The Relative Effects of Grazing By Bison and Cattle on Plant Community Heterogeneity In Northern Mixed Prairie

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ABSTRACT

Since northern mixed prairies evolved under the influence of bison, grazing may be an important process maintaining diversity in these ecosystems. However, it is unclear whether grazing by cattle has the same ecological consequences as grazing by bison. I surveyed plant communities that were grazed at a range of intensities by bison or cattle, or were mechanically mowed. I used generalized linear mixed models and geostatistical techniques to evaluate the effects of grazing intensity and species of grazer on structural and floristic responses, and analysis of variance to evaluate the effects of mowing. I found that both grazing and mowing increased diversity and reduced evenness of the plant community. Spatial patterns of grazing were similar for bison and cattle, although bison created more discrete patches at the highest intensities of grazing. My results suggest that despite some differences in their selective preferences, the two species may have similar ecological effects.

EXECUTIVE SUMMARY

Because of the keystone role that bison grazing played during the evolution of central North American grasslands, grazing by domestic cattle is sometimes considered to be a useful tool to promote taxonomic and patch diversity. However, there is no agreement within scientific literature as to whether cattle function as ecological equivalents to bison. To determine whether bison and cattle have similar effects on upland northern mixed prairie plant communities, I surveyed vegetation in 17 grazed and ungrazed landscapes in Grasslands National Park, Saskatchewan, Canada. Using an information-theoretic approach, I determined that the relative density of fecal pats within each ~80 hectare landscape could serve as a proxy for grazing intensity. I used generalized linear mixed-effects models to quantify the effects of grazing intensity, species of grazer, year, and interactions between these variables on plant community responses. I used semivariance analyses and Moran's *I* to quantify the effect of grazing on vegetation patchiness. I also indirectly assessed the importance of herbivore selectivity for maintaining species diversity by monitoring vegetation in two mowed/unmowed transects, and using analysis of variance to quantify the effect of one year of nonselective mechanical defoliation. Plant species diversity increased and evenness decreased with grazing and with mowing, indicating that competitive release may be more important than herbivore selectivity for determining plant community responses to grazing in the study ecosystem. For the most part, grazing by bison and cattle also had similar effects on vegetation structure, including patch size and discreteness. These results suggest that bison and cattle grazing at similar intensities may have similar effects on the structure and composition of northern mixed prairie plant communities.

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1.0 INTRODUCTION

1.1 BACKGROUND

Grassland ecosystems once dominated the North American continent, but were largely converted to other land uses following European settlement (Samson et al. 2004). Conversion and alteration of grasslands continues to the present day, compounding historic losses to make temperate grasslands one of the world's most threatened ecosystems (Hoekstra et al. 2005). Given that both publicly and privately managed grasslands provide important ecological services, including acting as reservoirs of biodiversity, ongoing threats to grassland ecosystems warrant a concerted and comprehensive conservation response (Hoekstra et al. 2005, Federal, Provincial and Territorial Governments of Canada 2010).

Conserving North American grasslands is challenging, in part because changes in land use have eliminated or negatively affected species and ecological processes that are considered to be keystone elements of these ecosystems (Knapp et al. 1999, Fuhlendorf et al. 2009). Prominent among these negative effects was the extirpation of Plains bison (*Bison bison*) in the late 1800s. Prior to European settlement, between 15 and 30 million bison are estimated to have been present within the Great Plains of North America (Hart and Hart 1997). Grazing by bison is understood to have been intermittent but at times very intense, as herds moved across vast areas and interacted with other disturbance agents such as drought and fire to produce a shifting mosaic of patches in different stages of succession (England and Devos 1969, Kay 1998, Fuhlendorf and Engle 2001). While the presence of large herbivores undoubtedly influenced the evolution of Great Plains ecosystems (Anderson 2006), and may therefore be important for securing conservation outcomes throughout the region (Grumbine 1994), the historic impacts of bison can neither be fully reinstated, nor fully understood (Fuhlendorf et al. 2010).

