

# Using evolutionary grazing histories to develop proactive conservation strategies for grassland systems

Bachelor thesis accompanying the Community Ecology Research course



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## Abstract

How do large herbivores affect grassland communities with regard to their evolutionary grazing histories? And how can we use this knowledge to develop conservation strategies for these areas?

This bachelor thesis aims to provide an answer to these questions by constructing an overview of the effects of grazing to a grassland system (with either a short or a long evolutionary history of grazing) in the absence or presence of large herbivores. Grazing is defined as a gradient from low to high grazing intensity (i.e. grazing can be “low”, “intermediate” or “high”). To construct this overview, first and foremost the generalized grazing model for grasslands created by Milchunas *et al.* (1988) is used. In addition, the intermediate disturbance hypothesis is used to clarify differences in magnitude of disturbance caused by grazing to different communities. Furthermore, it is considered how plant-plant interactions are altered in the presence of increasing grazing pressure by large herbivores. Grassland communities with a short evolutionary history are less resistant to stress induced by grazing than communities with a long evolutionary history. From a conservation point of view, low stocking rates are optimal for communities with a short evolutionary grazing history and intermediate stocking rates are optimal for communities with a long evolutionary grazing history. High stocking rates of large herbivores should always be avoided in grassland communities with a short evolutionary history of grazing, or else the system will become susceptible to invasion by exotic species and ultimately degrade. Abandoning grazing entirely results in a homogeneous vegetation structure dominated by a few plant species that outcompete all others, resulting in diminished habitat opportunities and diversity in higher trophic groups.

## Introduction

Certain plant communities are very sensitive to grazing by large herbivores and others are not (Milchunas *et al.*, 1988). Therefore, these large herbivores can be key determinants of grassland plant species composition and diversity (Bakker *et al.* and references therein, 2006). Species composition and diversity play key roles in the science of conservation (Olff and Ritchie, 1998). From the perspective of conservation biology, the goal is not to stop genetic (and thus evolutionary) change, not to try and conserve *de status quo*, but rather to ensure that populations may continue to respond to environmental change in an adaptive manner (Groom *et al.*, 2006). Since evolution is the only reasonable mechanism able to explain the patterns of biodiversity that we see in the world today, it offers a historical perspective on the dynamics of life (Groom *et al.*, 2006). So any conservation plan or strategy should be developed within an evolutionary framework (Meffe, 1993). Now, to continue this line of thought to grassland community managing. There have been many studies on the impacts of large herbivores on grassland communities (Krebs, 2006). However, commonly used models in these studies such as the predation hypothesis, the intermediate-disturbance hypothesis and the Huston hypothesis do not adequately explain the response of grassland plant communities to grazing by large herbivores (Milchunas *et al.* and references therein, 1988), because they do not take into account that the response of grassland communities to grazing is also (partly) explained by evolutionary grazing histories (Milchunas *et al.*, 1988). For example, as Milchunas *et al.* (1988) pointed out, grazing may or may not be a disturbance for a plant community depending on its evolutionary history. A generalized model, taking evolutionary grazing history into account, has therefore been proposed to explain the very different sensitivities of plant communities to grazing by large herbivores (Milchunas *et al.*, 1988) and has subsequently been validated by quantitative, meta-analyses of grazing studies from around the world (Milchunas and references therein, 2006).

The importance of evolutionary grazing history and community productivity in determining responses to grazing in plant community species composition was quantitatively assessed over 236 ungrazed-grazed comparisons from around the world (Milchunas and Lauenroth, 1993). At this global scale, sensitivity to grazing was more explained by ecosystem and environmental variables (evolutionary history of grazing, productivity) than by current grazing-related variables (intensity, years of protection) (Milchunas, 2006). Bakker *et al.* (2006) also pointed out that herbivore impact on grassland plant diversity is dependent on habitat productivity and herbivore size. They found that when large herbivores are present there is a positive correlation between primary production and species richness.

