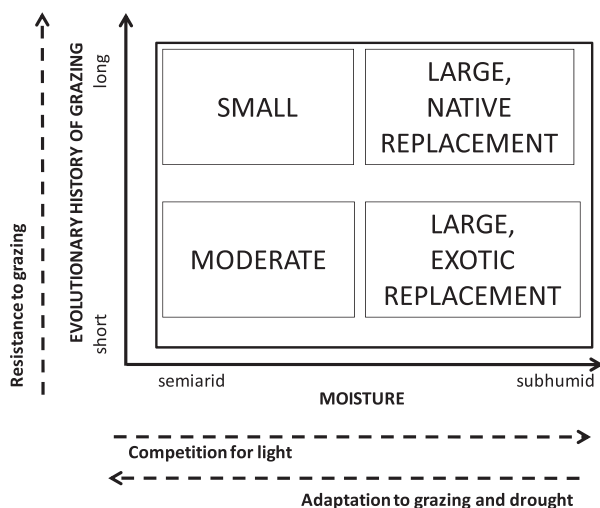
Fig. 1. Generalized model of the effect of grazing on community composition. The size of the effects is depicted as a function of moisture and the evolutionary history of grazing. Dashed arrows represent the major mechanisms proposed for the changes across each axis. Based on figure 3 of Milchunas *et al.* (1988), but restricted to changes in species composition.

confer on them higher competitive ability for aerial resources, but lower grazing resistance (Coughenour 1985; Herms & Mattson 1992). Another central mechanism was that as evolutionary history increased genotypes were more resistant to grazing (Fig. 1; Mack & Thompson 1982; Milchunas *et al.* 1988). As evolutionary history of grazing increases, plant species tend to have traits associated with resistance to grazing (Díaz *et al.* 2007), that is, tolerance in the form of rapid regrowth, or defence in the form of prostrate growth or silica content. The effect of evolutionary history of grazing on the amount of change of species composition as a response to grazing depended, in the generalized model, on the level of productivity. In low production systems, it added to the already present resistance to grazing derived from the adaptation to aridity and resulted in lower species changes. In high production systems, it generated a suite of species resistant to grazing that were more or less abundant according to the spatial variation of grazing intensity. Thus, the generalized model predicted similar amount of change of species composition in productive sites with long and short evolutionary history of grazing, but the mechanisms of species replacement were different. With a long history of grazing, grazing-susceptible species, which achieved dominance because of their ability to compete for light, were replaced by native, grazing-resistant species. With a short history of grazing, grazing-susceptible species were replaced by resistant species that were mostly exotic.

The model, originally based on a few case studies, was later tested by a meta-analysis that contrasted a number of situations across the world with different grazing regimes (Milchunas & Lauenroth 1993). The support for the model was partial (see in Appendix S1 a commentary by Milchunas, Lauenroth and Sala with a different interpretation). For the moisture axis, the results were as predicted by the model: as mean annual precipitation or productivity increased, the changes of species composition were larger (larger dissimilarity between grazing regimes). However, the proportion of variation of dissimilarity accounted for by mean annual precipitation was between low and moderate (15% overall, 13% for grasslands and shrublands, 40% for grasslands and 62% for shrublands). On the contrary, the evidence did not support the prediction for the interaction between evolutionary history of grazing and productivity. For grasslands and shrublands, as evolutionary history increased, the dissimilarity also increased at both ends of the moisture gradient, whereas for grasslands it increased at the subhumid end, and it did not change at the semiarid end. The proportion of variation of dissimilarity accounted for by evolutionary history of grazing was also between low and moderate (9% overall, 19% for grasslands and shrublands, 5% for grasslands and 5% for shrublands).

ADDING COMPLEXITY TO THE GENERALIZED MODEL

The generalized model proposed by Milchunas *et al.* (1988) was critical to understand and predict how grazing impacts species composition. More than 20 years since it was proposed, it remains as the standard reference to interpret the results of studies of grazing impact on plant communities. We will now focus on two central aspects of the model that could be improved by future research on grazing as a disturbance. First, the evolutionary history of grazing has some operational drawbacks. Second, other variables covarying with the axis of primary production may suggest additional mechanisms to explain why the effects of grazing on species composition increase with moisture or productivity. By proposing additional mechanisms, we are not suggesting that the originally proposed mechanisms are irrelevant. They most likely remain as the major mechanisms. However, considering additional mechanisms that are consistent with the model may help understand the variation of responses to grazing.