Today, most remaining North American grasslands are grazed at a moderate intensity for beef production (Holecheck et al. 2010). Some authors argue that areas grazed by beef cattle (*Bos taurus*) contribute to the conservation of grassland biodiversity by supporting extensive native plant communities (e.g., Fuhlendorf and Engle 2001, Brunson and Huntsinger 2008), but others maintain that cattle cannot act as ecological surrogates for bison, and thus cannot be used to comprehensively restore biodiversity in the Great Plains (e.g., Freese et al. 2007). However, the ecological consequences of deploying bison or cattle within a given landscape remain unclear, because the relative effects of these two species grazing within extensive ecosystems have mostly not been quantified (Fuhlendorf et al. 2010).

Given that North America’s grasslands have been drastically altered, not only would the reintroduction of bison grazing at intensities and spatial scales that approximate historic conditions be a major challenge (Fuhlendorf et al. 2010), but in the context of change, reintroducing past disturbances for their own sake may not be a sound approach to achieving conservation outcomes (Davies et al. 2009). By considering ecological disturbances through a mechanistic rather than historic lens, Davies et al. (2009) argue that managers will be better positioned to achieve specific desired outcomes, even as the dynamics of today’s ecosystems change along with climate, and other anthropogenic stressors. In order to clarify how grazing by bison and/or cattle might be used to optimize conservation outcomes in central North American grasslands, managers therefore require more information on the mechanisms driving species replacement in grazed plant communities.

In this study I examine the effects of grazing by bison and cattle on the structure, composition, and spatial patterning of vegetation in upland northern mixed prairie plant communities within Grasslands National Park (GNP), Saskatchewan, Canada. I also examine the effect of mechanical mowing on the elements comprising floristic diversity within the same study system. In so doing, I further the theoretical understanding of mechanisms driving plant community changes in response to selective and nonselective defoliation, and I offer practical recommendations for how grazing may be used to meet conservation objectives in northern mixed prairie ecosystems.

1.2 STUDY RATIONALE

The species present in plant communities today, their characteristics, and their interspecific interactions, reflect the history of past selective pressures (Mack and Thompson 1982). Central North American grasslands, including northern mixed prairie plant communities, evolved under the influence of periodic drought, fire, grazing, and the interaction of these disturbances (Fuhlendorf and Engle 2001, Anderson 2006). Adaptations that reflect this evolutionary history can help plants to avoid, to discourage and to tolerate defoliation by grazers. High densities of shoots that turn over rapidly, the presence of perennating organs, and the basal orientation of intercalary meristems in some grasses all facilitate regrowth following grazing disturbance (Mack and Thompson 1982, Coughenour 1985, Anderson 2006). Differences in the ability of plants to regrow following defoliation are a critical determinant of plant community changes (Augustine and McNaughton 1998), so evolutionary history is a primary factor in determining the response of grasslands to grazing (Milchunas et al. 1988, Cingolani et al. 2005).

Grazers alter competitive interactions among plant species in part by changing vegetation structure when they consume plant parts (Milchunas et al. 1988). When competition in ungrazed plant communities is primarily for above-ground resources, changes in vegetation structure associated with grazing (e.g., reduced canopy height, reduced foliar cover) may result in the increased availability of the resource that is limiting. Grazing-adapted plant species can often take advantage of the subsequent relaxation in competitive interactions to increase in dominance (Milchunas et al. 1988). For example, in tallgrass prairie plant communities the increase of light within the canopy following either grazing or mowing allows more species to flourish, leading to a shift in composition, and an overall increase in diversity (i.e., plant communities exhibit 'competitive release'; Collins et al. 1998). If a similar release occurs following plant defoliation in northern mixed prairie ecosystems, the relaxation of competitive interactions induced by either bison or cattle grazing could result in enhanced recruitment of the species-rich forb component into plant communities, and subsequent increases in floristic diversity (Bakker and Olff 2003, Towne et al. 2005).

Grazers also alter plant community competition by selectively consuming some plants and avoiding others (Augustine and McNaughton 1998). In this case, the fitness and/or abundance of preferred plant species may decline as they are grazed upon, allowing subordinate species to flourish (Anderson and Briske 1995, Hartnett at al. 1996). Although bison and cattle both primarily consume graminoid species, cattle also incorporate forbs and browse into their diets, whereas bison select against these subordinate forage classes when grazing in northern mixed prairie (Plumb and Dodd 1993). This difference in selective preferences could result in species-rich forb component increasing in plant communities grazed by bison, and in higher levels of floristic diversity within these plant communities compared to those grazed by cattle (Knapp et al. 1999).