Although evolutionary grazing history is nowadays accounted for in studies on the effects of grazing by large herbivores on grassland communities (Milchunas, 2006), there is still a demand for applying this knowledge in conservation endeavors. This is pointed out by Bakker *et al.* (2006), stating that in light of continuing global loss of native large herbivores from natural areas and continued introduction of livestock into new areas, the recognition of the trends shown by these results are critical for developing strategies of appropriate biodiversity conservation management.

So how do large herbivores affect grassland communities with regard to their evolutionary grazing histories? And how can we use this knowledge to develop conservation strategies for these areas? To answer these questions an overview of what happens to a grassland system (with either a short or a long evolutionary grazing history) when large herbivores are either absent or present is needed. This bachelor thesis will attempt to provide such an overview as a basis for conservation strategies. It is also important that this model will make a proactive conservation approach possible; one of the major developments needed in conservation is a shift from a reactive analysis of each crisis to a proactive science that permits us to anticipate developing crises and to prepare scientifically grounded contingency plans (Groom *et al.*, 2006). An ounce of prevention is worth a pound of cure.

### **Effects of grazing on grassland vegetation**

First we will discuss the effects of grazing in general. Second, we will take a closer look at some of the key processes that are affected by grazing. Finally, these effects will be summarized in table 1. Grazing by large herbivores (i.e. livestock and ungulates) results in both injury to individual plants and changes in community physiognomy (Milchunas *et al.*, 1988). In response to injury the community reacts to the grazing event directly by death or regrowth and indirectly by a regrowth response to the altered physiognomy. The mode and magnitude of the grazing action and of the community reaction are functions of the past history of the community (Milchunas *et al.*, 1988). So the reaction of the community to grazing will differ depending on the length of the evolutionary grazing history. It is to be expected that a community with a short history is less resistant to stress induced by grazing than a community with a long evolutionary history (Cingolani *et al.*, 2008; Milchunas *et al.*, 1988); the community with a long evolutionary grazing history has had more time to adapt to these circumstances.

Grazing in general is thought to increase plant diversity because of the direct consumption of competitively dominant species and indirect effects on plant competition. Furthermore, in the presence of large herbivores there is positive correlation between primary production and the change in species richness (Bakker *et al.*, 2006). The effects of herbivores on plant species richness and diversity vary depending on the type and abundance of herbivore species in a particular environment (Olff and Ritchie and references therein, 1998). For most systems a low or an intermediate grazing intensity yields the highest diversity. High grazing intensities are often detrimental to the system (Milchunas *et al.*, 1988; Olff and Ritchie, 1998; Andresen *et al.*, 1990; Smit *et al.*, 2009; Cingolani *et al.*, 2008).

Opposed to small herbivores, large herbivores produce consistent effects. They can consume large quantities of low-quality food (often tall, competitively dominant grassland plants) and create small disturbances across the landscape resulting in a diverse vegetation mosaic (Olff and Ritchie, 1998; Andresen *et al.*, 1990). Milchunas *et al.* (1988) also state that moderate grazing can create a mosaic vegetation pattern where short grasses dominate the relatively heavily grazed patches, mixtures of grasses dominate in moderately grazed patches and tall grasses dominate where ungrazed growth discourages grazing. Initially, these mosaics develop from small differences in the vegetation structure that were already present in the landscape due to some local variation in abiotic gradients (WallisDeVries *et al.*, 1999). WallisDeVries *et al.* (1999) found that when differences between patch types (i.e. short and tall) are easy to detect, the animals will follow a selective foraging pattern within a certain range (over time creating the vegetation mosaic). Grazing ungulates (i.e. large herbivores) prefer short, leafy areas of grasslands that contain relatively high concentrations of nutrients (McNaughton, 1984). However, this does not necessarily yield the highest intake rate; they therefore consume abundant low-quality forage (i.e. tall grasses) as well to bulk up and maximize daily intake (WallisDeVries *et al.* and references therein, 1999; Demment and Van Soest, 1985).