Operational limitations of the evolutionary history of grazing

Assigning a given evolutionary history of grazing to a site has proven to be complicated (Milchunas &

Lauenroth 1993; Lauenroth 1998; Adler *et al.* 2004). One of the difficulties is the lack of information on the historical population of herbivores with a spatial and temporal resolution that matches the requirement of users of the generalized model. We will illustrate this by describing in some detail the approaches followed by two studies that used the concept of evolutionary history of grazing. First, the most thorough review of the evidence for the generalized model (Milchunas & Lauenroth 1993) used the opinions of five experts who assigned to each site a value of 1 to 4 according to their knowledge of the evolutionary history of grazing. For each site, each expert had to combine the length and the intensity of grazing by large herbivores for the period between one million and one hundred years ago. Experts also included the certainty of their estimate (from 1 to 4 increasing certainty), which averaged between 2.0 for European sites and 3.1 for North American sites. Second, a thorough exploration of the evolutionary history of grazing as a potential explanatory variable of the diversity of plant traits assigned each site a category of evolutionary grazing based on the literature (Díaz *et al.* 2007). Sites were classified into either long or short evolutionary history of grazing based on the continuous occupation of large herbivores for the last 10 000 years. The resulting pattern of evolutionary history had a continental grain except for North America. South American sites were assigned a long evolutionary history of grazing, which contradicted the previous classification by Milchunas and Lauenroth (1993), which had assigned a short history to sites in that continent (average 1.7 in the 1–4 scale mentioned above). North America was the only continent with both long and short history sites, which likely resulted from a better knowledge of its paleoecology. These two examples illustrate that our capability to use the evolutionary history of grazing as an explanatory variable may be too coarse (continental scale, few classes) and uncertain (low certainty, subjective opinion, low consistency between studies).

The lack of hard evidence with good resolution on the evolutionary history of grazing makes it tempting to include plant traits as evidence. As was previously noticed (Lauenroth 1998), this is dangerous, circular thinking. Plant traits associated with a long evolutionary history, such as spines, or silica content should be defined *a priori* and be fully independent of observed patterns of response of the species to grazing.

Another pending issue on the quantification of the evolutionary history of grazing is the relevant time frame that should be taken into consideration (Fig. 2). This time frame has varied significantly among studies. Leaving out the last 100 years as ecological time, evolutionary time was considered within a time frame of about one million (Milchunas & Lauenroth 1993) to 10 000 (Díaz *et al.* 2007), to 2000 years
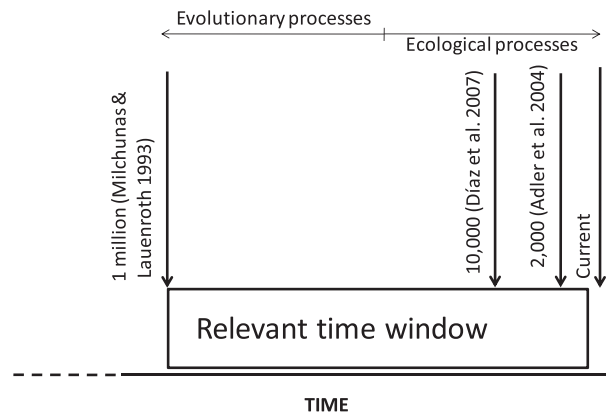

Fig. 2. Different authors have used different time windows as relevant to assign the evolutionary history of grazing to a site. The size of the time window implies different processes and thus different mechanisms for the role of evolutionary history of grazing as an explanatory variable of the effects of grazing on species composition. Notice that the window does not include the last 100 years, which are considered ecological time (Milchunas & Lauenroth 1993).

(Adler *et al.* 2004). How long and recent should the continuous presence of herbivores be to be relevant as a selective force on plants? Short-term evolutionary history may be insufficient for species-level adaptations to the evolutionary history of grazing, so most changes of species composition will stem from ecological processes, such as the migration of species previously adapted under conditions prevailing outside of the time/space frame (Fig. 2). In contrast, long-term evolutionary history may include evolutionary processes, such as speciation, that took place in the system under study. These issues are not exclusive of the evolutionary history of grazing, but apply to any other selective force.