Selective grazers also express their preferences at multiple spatial and temporal scales, grazing at some locations within a landscape and avoiding others based on several interacting biotic and abiotic factors (Bailey et al. 1996). The resulting spatial variability of vegetation structure in grazed landscapes may allow for the coexistence of more species, and therefore, a more diverse plant community (Adler et al. 2001, Fuhlendorf and Engle 2001, Bakker and Olff 2003). Whether the number and extent of different niches created by heterogeneous grazing depends on which species of grazer is deployed within a given landscape remains unclear. The selective preferences of bison and cattle necessarily differ because of differences in the morphology, physiology, environmental tolerance, and social behaviours between the two species (Damhoureyeh and Hartnett 1997). However, the full ecological implications of bison and cattle expressing their selective behaviours at multiple scales have not been documented, because most comparative experiments have been conducted in small pastures, thereby eliminating the complexity and variation inherent to large natural landscapes (Fuhlendorf et al. 2010).

Non-grazing behaviours such as wallowing and the deposition of dung and urine may also generate spatial patterns of soil and vegetation characteristics, including nutrient availability, primary productivity, and species diversity, primarily at small spatial scales (Augustine and Frank 2001, McMillan et al. 2011). Bison and cattle differ in their expression of these behaviours, the most striking difference being that cattle do not engage in wallowing. Since wallowing creates localized patches of bare soil that are a few metres to many metres in diameter within which there is little competition for colonizing plant species, bison may maintain higher levels of small-scale diversity than cattle (Trager et al. 2004, McMillan et al. 2011). Since the spatial scale and pattern of environmental heterogeneity can influence population dynamics of native flora and fauna, as well as other ecosystem processes (Turner 1989, Adler et al. 2001), differences in the spatial patterns of disturbance generated by bison and cattle may have important implications for whether the two species of grazer are equally suitable for meeting conservation objectives in northern mixed prairie.

The presence of both bison and cattle in different parts of Grasslands National Park provides a unique opportunity to examine the ecology of extensively grazed tracts of northern mixed prairie. If competitive release is the primary mechanism by which species replacement occurs in grazed plant communities within this ecosystem, then the elements comprising floristic diversity should respond similarly to grazing by bison and cattle, and to mechanical mowing (i.e., nonselective defoliation). Alternatively, if plant species replacement is being driven by selective grazing on preferred species, then each species of grazer may have different effects on the elements comprising diversity. By examining responses of individual plant species to grazing by bison and cattle, the relative importance of differences in forage preferences for driving plant community changes can be clarified. Finally, if spatial heterogeneity is the primary factor allowing for the co-existence of more species in grazed plant communities, then bison and cattle may have different effects on the elements comprising diversity. The relative importance of this factor in determining plant community changes can be clarified by examining the spatial scale at which vegetation structure varies in areas grazed by bison or cattle.

1.3 PROBLEM STATEMENT

There are significant gaps in the literature regarding the different ecological effects of bison and cattle grazing in complex natural systems. No peer-reviewed studies have examined the relative effects of each herbivore grazing in pastures larger than 300 hectares (ha), in part because scientists have traditionally aimed to reduce eliminate or reduce the effects of natural variability, and in part because differences in the typical management of each species of grazer make direct comparisons logistically challenging (Fuhlendorf et al. 2010). In northern mixed prairie, one study compared grazing ecology of bison and cattle while holding management constant, but only within four, 48-ha experimental units (Plumb and Dodd 1993).