### *Community composition*

Community composition can be defined as the way in which populations of different species, living close enough together for potential interaction, are assembled (Campbell *et al.*, 2008). Since grazing can affect species richness, diversity, disturbance, productivity and plant interactions, all of which are processes that can contribute to the composition of a community (Olf and Ritchie, 1998; Bakker *et al.*, 2006; McNaughton, 1979; Milchunas *et al.*, 1988; Daleo and Iribarne, 2009), it is an important factor to take into account when studying the effects of large herbivores on grassland communities. It should be noted however, that community structure can be affected rather differently by grazing herbivores depending on their forage strategy; the difference is caused by specialist herbivores that can either consume competitively dominant or competitively inferior species (Milchunas *et al.* and references therein, 1988; Krebs, 2009). Yet, to simplify our model, we will be focusing on generalist herbivores only.

The following summarized case studies are used to clarify the response of ecosystems with different evolutionary grazing histories to different grazing intensities by large herbivores; during the early 1900s the bunchgrass steppe of western North America, an area with a short evolutionary history of grazing, was under a high a grazing pressure (Milchunas *et al.*, 2008). These heavily grazed areas were susceptible to invasion by exotics, altering the community composition (Milchunas *et al.*, 1988). These exotics, or invasive species, are often competitively superior in exploiting limited resources such as water or nutrients (Campbell *et al.*, 2008). It is also possible that they are not affected by natural predators (i.e. large herbivores) and diseases that would otherwise keep their population in check (Campbell *et al.*, 2008). This explains why exotics can have such a large effect on the community composition. Such a high grazing intensity will eventually degrade the system as observed by Rickard (1985) where areas around watering tanks showed not only invasion by exotics but also a lot of bare ground. After 4 years of Intermediate grazing in one of the undisturbed North American areas, the community composition did not significantly change (Rickard, 1985). Furthermore, Sneva *et al.* (1984) found parallel temporal changes in community composition inside and outside exclosures after a 36 years of moderate grazing and grazing-exclosure treatment in eastern Oregon.

However, a comparison between 20-year-old exclosures and areas under low and high grazing pressures in the Patagonian steppe in southern Argentina showed a clear change in species composition with increasing grazing pressure (Milchunas *et al.*, 1988; Schlichter *et al.*, 1978); so although the community composition can change over time, intermediate and low grazing pressures by large herbivores do not seem to consistently affect the composition of the community. It is worth noting however, that these changes are much greater than in grasslands with a long evolutionary history of grazing (Milchunas *et al.*, 1988). An example of what happens to community composition when large herbivores are absent can be found in a 9 years grazing experiment by Andresen *et al.* (1990), carried out in the mainland salt marsh of the Leybucht (Niedersachsen). They discovered that abandoning grazing initially results in well developed, species rich communities, but that the characteristic species of the community will disappear within 10 years. So absence of large grazers has a negative effect on species richness in areas with a long evolutionary history of grazing (Andresen *et al.*, 1990). In areas with a short evolutionary history of grazing the composition of the community is also negatively affected by absence of large herbivores as mentioned earlier, i.e. some grazing by large herbivores is required to promote structural and species diversity (Milchunas *et al.*, 1988; McNaughton, 1979; Knapp *et al.*, 1999).