The phylogeny of the grass family could become a framework for the analysis of the evolutionary history of grazing. There is ample evidence of the coevolution of grasses and grazers (Stebbins 1981; McNaughton 1984). However, grass phylogeny (Kellogg 2000, 2001; GPWG 2001) does not show a clear association with herbivory but instead suggests broad patterns of adaptation to shade/open environments, high or low temperature, or high or low water availability (Edwards & Smith 2010). Grass phylogeny does not show how the acquisition of traits to resist grazing could have driven grass evolution. If we knew how certain grazing-related traits were distributed across the phylogeny of the family or across certain subordinate groups, we could infer whether grazing was a more important evolutionary force in the evolution of certain genera or species than in others. Then, through the dominance of these groups in the field we could infer more directly the evolutionary history of grazing of the site. As indicated
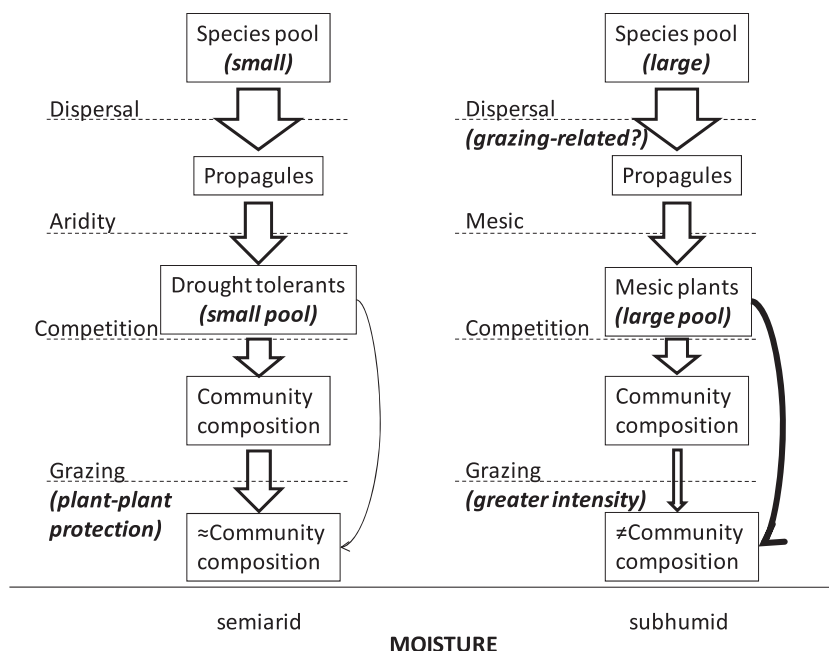
Fig. 3. Formalization of the generalized model of Milchunas *et al.* (1988) under the logic of community assemblage through environmental filters. Only the gradient of moisture is shown. Additional mechanisms that may explain why grazing impact on species composition increases with productivity were added between brackets (bold and italic). These additional mechanisms are the increase of the species pool size and the intensity of grazing in subhumid sites, and the increase of plant to plant protection from grazing in semiarid sites. Dispersal effects are highlighted, but remain undefined.

above, this should be done with caution because there is a high chance of circularity if the interpretation of grazing-related traits is based on the response of the species to grazing.

In contrast to the lack of association between grazing and broad phylogenetic patterns, grazing has clear links to intraspecific and intrageneric differentiation of grasses. A number of studies have shown intraspecific variation in grazing-related traits. Grazing ecotypes differ in plant height, tillering, leaf morphology, growth rates and response to defoliation (e.g. McNaughton 1984). There are also cases of contrasting adaptation to grazing between species of the same tribe (Caldwell *et al.* 1981). These strong microevolutionary changes suggest that the spatial pattern of evolutionary history of grazing may be fine-grained. For example, differences between prairie dog on-colony and off-colony sites separated by a few metres were responsible for large differences within grass species in a mixed-grass prairie (Painter *et al.* 1989). Interestingly, however, species from the drier shortgrass steppe did not show strong intraspecific differences in the response to defoliation (Kotanen & Bergelson 2000), which agrees with the predictions of the generalized model. In summary, assigning an evolutionary history to a site may require a knowledge of past herbivore distribution much more detailed than the current at the continental scale.