1.3.1 Estimating grazing intensity of bison and cattle using density of fecal pats and stocking rates

Bison managed for conservation objectives usually graze in large natural areas with minimal interference from managers, whereas domestic cattle tend to graze in smaller pastures with higher investment from managers in the form of fences, herding, and supplemental water and mineral sources (Hartnett et al. 1997, Steuter and Hidinger 1999). In general, these differences are also true of the management of bison and cattle in GNP, where the former graze year-round in one ~18,000-ha pasture at a low stocking rate, and the latter graze seasonally in several ~300-ha pastures at a range of stocking rates. However, even cattle pastures in GNP are large enough that animals must make foraging decisions at several spatial and temporal scales, so both bison and cattle are expected to have heterogeneous impacts throughout their respective pastures (Coughenour 1991, Bailey et al. 1996). Comparisons between the effects of grazing by bison and cattle based solely on stocking rates cannot account for within-pasture variability, and therefore, cannot accurately reflect the range of intensities at which the two herbivores graze, nor be used to model the full range of effects of grazing. Since no approach to modeling grazing intensity at spatial and temporal scales that would be appropriate for comparing the effects of bison and cattle grazing in complex natural landscapes has been validated in the literature, my study will not only facilitate direct comparisons between the ecological effects of bison and cattle in GNP, but will fill a gap in the literature by providing a method for monitoring the effects of grazing in extensive wilderness or working landscapes where grazing intensity is difficult to quantify.

1.3.2 Relative effects of grazing by bison and cattle on plant community heterogeneity in northern mixed prairie

The majority of studies that have compared bison and cattle have focused on physiological rather than ecological differences between the two species of grazer (Fuhlendorf et al. 2010). Most studies comparing bison and cattle have also been conducted in tallgrass prairie ecosystems (e.g. Damhoureyeh and Hartnett 1997, Towne et al. 2005), where higher net primary productivity means that structural responses to grazing may be more pronounced, average stocking rates may be significantly higher, and plant community responses to grazing may be controlled by different ecological mechanisms than in northern mixed prairie. Given the lack of studies comparing bison and cattle on large, complex landscapes in northern mixed prairie ecosystems, this study fills a significant gap in the literature on these two herbivores, informing both the theoretical understanding of grazing as an ecological process, and clarifying the suitability of each herbivore for natural area management.

1.4 RESEARCH OBJECTIVES

In this study, I aim to (a) identify a method of quantifying grazing intensity that facilitates direct comparisons between the effects of bison and cattle grazing in extensive landscapes, and (b) to use this method to address whether differences in foraging and non-foraging behaviours between bison and cattle result in the two having different effects on vegetation structure, plant community composition, floristic diversity and/or spatial heterogeneity when grazing at comparable intensities.

Specifically, in Chapter 2, I will examine the utility of several proxies based on the density of fecal pats and stocking rate for comparing the effects of each species of grazer. In Chapter 3, I will address the following questions:

- What are the relative impacts of bison and cattle grazing on plant community composition, including on the proportions of specific plant species in the community, and on the elements of floristic diversity?
- Does simulated nonselective grazing (i.e., mowing) have comparable impacts to either bison grazing or cattle grazing on the elements of floristic diversity?
- What are the relative impacts of bison and cattle grazing on plant community structure? Is the spatial pattern of vegetation structure similar under similar intensities of grazing by each species?

The answers to these questions will help to clarify what mechanisms drive plant community changes in response to grazing, and therefore, whether bison and cattle are ecologically equivalent disturbance agents when grazing in northern mixed prairie plant communities. Chapter 4 synthesizes the implications of my results for ongoing monitoring of the effects of grazing in GNP, and in other extensive landscapes.

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2.0 ESTIMATING GRAZING INTENSITY OF BISON AND CATTLE USING DENSITY OF FECAL PATS AND STOCKING RATES

2.1 ABSTRACT

Grazing intensity influences ecological dynamics of rangelands but is difficult to quantify, so proxies for grazing intensity are sometimes used to monitor the effects of grazing. Several studies have used the density of fecal pats as a proxy for grazing intensity; however, none have verified whether this proxy corresponded well to actual grazing intensity, and if so, over what spatial and temporal scales. To determine what proxies are most effective at modeling the effects of grazing by bison (*Bison bison*) and cattle (*Bos taurus*), I monitored 10 grazing intensity-related response variables in 100, 0.1-hectare patches in 2010 and 2011 in Grasslands National Park, Saskatchewan, Canada. Patches were nested within 17 grazed and ungrazed landscapes, each representing approximately 80 hectares (SD = 25) of upland grassland. I compared effects of year, stocking rate, and three potential proxies for grazing intensity based on the density of fecal pats at the patch and landscape scales as predictor variables, including a new proxy I introduce called Constrained Relative Use (CRU · patch^{-1}), using Akaike's Information Criterion (AIC$_c$) for small sample sizes. Year was an important predictor of most plant community responses. Landscape-scale proxies were important for modeling structural responses to grazing by bison and cattle. Constrained Relative Use was valuable for modeling changes in plant community composition in cattle pastures. None of the proxies were successful at modeling compositional changes associated with bison grazing, perhaps because sites had been grazed at relatively low intensities since bison were introduced in 2006. My results show that proxies based on fecal pat densities can be used to quantify grazing intensity of bison and cattle at appropriate spatial and temporal scales.