## Diversity and productivity

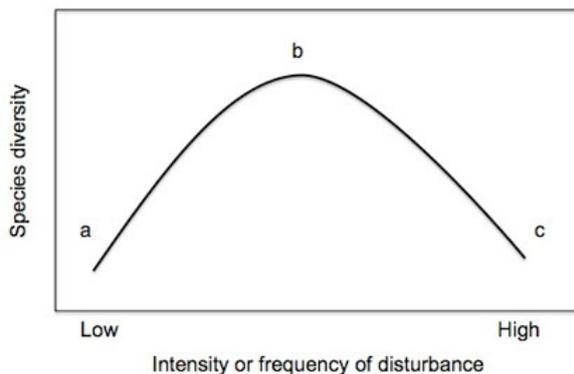
Plant diversity and productivity will be discussed together because they are so closely linked to one another. Generally, more diverse sites are more productive and this can also be a reason to conserve biodiversity (Campbell *et al.* and references therein, 2006). As a result of the reduction in competitive exclusion an increase in diversity (and therefore productivity) would be expected at intermediate levels of grazing (Milchunas *et al.*, 1988). Milchunas *et al.* (1988) describe quite clearly what happens to diversity with changing grazing intensity for both short and long evolutionary histories of grazing; grasslands with a long history of grazing are composed of grasses with varying heights as a result of divergent selection in the past for grazing tolerance and canopy dominance. When large herbivores are absent, only a few tall species (i.e. canopy dominant species) dominate the area and diversity is low (Andresen *et al.*, 1990; Milchunas *et al.*, 1988). Under low grazing pressure the same trend occurs, but diversity is slightly increased because of the grazing action (Milchunas *et al.* and references therein, 1988). Moderate grazing can create a mosaic vegetation pattern where short grasses dominate the relatively heavily grazed areas, mixtures of grasses dominate in moderately grazed patches and tall grasses dominate where ungrazed growth discourages grazing; this mosaic of growth forms increases diversity (WallisDeVries *et al.*, 1999). Diversity will decline as short grasses start to dominate more and more in areas with increasingly high grazing pressures (Olf and Ritchie, 1998). Grassland communities with a short evolutionary history of grazing have a greater potential to be changed by grazing than grasslands with a long evolutionary history of grazing; these communities are primarily composed of tall grasses that have a low tolerance for grazing (Milchunas *et al.* and references therein, 1988). Over time, selection has mainly promoted canopy dominance in these grassland plants (Milchunas *et al.*, 1988). Diversity is low when large herbivores are absent; the area is dominated by tall, competitively dominant species (Andresen *et al.*, 1990). At low grazing intensity, diversity is rapidly increased because of the growth in abundance of inferior canopy competitors (McNaughton, 1983) and a higher potential to be invaded by exotics (Naeem *et al.*, 2000; Milchunas *et al.*, 1988). This increase is short-lived if grazing intensity increases (i.e. intermediate and high); grazing has a significant effect on canopy structure (Milchunas *et al.*, 1988) and as grazing increases, the mortality due to grazing becomes a larger factor than the relaxation of competitive interactions, leading to a rapid decrease in diversity (Schlichter *et al.*, 1978). If grazing pressure is then not reduced, the system will degrade (Cingolani *et al.*, 2008; Rietkerk *et al.*, 2000).

So how does productivity fit in to all of this? More or less according to the previous expectation mentioned earlier, where diversity increases when productivity increases (Bakker *et al.*, 2006). Bakker *et al.* (2006) did a 7-years field study across a productivity gradient at several grassland sites in North America and Europe, separating the effects of primary productivity and herbivores of different body sizes (i.e. small and large herbivores) on plant species richness. They found that grazing by large herbivores increased plant diversity at high productivity, but decreased diversity at low productivity. However, when large herbivores were absent, there were no consistent effects along the productivity gradient. As previously mentioned, ungrazed areas are dominated by tall, competitively dominant species, so productivity is high in these areas (i.e. for both short and long evolutionary grazing histories) (Andresen *et al.*, 1990). When large herbivores are present, the increase in productivity by tall grass species will be counteracted by the decrease in productivity due to defoliation by grazing (Bakker *et al.*, 2006; Milchunas *et al.*, 1988). This effect is the same for grassland communities, no matter the length of the evolutionary grazing history of the community (Milchunas *et al.*, 1988). For intermediate and high grazing pressures the different evolutionary histories of grazing (i.e. short or long) yield different responses. Communities with a long evolutionary history of grazing continue to experience the balancing effect that also takes places under low grazing pressures, followed by a decrease in production at high grazing pressures due to massive reduction of biomass (Milchunas *et al.*, 1988). This decrease in production already starts at intermediate grazing pressures for communities with a short evolutionary history of grazing, because the tall grasses in these communities have slow rates of regrowth (Milchunas *et al.*, 1988). Therefore high grazing pressure finally results in a degraded system (Cingolani *et al.* and references therein, 2008; Rietkerk *et al.*, 2000).