Additional mechanisms along the axis of primary productivity

The composition of a plant community has been presented as the result of a series of steps that starts with a regional pool of species and ends with the final composition of species. Thus, community composition results from the action of a sequence of filters or sieves through which some species are deleted and others retained: availability of species, dispersal, abiotic filters and biotic filters (Keddy 1992; Díaz *et al.* 1998, 1999; Wilson 2004). This logic is particularly well suited to address the effects of disturbances on community composition (Keddy 1992), but it has not been applied to the generalized model of the effect of grazing and its further developments (Milchunas & Lauenroth 1993; Cingolani *et al.* 2005). Analysed under this logic, the generalized model focused on the effect of an abiotic filter, moisture or rainfall, interacting with a biotic filter, competition. This combination determined the result of grazing (Fig. 3). In the model, the availability of water (Milchunas *et al.* 1988) and of soil resources in general (Milchunas *et al.* 1988; Cingolani *et al.* 2005) is a major abiotic filter that ultimately determines the response of the community to grazing. We will here analyse the role played by the size of the species pool, the process of dispersal, the intensity of grazing and the strength of other biotic interactions

across the gradient of primary productivity (Fig. 3). These additional mechanisms are not proposed as alternative mechanisms to competition, but as reinforcing mechanism that may generate the pattern predicted by the model and observed by later empirical studies.

Availability of species

As the availability of species in the regional pool increases, the changes in species composition triggered by grazing will be larger (Fig. 3). The species composition of a plant community ultimately depends on the availability of species at a broader scale (Ricklefs 1987; Keddy 1992). The regional pool of available species is the set of species in a region that may potentially live in the target community (Partel et al. 1996). If the size of the regional pool increased with rainfall or primary production, species availability would be an alternative mechanism for the pattern of species change induced by grazing across the gradient. For a given alpha diversity, there will be more potential for changing species composition as the pool size increases. We will here analyse this prediction based on patterns of richness among some case studies that were paradigmatic in formulating the generalized model (Milchunas et al. 1988; Partel et al. 1996): the Patagonian steppe and the shortgrass steppe, as low-production systems, and the Serengeti and the Flooding Pampa grasslands, as high-production systems.

As a general rule, species richness of rangeland increases with mean annual precipitation and primary productivity across regional gradients (Adler & Levine 2007; Anderson et al. 2007). In agreement with this general pattern, in the semiarid Patagonian steppe and in the shortgrass steppe regional richness is low. The Patagonian grass-shrub steppe has a total richness of 62 species and an average stand richness of 26 species (Golluscio et al. 1982). The uplands of the shortgrass steppe have a total of 107 species (Lauenroth 2008), and each stand has an average of 15–27 species (Milchunas et al. 1989). In contrast, the highly productive Serengeti and Flooding Pampa grasslands, which exhibit large changes in species composition as a result of grazing, have a larger regional species pools. In the Flooding Pampa, mesophytic meadows have a pool of 223 species and a stand richness of 33–39 species (Perelman et al. 2001). In the Serengeti, Anderson et al. (2007) found a total of 317 species: species richness ranged between 7 and 25 for a 10-m^2 area and between 12 and 45 for a 100-m^2 area, which is roughly similar to the Flooding Pampa's 33–39 species for a 25-m^2 sample area. All these data show that wet, high-production grasslands have more species regionally available than dry, low-production systems. Moreover, the increase of the pool size is much larger than the

increase of stand richness, which indicates that as productivity increases there are proportionally more species available to colonize a patch disturbed by grazing. Certainly, more data are needed to confirm the pattern, but these four example areas, the same used by Milchunas et al. (1988) to illustrate their model, suggest that regional species availability increases with primary production. The potential role of species availability is highlighted also by seed addition experiments combined with grazing: a common response is that grazing does not produce the expected changes in species composition unless seeds of the target species are added (Oesterheld & Sala 1990; Martin & Wilsey 2006).

The increasing size of the species pool as productivity increases could then become one additional mechanism for the larger changes of species composition induced by grazing in high- than in low-production grasslands. The size of the regional species pool represents the potential set of species that may be added as a result of grazing. Thus, as rainfall and productivity increase across regional gradients, there is a larger potential for species change, just as predicted by the generalized model, but through a new mechanism, different from competition.

What is the implication of the existence of this potential additional mechanism? As indicated above, the evidence for the prediction of the generalized model across the gradient of production is strong but not perfect: a significant amount of variation of species composition response to grazing remains unexplained. Thus, some deviation of the responses could be accounted for by species availability (e.g. because of the regional abundance of exotic species). The dissimilarity between grazed and ungrazed situations that arises from species additions requires the regional availability of species to be added. Thus, although the original mechanism proposed by the generalized model suffices to qualitatively explain the response, the size of the species pool may be responsible for some of the quantitative differences of response.