Key words. *Bison bison*, *Bos taurus*, information-theoretic approach, northern mixed prairie, rangeland monitoring, spatial scale

2.2 INTRODUCTION

Both ecological and agronomic outcomes on rangelands are determined in large part by grazing intensity (Bransby et al. 1988, Holechek et al. 1999). However, many evaluations of the effects of grazing lack quantitative estimates of the intensity at which rangeland ecosystems are grazed (Milchunas and Lauenroth 1993). Studies that do quantify grazing intensity typically do so at only one spatial scale, despite the fact that grazing intensity within a given pasture is never uniform, especially in large pastures (Andrew 1988, Holechek et al. 2010). By only considering one level of grazing intensity per pasture, we may hamper our ability to determine the relative influence of grazing compared with other influential variables, such as climatic variability (Fuhlendorf et al. 2001), grazing systems (Barnes et al. 2008), and species of grazer (Allred et al. 2011). A method of quantifying grazing intensity that can account for the effects of grazing at multiple spatial and temporal scales may, therefore, assist in efforts to clarify the full range of effects that grazers have on rangelands.

Grazing intensity refers to the cumulative effects that grazers have on rangelands during a given time period (Holechek et al. 1998). These effects include consumption of plants, as well as trampling, wallowing, defecating, and other behaviours, which may influence soil compaction and nutrient dynamics, niche creation and colonization, seed dispersal, and other ecosystem responses (Huntly 1991, Hobbs 1996, Olff and Ritchie

1998). Thus, grazing has a variety of direct and indirect effects on ecological processes, including on plant competition (Augustine and McNaughton 1998, Collins et al. 1998, Bakker and Olff 2003). Over time, grazing can result in changes in floristic diversity and plant community composition, with the nature of the response depending on the level of grazing intensity, and on environmental moisture and evolutionary history of grazing within a given system (Milchunas and Lauenroth 1993, Cingolani et al. 2005).

Various qualitative and quantitative techniques have been used to evaluate the level of grazing intensity at a given site. In published literature, the most common quantitative approach has been to measure the percent of forage utilized by grazing animals, i.e., the difference in standing crop between temporarily caged and uncaged, grazed plots (Milchunas and Lauenroth 1993). This approach has a long history of use in rangeland management, but has also received substantial criticism (e.g., Sharp et al. 1994, McNaughton et al. 1996, Scarnecchia 1999). One issue with evaluating grazing intensity based on percent utilization data is that, by chance, the amount of vegetation in grazed areas can be greater than the amount in adjacent ungrazed caged areas, resulting in negative values of forage utilization being calculated. The more heterogeneous the plant community, and/or the distribution of grazing pressure, the higher the possibility of this spurious result (Bork and Werner 1999). Additionally, exclusion cages themselves may alter the microenvironment in such a way that forage production within or around the caged area is affected (Owensby 1969). Significant time and effort are therefore required to determine the percent of forage utilized with reasonable accuracy and precision (Smith et al. 2005). Furthermore, percent utilization data may not accurately reflect grazing intensity within a given year, because of the potential for vegetation to regrow after it has been defoliated (McNaughton et al. 1996). This calls into question the appropriateness of basing estimates of grazing intensity on percent utilization data, and on other methods of quantifying grazing intensity that rely on univariate measures of vegetation structure (e.g., stubble height, residual biomass).