## Disturbance

Since disturbance can be a whole range of factors, e.g. predation, herbivory, fluctuations in physical factors and catastrophes such as fires (Krebs, 2009), it is important to first define a measure of disturbance to use for the creation of this thesis' model. In the creation of our model we will define disturbance as a discrete, punctuated killing, displacement, or damaging of one or more individuals that directly or indirectly create an opportunity for new individuals to become established. This definition was also used by Milchunas *et al.* (1988) to create a generalized grazing model for grasslands and was adopted from Sousa (1984). The intermediate disturbance hypothesis (Fig. 1) is often used to describe the general effect of disturbance on a community (Krebs, 2009). The problem with applying this model to grazing is that it does not take evolutionary grazing history into account; grazing may or may not be a disturbance for a plant community depending on its evolutionary history of grazing (Milchunas *et al.*, 1988).

If a community has evolved with grazing (i.e. intermediate grazing pressure; natural population), then both increasing and decreasing grazing pressure can be considered disturbances (Milchunas *et al.*, 1988). Though this will be apparent for the extremes (i.e. when large herbivores are absent and when grazing pressure is high) (Krebs, 2009), this will not be the case for low and intermediate grazing pressures; grazing can be a disturbance to an individual plant, but does not have to be at the community level, because of the mosaic vegetation structure (Milchunas *et al.*, 1988). In the vegetation mosaics the negative effects on tall grasses can be compensated by the positive effects on short grasses (Milchunas *et al.*, 1988; Krebs and references therein, 2009). So the net effect will be around 0. Communities that have evolved with a short grazing history will experience similar effects to communities that have evolved with a long grazing history, but the effects will be more severe (Milchunas and references therein, 2006). This is due to the communities' lower tolerance to grazing (Milchunas *et al.*, 1988; Milchunas, 2006). Disturbance will have pronounced effects starting at intermediate grazing pressures and reaching its climax at high grazing pressures, resulting in a degraded system (Cingolani *et al.* and references therein, 2008; Rietkerk *et al.*, 2000). This can also be predicted by Grime's theory of plant strategies from 1979, stating that if stress and disturbance are too severe, there is no fitting strategy possible and therefore no plant can survive (Krebs, 2009).

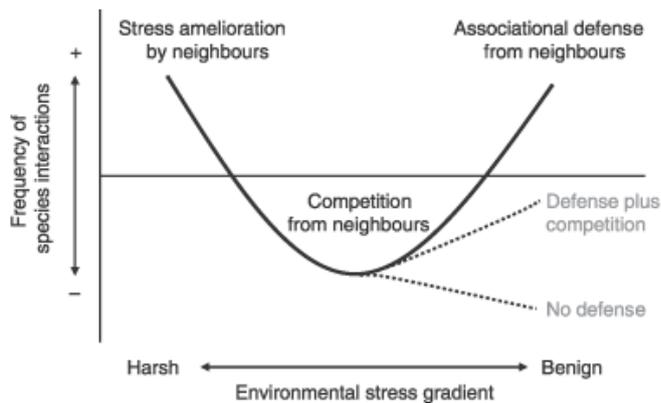


**Figure 1:** The intermediate disturbance hypothesis (IDH). (A) Species diversity is low at low disturbance frequency because of competitive exclusion. An increase in disturbance would increase diversity. (B) Species diversity is higher at intermediate disturbance frequency due to a mix of good colonizer and good competitor species. (C) Species diversity is low at high disturbance frequency because only good colonizers or highly tolerant species can persist. A reduction in disturbance would increase diversity. The model assumes succession to proceed from right to left (Krebs, 2009; Nature Education, 2011).