Dispersal

Grazing herbivores play a significant role in the dispersal of fruits and seeds. Most classifications of dispersal modes are based on the agent of dispersal and largely rely on morphological clues of the propagule. Major dispersal agents are wind (anemochory), water (hydrochory), animals (zoochory) and the plants themselves (autochory) (Levin et al. 2003). Dispersal of grassland species by grazing herbivores has been underestimated because many species with no particular seed or fruit morphology are dispersed by herbivores (Janzen 1984). The two most common mechanisms are seed deposition within feces, and the

transport of seeds attached to the surface of the animal. A high proportion of the species present in various grassland communities germinate in dung of several herbivore species (Pakeman 2001; Pakeman *et al.* 2002; Myers *et al.* 2004). In addition, plants of many herbaceous species are transported long distances by migrating herds of herbivores that carry them attached to their skin (Sorensen 1986; Manzano & Malo 2006) and may even facilitate their establishment through small-scale disturbances (Milchunas *et al.* 2008).

Does dispersal play a role in the patterns predicted by the generalized model? This would be the case if the dispersal spectra of species changed across the gradient of production and, in particular, if the dispersal by herbivores changed across the gradient. There is very little evidence for these possibilities. The dispersal spectra of vegetation do change across environmental gradients, such as water availability and soil fertility (Willson *et al.* 1990). However, due to the high proportion of species with no apparent dispersal mechanism that are actually dispersed by animals, these patterns are largely inconclusive. The types of dispersal associated with grazing intensity are also contradictory (McIntyre & Lavorel 2001; Pakeman 2004).

Even if dispersal does not have a clear variation with the gradients of the generalized model, it has such an impact that it may be a major source of the variation not explained by the model. For example, the conversion of Texas grasslands and savannas into dense woodlands has been tracked to the dispersal of *Prosopis glandulosa*, which, once established, facilitates the dispersal of other woody species by birds (Archer *et al.* 1988; Brown & Archer 1988). Dispersal is a critical step in the logic of community assemblage that we are following. In contrast to the previous step, species availability, for which we had evidence of a variation across the gradient of production, there is no clear direction in which grazing and dispersal may interact across that gradient (Fig. 3).

Covariation of production and grazing intensity

The generalized model assumed an increase of grazing intensity across the gradient of productivity because above-ground/below-ground ratios of biomass increased, and thus the proportion of total biomass removed by grazers also increased (Milchunas *et al.* 1988). The model was not explicit about variations of the proportion of above-ground productivity consumed across the axis, which is a common way of expressing grazing intensity, but stated that the impact of grazing on community physiognomy increased with production. The test of the model (Milchunas & Lauenroth 1993) showed that the pro-

portion of above-ground production consumed remained fairly constant or slightly decreased as productivity increased. Then, the increasing change of species composition induced by grazing across the gradient resulted from a given percentage of above-ground removal having contrasting effects at both ends of the gradient (Milchunas & Lauenroth 1993). The evidence for this pattern of above-ground grazing intensity came from reported estimates in the papers included in the review, either in the form of percentages of consumption or as herbivore density that was translated to consumption according to animal weight.

Other estimates of herbivore density showed that the proportion of above-ground consumption or grazing intensity increased across regional gradients of rangeland primary production. The biomass of herbivores increased exponentially with primary production at a regional scale, both for natural and livestock systems (McNaughton *et al.* 1989; Oesterheld *et al.* 1992, 1999; Fritz & Duncan 1994; Cebrian & Lartigue 2004). As a consequence, the percentage of above-ground production consumed increased with primary production from around 20–30% in the low end of the productivity gradient to 70–80% in the high end. The evidence for these patterns was mostly based on animal density surveys at different scales correlated with either rainfall or its translation into productivity by empirical models. According to these patterns, there could be an additional mechanism for the larger changes in species composition induced by grazing across productivity gradients: the average grazing intensity expressed as a proportion of above-ground production removed by herbivores increases with productivity thus reinforcing the mechanism of canopy opening initially present in the generalized model (Fig. 3).

The contrast between the patterns of above-ground consumption reported by Milchunas and Lauenroth (1993) and other sources (McNaughton *et al.* 1989; Oesterheld *et al.* 1992, 1999; Fritz & Duncan 1994; Cebrian & Lartigue 2004) is intriguing, and we do not have an explanation for it. Although the predictions of the generalized model are not altered by how the controversy is resolved, the potential mechanisms for those predictions will be affected. One of the important findings of the test of the generalized model was that where grazing occurs was more important than how it is done (Milchunas & Lauenroth 1993). The second set of evidence discussed here indicates that where and how grazing occurs are intimately related because as production increases herbivore density increases more than proportionally, and the relative consumption of above-ground production also increases, which would become an additional mechanism leading to the predictions of the generalized model.