Since grazing intensity refers not only to utilization of forage but to all effects that grazers have on rangelands, an alternative approach to its quantification is to measure a diverse suite of response variables. Incorporating numerous variables into qualitative evaluations of grazing intensity is commonplace. For example, the level of grazing at a given site may be classified as low, medium, or high, based in part on visual estimations of variables like vegetation patchiness, the degree to which palatable species have been defoliated, and the extent of trampling and dunging effects (Anderson and Currier 1973, Jasmer and Holechek 1984, WallisDeVries and Raemakers 2001). Guidelines for the qualitative assessment of grazing intensity based on past observations within a specific ecosystem can produce repeatable results that are useful for evaluating variability in livestock use within a given pasture (Holecheck and Galt 2000). However, the accuracy and reliability of qualitative assessments is lessened when guidelines that apply to a given ecosystem or management regime are applied elsewhere. In contrast to qualitative approaches, quantitative evaluations of grazing intensity are typically based on one or two dependent variables. Beever et al. (2003) demonstrated, however, that a multifaceted approach to quantifying grazing intensity can be more effective at assessing the intensity of disturbance than monitoring a single response variable. In their study on the ecological effects of feral horses, the authors monitored a number of disturbance-sensitive variables to evaluate the degree of herbivore disturbance across the landscape, and found these out-performed vegetative data in distinguishing between grazed and un-grazed sites. However, monitoring numerous response variables may be complicated and time consuming, and is therefore not always feasible. Further, the methods of Beever et al. (2003) must be adjusted if they are to be used in other ecosystems, and with other species of grazers.

Given limited time and effort to dedicate to monitoring, various proxies for grazing intensity have been used in grazing studies. The most prominent example is the use of distance to water to describe a grazing intensity gradient, based on the ‘piosphere’ concept (Lange 1969, Ludwig et al. 1999, Todd 2006), but other proxies have also been used, including herbivore track density (Pringle and Landsberg 2004) and fecal pat density (Julander 1955, Mueggler 1965, Milchunas et al. 1989, Abensperg-Traun et al. 1996, Dale et al. 1999, Riginos and Hoffman 2003, Tadey 2006, Vulliamy et al. 2006, Manthey and Peper 2010). Proxies are advantageous because they account for effects of grazers other than defoliation without the need to include multiple predictors in statistical models, thereby retaining degrees of freedom, and thus statistical power (Quinn and Keough 2002). Furthermore, proxies can serve as continuous predictors of grazing intensity, which may be more powerful at detecting the effects of grazing than categorical measures, and allow for modeling non-linear responses to grazing intensity (Andrew 1988, Milchunas et al. 1988, Koper et al. 2008).

While some studies use proxies to represent within-pasture variation in grazing intensity, most use evaluations of grazing intensity that have been averaged across entire pastures (especially stocking rate; e.g., Olson et al. 1985, Gillen et al. 2000, Smart et al. 2010). However, herbivores make habitat selection decisions at several spatial and temporal scales, resulting in heterogeneous landscape use (Bailey et al. 1996). Even in managed grazing systems, spatial patterns of utilization may emerge (Barnes et al. 2008), so a targeted level of utilization is unlikely to be realized at any single point within a given pasture. As a result, local effects of grazing cannot necessarily be predicted using estimates of grazing intensity that are averaged across entire pastures (Coughenour 1991). Rather, proxies for grazing intensity that can be calculated at local scales may be required to model local effects more accurately.

In the northern mixed prairie, cattle typically graze in large pastures that encompass heterogeneous landscape elements. Since stocking rate is calculated at the pasture scale, it may fail to accurately predict the effects of cattle grazing at a local scale. Despite the fact that areas with high densities of fecal pats do not always correspond with the most heavily grazed areas within a single season (Julander 1955, Kohler et al. 2006), measures based on the density of fecal pats may effectively represent grazing intensity of cattle over time (Mueggler 1965, Milchunas et al. 1989). Therefore, fecal pat densities may serve as useful proxies for modeling effects of grazing among continuously grazed sites in northern mixed prairie. Advantages of this approach include the fact that fecal pat counts are relatively simple to conduct, and pat densities can be calculated over several ecologically important spatial scales.

I calculated three potential proxies for grazing intensity based on fecal pat densities at the patch scale (sensu Bailey et al. 1996; representing a localized cluster of feeding stations) and the landscape scale (sensu Senft et al. 1987; encompassing a variety of plant communities or large patches). I evaluated these by testing how well each corresponded to several plant community responses in a northern mixed prairie grazed by cattle at wide a range of stocking rates. My objectives were to determine whether any of my potential proxies for grazing intensity were better at describing the observed variability in vegetation structure or composition than stocking rate, and if so, proxies calculated at which spatial scale(s) were best.