## Plant interactions - Competition & Facilitation

When looking at plant interactions, the stress gradient hypothesis (SGH) is essential. The SGH predicts that the importance of competitive effects is higher under benign environmental conditions, whereas facilitative effects increase in importance as environmental stress (either biotic or abiotic) increases; so it predicts a shift from net negative interactions (i.e. competition) in benign environments towards net positive (i.e. facilitation) in harsh environments (Daleo and Iribarne, 2009; Smit *et al.*, 2009). Recent studies show a hump-shaped relationship between environmental stress and plant interactions (Smit *et al.*, 2009; Crain, 2008). So it can be assumed that at intermediate grazing pressures the net effect of the communities' plant interactions can be neutral due to the balancing act of competition and facilitation. The model (Fig. 2) by Bertness and

Callaway (1994), and further refined by Crain (2008), partly confirms this, predicting that positive interactions between species will dominate in harsh physical environments due to neighbour buffering and stress heightening, negative interactions will dominate intermediate environments due to intense competition, and positive interactions will be increasingly frequent in physically benign environments that have high consumer pressure because species benefit from neighbours that offer predator refuge and associational defence (Crain, 2008). This does not completely match with this thesis' model because the "intense competition" mentioned by Bertness and Callaway (1994) is less intense because of the vegetation mosaics that develop at intermediate grazing pressures (WallisDeVries et al., 1999). Furthermore, also noted by Crain (2008), it may not apply as consistently in the benign end of environmental gradients where consumer 'stress' and therefore species interactions are more variable (see dotted line).



**Figure 2:** Conceptual model predicting the frequency of positive and negative species interactions between primary space holders across environmental stress gradients. The Bertness and Callaway model (solid line) may not apply as consistently in the benign end of environmental gradients where consumer 'stress' and therefore species interactions are more variable (Crain, 2008).

Milchunas et al. (1988) suggested that feedback mechanisms between plants and animals are well developed in grasslands with a long evolutionary history of grazing. These feedback mechanisms are noticeable in the ability of communities to switch rapidly between facilitation and competition depending on grazing intensity. In systems with short evolutionary grazing histories these feedback mechanisms are not well developed (Milchunas *et al.*, 1998). Both communities with a short and a long evolutionary history of grazing have in fact a history of grazing, albeit short for some communities, so completely abandoning grazing can result in a shift from net neutral interactions to net negative interactions (Milchunas *et al.*, 1988; Smit *et al.*, 2009; Andresen *et al.*, 1990). Such a community, that developed with grazing, will get dominated by tall, competitively dominant species if large herbivores are no longer present (Smit *et al.*, 2009, Milchunas *et al.*, 1988). Looking at the other extreme, when grazing intensity is high, those tall, competitively dominant species are removed by the grazing and consequent disturbance action (Bakker *et al.*, 2006; Milchunas *et al.*, 1988). This shifts the system from net neutral interactions at low and intermediate grazing intensities to net positive interactions, making the community primarily a facilitative one (Daleo and Iribarne, 2009; Smit *et al.*, 2009). However, this shift from net neutral to net positive interactions will take place sooner for a community with a short evolutionary history of grazing than for a community with a long evolutionary history of grazing (Milchunas *et al.*, 1988). This is because communities with a short evolutionary history of grazing have feedback mechanisms that are not well developed (Milchunas *et al.*, 1988); the system is then less responsive to the stress induced by grazing, resulting in a degraded system at high grazing intensities (Smit *et al.*, 2009) and susceptible to exotic invasion (Naeem *et al.*, 2000).

## The model

This bachelor thesis suggests the following model (Table 1) that lists important directional changes to processes that are essential to the configuration of grassland community structure. In this table positive influences are defined as “+”, negative influences are defined as “-“ and neutral influences are defined as “0”. In general the model shows that grasslands with a short evolutionary grazing history are not tolerant to a high intensity of grazing by large herbivores and that all directional responses are limited to the “absent”, “low” and “intermediate” categories. Alternatively, grasslands with a long evolutionary history of grazing are able to withstand intermediate grazing pressures and will also be able to recover from high grazing pressures if timeous management interventions (i.e. reduced stocking rate) are implemented.