Positive biotic interactions

Facilitative interactions are more frequent in arid and semiarid than in subhumid and humid conditions (Callaway 2007). Palatable species are often protected from grazing by less palatable neighbours (Milchunas & Noy-Meir 2002) and this type of relationship has been most often described for low production environments, such as alpine or dry steppe communities (Rebollo *et al.* 2002; Oesterheld & Oyarzabal 2004; Callaway *et al.* 2005). These indirect facilitative interactions would have the same consequences as predicted by the generalized model and thus could become an additional mechanism (Fig. 3): in dry environments, these interactions that protect plants from herbivory would be strong and thus species composition would change less after grazing than in humid environments where these interactions are weaker.

SYNTHESIS AND FUTURE LINES OF RESEARCH

More than 20 years later, the generalized model remains as the best explanation of why grazing differentially affects species composition of plant communities. In this article, we have further developed some early concerns with the operational problems of evolutionary history, and incorporated the logic of environmental filters of community assemblage in order to point to potential mechanisms that could be operating across the axis of primary productivity, most of them likely in the same direction as the originally proposed predictions of the model. The evolutionary history of grazing is a powerful concept to explain the variation of the impact of grazing on species composition, but it is a limited operational variable due to the coarse availability of data on past herbivore distribution. The mechanisms originally invoked to explain the influence of the gradient of moisture or productivity may be enriched with other potential mechanisms that may produce similar results. The size of the regional pool of species, the intensity of grazing and the strength of biotic interactions that protect plants from herbivores change across the gradient of productivity in a manner consistent with the predictions of the generalized model. Using the logic of environmental filters to explain community assemblage, we can see how these mechanisms may drive, together with the original mechanisms, the increasing effect of grazing on species composition as productivity increases (Fig. 3).

The future lines of research that arise from this analysis relate to each of the two axes of the generalized model. For the evolutionary history of grazing axis, it is clear that we need to map the evolutionary impact of grazing on the phylogeny of grasses as a family highly relevant to rangelands. Are there certain groups within the family that exhibit more traits related specifically to grazing tolerance or avoidance? Can these influences of grazing be discriminated from the influence of aridity? It is also necessary to define the time window of evolutionary history that is relevant for the problem of explaining differences in species composition. Obviously, we need to gain more spatial and temporal precision on the past distribution and abundance of herbivores.

For the productivity axis, we need experimental control of the species pool size (e.g. seed addition experiments), dispersal and grazing intensity to evaluate if these mechanisms are important. Surprisingly, the mechanisms proposed by the generalized model have remained largely untested. A recent paper (Quiroga *et al.* 2010) claims to be the first to show direct experimental evidence of convergence between aridity and grazing as selective pressures acting on both drought resistance and grazing resistance. Thus, the mechanisms considered by the generalized model and the mechanisms proposed here need to be tested under different conditions if we want to progress from observing patterns to a mechanistic understanding of why different communities respond differently to grazing.

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REFERENCES

Adler P. B. & Levine J. M. (2007) Contrasting relationships between precipitation and species richness in space and time. *Oikos* **116,** 221–32.

Adler P. B., Milchunas D. G., Lauenroth W. K., Sala O. E. & Burke I. C. (2004) Functional traits of graminoids in semiarid steppes: a test of grazing histories. *J. Appl. Ecol.* **41,** 653–63.

Anderson T. M., Metzger K. L. & McNaughton S. J. (2007) Multi-scale analysis of plant species richness in Serengeti grasslands. *J. Biogeogr.* **34,** 313–23.

Archer S., Scifres C., Bassham C. R. & Maggio R. (1988) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodalnd. *Ecol. Monogr.* **58,** 111–27.

Brown J. R. & Archer S. (1988) Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: the role of domestic herbivores. *Vegetatio* **73,** 73–80.

Caldwell M. M., Richards J. H., Johnson D. A., Nowak R. S. & Dzurec R. S. (1981) Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* **50,** 14–24.

Callaway R. M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht.

Callaway R. M., Kikodze D., Chiboshvili M. & Khetsruruani L. (2005) Unpalatable plants protect neighbors from grazing and increase plant community diversity. *Ecology* **86,** 1856–62.

Cebrian J. & Lartigue J. (2004) Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecol. Monogr.* **74,** 237–59.

Cingolani A., Noy-Meir I. & Díaz S. (2005) Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecol. Appl.* **15,** 757–73.

Clements F. E. (1916) *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institute Washington Publications, Washington.