2.2.1 Estimating grazing intensity of bison and cattle

A proxy capable of representing grazing intensity over multiple spatial and temporal scales could be particularly useful for comparing the ecological effects of native and domestic herbivores. Historically, herds of Plains Bison (*Bison bison*) grazed North America's Great Plains, responding to and interacting with intrinsic features of the landscape as well as extrinsic elements (e.g., disturbances like fire; Fuhlendorf et al. 1999). Since both the intrinsic and extrinsic features of complex natural landscapes were and are inherently variable (Ludwig and Tongway 1995, HilleRisLambers et al. 2001, Fuhlendorf et al. 2006), grazing by bison generated a pattern of disturbance that varied in space and time (Hartnett et al. 1996, Knapp et al. 1999, Fuhlendorf and Engle 2001). Today, bison managed for conservation objectives typically graze in large natural areas with minimal interference from managers, allowing some of these historical disturbance processes to persist, albeit at a dramatically reduced extent (Gates et al. 2010). Domestic cattle (*Bos taurus*) have replaced bison as the dominant grazer on the Great Plains, and tend to graze in smaller pastures, with higher investment from managers in the form of fences, herding, and supplemental water and mineral sources (Hartnett et al. 1997, Steuter and Hidinger 1999). Due in part to the differences in management used with each herbivore, the relative ecological effects of bison and cattle remain largely unknown.

Even when management differences are controlled for, the relative ecological effects of grazing by bison and cattle have been obscured by the tendency to study grazing effects in small pastures, in isolation from the inherent variability herbivores encounter in natural ecosystems (e.g., Plumb and Dodd 1993, Towne et al. 2005). To understand the relative ecological effects of bison and cattle, it has been suggested that studies should acknowledge and account for the variability inherent in grassland ecosystems, and the way each grazer interacts and responds to the heterogeneous features of natural landscapes (Allred et al. 2011). A proxy capable of representing the intensity at which bison and cattle graze within a natural ecosystem would enable direct comparisons of the effects of grazing by each herbivore at ecologically relevant scales, thus facilitating quantitative analyses of the relative effects of each species of grazer that better reflect the way each interacts with natural variability.

In Grasslands National Park (GNP), located in southern Saskatchewan, Canada, both bison and cattle graze in pastures large enough to encompass a multitude of heterogeneous landscape elements. Quantifying the effects of herbivore disturbance in this context is challenging, as each species of grazer interacts with landscape heterogeneity to produce effects that are variable in space and time. Furthermore, bison and cattle in GNP are subject to different management regimes, with bison being present in one large pasture year-round, and cattle being seasonally stocked in smaller pastures at a wide range of rates. As noted above, stocking rate, the only proxy for grazing intensity that can be readily estimated for both herbivores, is calculated at the pasture scale, and so may fail to accurately predict the effects of grazing at a local scale.

While measures based on the density of fecal pats have been used and defended elsewhere as representing grazing intensity over time, direct comparisons of fecal pat densities under bison and cattle may be confounded by numerous factors. These include different rates of defecation and/or fecal pat breakdown based on species of grazer (given differences in diets and abilities to digest forage; Schaefer et al. 1978, Hawley et al. 1981, Van Vuren 1984), and the fact that bison and cattle in GNP spend different lengths of time in different sized pastures.

I evaluated how well stocking rate and three other potential proxies for grazing intensity corresponded to a number of structural and compositional plant community responses in areas grazed by bison and by cattle within GNP, to determine whether the proxies performed reliably despite the potentially confounding factors associated with species and/or management differences. In addition to the objectives outlined above, I aimed to determine whether any of my potential proxies could be used to directly compare grazing intensities of bison and cattle, and if so, how similar the intensities of grazing by bison and cattle were within the study area.