A negative effect on community composition is defined as the replacement of a diverse community by only a limited range of plant species adapted to cope with the extreme conditions (i.e. competitive tall species outcompete short, stress tolerant species where grazers are absent, and short stress tolerant species replace tall, light competitive species where grazing pressures approach the upper limit). A neutral effect on community composition is found where a diverse plant community is maintained in the presence of large grazers. Both species richness/diversity and productivity have a straightforward definition of negative, positive and neutral effects; a negative effect is defined as a decrease, a positive effect as an increase and a neutral effect as being stable. For disturbance a negative effect means an increase in disturbance on the community whereas a positive effect means a decrease in disturbance. A neutral effect means that the disturbance to the community neither increases, nor decreases. Plant interactions are defined as negative when the community is dominated by tall, competitive species. If the community is dominated by short, facilitative species, then plant interactions are noted as positive. Plant interactions are deemed neutral when competition is compensated by facilitation.

**Table 1:** An overview of directional responses of grassland ecosystems with either a short or a long evolutionary grazing history when large herbivores are absent or present. Presence of large herbivores has been divided into three categories: low, intermediate and high. The effect on a process can be negative (-), positive (+) or have a net outcome of zero (0). In some cases the system is unable to cope with the effects of the large herbivores and simply gets degraded.

Processes	Evolutionary Grazing History								# Ref.	References
	Short				Long					
	Large Herbivores				Large Herbivores					
	Absent	Low	Intermed.	High	Absent	Low	Intermed.	High		
Community composition	-	0	-	degraded	-	0	0	-	4	(Andresen <i>et al.</i> , 1990; Milchunas <i>et al.</i> , 1988; Rickard, 1985; Sneva <i>et al.</i> , 1984)
Species richness/Diversity	-	+	-	degraded	-	+	+	-	4	(Bakker <i>et al.</i> , 2006; McNaughton, 1983; Milchunas <i>et al.</i> , 1988; Schlichter <i>et al.</i> , 1978)
Disturbance	-	0	-	degraded	-	0	0	-	2	(Krebs, 2009; Milchunas <i>et al.</i> , 1988)
Productivity	+	0	-	degraded	+	0	0	-	2	(Bakker <i>et al.</i> , 2006; Milchunas <i>et al.</i> , 1988)
Plant interactions:	-	0	+	degraded	-	0	0	+	3	(Daleo and Iribarne, 2009; Milchunas <i>et al.</i> , 1988; Smit <i>et al.</i> , 2009)

### *Possible limitations to the model*

This thesis' model attempts to provide a generalized prediction for responses of ecosystems with differing evolutionary grazing histories, however it must be acknowledged that overriding environmental gradients (such as different latitudinal moisture regimes) would require more careful interpretation (Olf and Ritchie, 1998; Milchunas *et al.*, 1988). In the model, different measures of parameters have been lumped together, and perhaps compared when they should not have been (Milchunas *et al.*, 1988; Milchunas, 2006). For instance, the data from the generalized model for grasslands by Milchunas *et al.* (1988) is all assessed along a moisture gradient (i.e. semiarid to subhumid, lacking humid). Most of their data used for this thesis was on subhumid grasslands. However, here we note that the response to grazing differs along the moisture gradient (Milchunas *et al.*, 1988). Semiarid grassland communities with a long evolutionary history of grazing do not show the characteristic bell-curve response that their subhumid counterparts do; instead they show a slightly negative relation between diversity and increasing grazing intensity (Milchunas *et al.*, 1988). The very nature of this extreme environment restricts the overall diversity, and the range over which abiotic conditions can vary is limited to what is generally considered a "harsh" condition for natural diversity to occur (Milchunas *et al.* and references therein, 1988). This altered response to grazing is probably due to evolutionary increased drought tolerance; water stress and grazing stress are similar in that both periodically result in partial loss of organs (Milchunas *et al.*, 1988). Therefore a community adapted to drought, is a community adapted to grazing (Milchunas *et al.*, 1988). Not only does the moisture gradient affect diversity, it also affects disturbance (Milchunas *et al.*, 1988). Disturbances can be either exogenous (destabilizing) or endogenous (stabilizing) (Milchunas, 2006). However, differentiating between these two classes of disturbance is what is attempted to be done with respect to approach to management (Milchunas, 2006). Often it is not an either/or situation, but rather when does a particular disturbance become destabilizing? If the disturbance is destabilizing, then management strictly for conservation purposes would suggest its removal, unless any alternatives result in equal or greater destabilizing disturbances (Milchunas, 2006). If, however, the disturbance is destabilizing and it remains, it may be considered "sustainable" only if an alternate state is not the permanent end state (Milchunas, 2006). If an alternate stable state is reached through deflection by some other force, then the previous reference point is no longer valid for evaluating the subject disturbance (Milchunas, 2006).