Connell J. H. & Slatyer R. O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* **111,** 1119–44.

Coughenour M. B. (1985) Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Ann. Mo. Bot. Gard.* **72,** 852–63.

Díaz S., Cabido M. & Casanoves F. (1998) Plant funtional traits and environmental filters at a regional scale. *J. Veg. Sci.* **9,** 113–22.

Díaz S., Cabido M., Zak M., Martínez Carretero E. & Araníbar J. (1999) Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *J. Veg. Sci.* **10,** 651–60.

Díaz S., Lavorel S., McIntyre S. *et al.* (2007) Plant trait responses to grazing – a global synthesis. *Glob. Change Biol.* **13,** 313–41.

Drury W. H. & Nisbet I. C. T. (1973) Succession. *J. Arnold Arbor.* **54,** 331–68.

Dyksterhuis E. J. (1949) Condition and management of rangeland based on quantitative ecology. *J. Range Manage.* **41,** 450–9.

Edwards E. J. & Smith S. A. (2010) Phylogenetic analyses reveal the shady history of C4 grasses. *Proc. Natl. Acad. Sci. USA* **107,** 2532–7.

Fritz H. & Duncan P. (1994) On the carrying capacity for large ungulates of African savanna ecosystems. *Proc. Roy Soc. Lond. (B)*. **256,** 77–82.

Golluscio R. A., León R. J. C. & Perelman S. (1982) Caracterización fitosociológica de la estepa del oeste de Chubut: Su relación con el gradiente ambiental. *Boletin Sociedad Argentina Botanica.* **21,** 299–324.

GPWG (2001) Phylogeny and subfamilial classification of the grasses (Poaceae). *Ann. Mo. Bot. Gard.* **88,** 373–430.

Herms D. A. & Mattson W. J. (1992) The dilemma of plants: to grow or defend. *Q. Rev. Biol.* **67,** 283–335.

Janzen D. H. (1984) Dispersal of small seeds by big herbivores: foliage is the fruit. *Am. Nat.* **123,** 338–53.

Keddy P. A. (1992) Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* **3,** 157–64.

Kellogg E. A. (2000) The grasses: a case study in macroevolution. *Annu. Rev. Ecol. Syst.* **31,** 217–38.

Kellogg E. A. (2001) Evolutionary history of the grasses. *Plant Physiol.* **125,** 1198–205.

Kotanen P. M. & Bergelson J. (2000) Effects of simulated grazing on different genotypes of Bouteloua gracilis: how important is morphology? *Oecologia* **123,** 66–74.

Lauenroth W. K. (1998) Guanacos, spiny shrubs and the evolutionary history of grazing in the Patagonian steppe. *Ecología Austral* **8,** 211–15.

Lauenroth W. K. (2008) Vegetation of the shortgrass steppe. In: *Ecology of the Shortgrass Steppe* (eds W. K. Lauenroth & I. C. Burke) pp. 70–83. Oxford Univ. Press, Oxford.

Levin S. A., Muller-Landau H. C., Nathan R. & Chave J. (2003) The ecology and evolution of seed dispersal: a theoretical perspective. *Annu. Rev. Ecol. Syst.* **34,** 575–604.

McIntyre S. & Lavorel S. (2001) Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. *J. Ecol.* **89,** 209–26.

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

McNaughton S. J. (1984) Grazing lawns: animals in herds, plant form, and coevolution. *Am. Nat.* **124,** 863–86.

McNaughton S. J., Oesterheld M., Frank D. A. & Williams K. J. (1989) Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* **341,** 142–4.

Mack R. N. & Thompson J. N. (1982) Evolution in steppe with few large, hooved mammals. *Am. Nat.* **119,** 759–73.

Manzano P. & Malo J. E. (2006) Extreme long-distance seed dispersal via sheep. *Front. Ecol. Environ.* **4,** 244–8.

Martin L. M. & Wilsey B. J. (2006) Assessing grassland restoration success: relative roles of seed additions and native ungulate activities. *J. Appl. Ecol.* **43,** 1098–109.

Milchunas D. G. & Lauenroth W. K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol. Monogr.* **63,** 327–66.

Milchunas D. G. & Noy-Meir I. (2002) Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* **99,** 113–30.

Milchunas D. G., Sala O. E. & Lauenroth W. K. (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Nat.* **132,** 87–106.

Milchunas D. G., Lauenroth W. K., Chapman P. L. & Kazempour M. K. (1989) Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* **80,** 11–24.

Milchunas D. G., Lauenroth W. K., Burke I. C. & Detling J. K. (2008) Effects of grazing on vegetation. In: *Ecology of the Shortgrass Steppe: A Long Term Perspective* (eds W. K. Lauenroth & I. C. Burke) pp. 389–446. Oxford University Press, New York.

Myers J. A., Vellend M., Gardescu S. & Marks P. L. (2004) Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* **139,** 35–44.

Oesterheld M. & Oyarzabal M. (2004) Grass-to-grass protection from grazing in a semi-arid steppe. Facilitation, competition, and mass effect. *Oikos* **107,** 576–82.

Oesterheld M. & Sala O. E. (1990) Effects of grazing on seedling establishment – the role of seed and safe-site availability. *J. Veg. Sci.* **1,** 353–8.

Oesterheld M., Sala O. E. & McNaughton S. J. (1992) Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature* **356,** 234–6.

Oesterheld M., Loreti J., Semmartin M. & Paruelo J. (1999) Grazing, fire, and climate effects on primary productivity of grasslands and savannas. In: *Ecosystems of Disturbed Ground* (ed. L. Walker) pp. 287–306. Elsevier, Amsterdam.

Painter E. L., Detling J. K. & Steingraeber D. A. (1989) Grazing history, defoliation, and frequency-dependent competition -Effects on 2 North American grasses. *Am. J. Bot.* **76,** 1368–79.

Pakeman R. J. (2001) Plant migration rates and seed dispersal mechanisms. *J. Biogeogr.* **28,** 795–800.

Pakeman R. J. (2004) Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *J. Ecol.* **92,** 893–905.

Pakeman R. J., Digneffe G. & Small J. L. (2002) Ecological correlates of endozoochory by herbivores. *Funct. Ecol.* **16,** 296–304.

Partel M., Zobel M., Zobel K. & van der Maarel E. (1996) The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos* **75,** 111–17.

Perelman S., León R. & Oesterheld M. (2001) Cross-scale vegetation patterns of Flooding Pampa grasslands. *J. Ecol.* **89,** 562–77.

Quiroga R., Golluscio R., Blanco L. & Fernandez R. (2010) Aridity and grazing as convergent selective forces: an experiment with an Arid Chaco bunchgrass. *Ecol. Appl.* **20,** 1876–89.

Rebollo S., Milchunas D. G., Noy-Meir I. & Chapman P. L. (2002) The role of a spiny plant refuge in structuring grazed shortgrass steppe plant communities. *Oikos* **98,** 53–64.

Ricklefs R. E. (1987) Community diversity: relative roles of local and regional processes. *Science* **235,** 167–71.

Sala O. E., Parton W. J., Joyce L. A. & Lauenroth W. K. (1988) Primary production of the central grassland region of the United States. *Ecology* **69,** 40–5.

Sampson A. W. (1917) Succession as a factor in range management. *J. For.* **15,** 593–6.

Sorensen A. E. (1986) Seed dispersal by adhesion. *Annu. Rev. Ecol. Syst.* **17,** 443–63.

Stebbins G. L. (1981) Coevolution of grasses and herbivores. *Ann. Mo. Bot. Gard.* **68,** 75–86.

Westoby M., Walker B. & Noy-Meir I. (1989) Opportunistic management for rangelands not at equilibrium. *J. Range Manage.* **42,** 266–74.

Willson M. F., Rice B. L. & Westoby M. (1990) Seed dispersal spectra – a comparison of temperate plant communities. *J. Veg. Sci.* **1,** 547–62.

Wilson J. B. (1999) Mechanisms of species coexistence: twelve explanations for Hutchinson's 'paradox of the plankton': evidence from New Zealand plant communities. *N. Z. J. Ecol.* **13,** 17–42.

Wilson J. B. (2004) Assembly rules in plant communities. In: *Ecological Assembly Rules: Perspectives, Advances, Retreats* (eds E. Weiher & P. A. Keddy) pp. 130–64. Cambridge University Press, Cambridge.

Sala O. E., Oesterheld M., León R. J. C. & Soriano A. (1986) Grazing effects upon plant community structure in subhumid grasslands of Argentina. *Vegetatio* **67,** 27–32.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Some clarifications on interpreting the generalized grazing model of Milchunas, Sala, & Lauenroth (1988) and the quantitative grazing models of Milchunas & Lauenroth (1993) with reference to Oesterheld & Semmartin (2011). By Daniel G. Milchunas, William K. Lauenroth & Osvaldo E. Sala.