## Conclusion and discussion

So how do large herbivores affect grassland communities with regard to their evolutionary grazing histories? And how can we use this knowledge to develop conservation strategies for these areas?

The effects of grazing, or lack thereof, by large herbivores on a community with either a short or a long evolutionary history are summarized in table 1. The table can be used to predict in which ecosystems large herbivores play a key role in maintaining the system. This can then be used to choose whether to exclude these large herbivores or to include them with a certain stocking rate (Bakker *et al.*, 2006; Andresen *et al.*, 1990). The first point that the table makes clear is that high stocking rates of large herbivores should always be avoided in grassland communities with a short evolutionary history of grazing, because of the degradation risk for the community (Milchunas *et al.*, 1988; Milchunas, 2006; Bakker *et al.*, 2006). Grassland communities with a long evolutionary history of grazing will also experience negative effects to community composition, diversity and productivity at high stocking rates, but because the community had more time to develop under grazing, the system will most likely be able to avoid degradation if timeous management interventions (e.g. reduced stocking rate) are implemented (Milchunas *et al.*, 1988; Krebs, 2009; Bakker *et al.*, 2006). Abandoning grazing entirely would also be a bad management strategy, since this results in a low diversity vegetation structure where species composition and plant interactions are negatively influenced (Milchunas *et al.*, 1988; Smit *et al.*, 2009; Andresen *et al.*, 1990; Owen and Wiegert, 1981). However, such a community can be highly productive, which is of interest when managing grasslands for hay or the cultivation of cereals, but from a conservation point of view, where the focus is on maximizing biodiversity, this is not a successful strategy (Bakker *et al.*, 2006). So when focussing on creating and maintaining a high diversity grassland, with a healthy community composition and optimal plant interactions, low and intermediate stocking rates of large herbivores are the way to go. Low stocking rates would then be optimal for communities with a short evolutionary grazing history and intermediate stocking rates would be optimal for communities with a long evolutionary grazing history.

While this model can be an aid in creating a proactive grassland conservation management strategy for a community with a known evolutionary grazing history, it is recommended to test the predictable power the model has. For this we should use the model to create a conservation advise for an area (i.e. community or ecosystem) that already has a proper working conservation management plan. If the two match, that is indication that it is in fact a good model to use in constructing these conservation recommendations. This should then be repeated for different areas to exclude stochasticity.

## Future research

This model, although far from perfect, provides a starting point for future research. So it is needed that a new, long-term research project is set up where all the processes used in this model (and more) are measured in exactly the same way for different, preferably paired, grassland communities and for different evolutionary grazing histories (Olf and Ritchie, 1998; Cingolani *et al.*, 2008; Bakker *et al.*, 2006). Perhaps evolutionary grazing history should also be studied as a wider gradient instead of just short or long, in order to create a more precise model and therefore provide a better basis for creating conservation management strategies (Cingolani *et al.*, 2008; Smit *et al.*, 2009). Although the invasion of exotic species has not been discussed in detail in this thesis, it is definitely interesting from a conservation point of view, because the probability of a grassland community being invaded by exotic plant species is affected by grazing intensity (Knops *et al.*, 1999; Naeem *et al.*, 2000). In general, plant diversity increases the resistance to invasion; high diversity increase the competitive environment of communities and makes them more difficult to invade (Naeem *et al.*, 2000). However, as Naeem *et al.* (2000) mentioned, extrinsic factors (e.g. disturbance, climate, or soil fertility) covary with biodiversity and invasion, making this a difficult factor to predict. So the inclusion of "invasion by exotics" in a future study is recommended to further improve the model.

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