2.3 METHODS

2.3.1 Study area

This study was conducted in Grasslands National Park, located in southern Saskatchewan, Canada (49°15’ N, 107°00’ W; Fig. 1). The area’s topography is rough to rolling, supporting a wide range of landscapes with variable drainage conditions, soil types, and plant communities characteristic of northern mixed prairie (Coupland 1950). Vegetation within my study sites was composed of a mixture of mid-height cool-season grasses (e.g., *Elymus lanceolatus* [Scribn. & J. G. Sm.] Gould, *Hesperostipa* spp. [Elias] Barkworth, *Pascopyrum smithii* [Rydb.] Barkworth & D. R. Dewey), warm-season shortgrasses (e.g., *Bouteloua gracilis* [Kunth] Lag. ex Griffiths), forbs (e.g., *Artemisia* *frigida* Willd., *Phlox hoodii* Richardson, *Sphaeralcea coccinea* [Nutt.] Rydb.), and shrubs (e.g., *Artemisia cana* Pursh). Over the long term, the area received an average of 348 mm of annual total precipitation, approximately 70% of which was received as summer rainfall (between April and September; Environment Canada 2011*a*). During the study period, summer rainfall in the area was higher than the long-term average (14% and 22% above average in 2010 and 2011, respectively; Environment Canada 2011*b*).

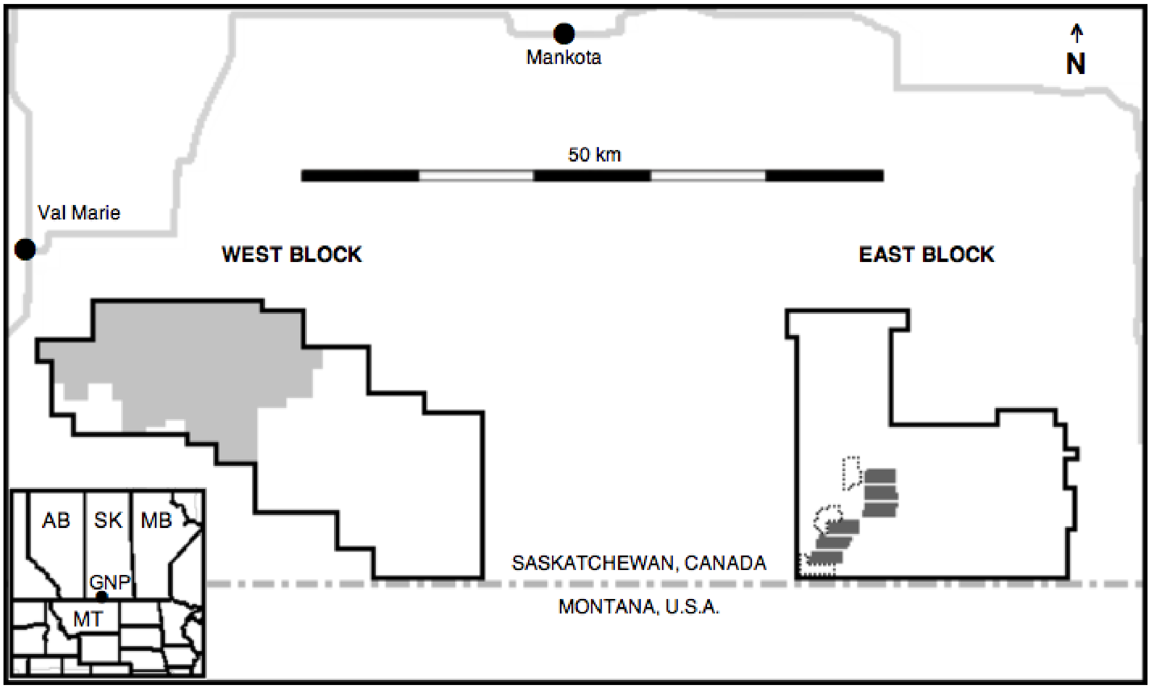

Figure 1. Location of grazed and ungrazed pastures within Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. The bison pasture is shaded light gray, cattle pastures are dark gray, and control pastures are indicated with dotted lines.

2.3.2 Study design

Cattle pastures. The East Block of GNP contained six cattle pastures (~300 hectares [ha] each) that were seasonally grazed by Angus and Hereford yearling steers from 2008 to 2011, and three adjacent pastures that served as ungrazed controls (*n* = 9; Fig. 1).

Livestock had not grazed these areas for approximately 15 years prior to the re-introduction of cattle in 2008 (Koper et al. 2008). Each cattle pasture contained a natural water source, and at least the following three broad vegetation types: riparian shrublands, valley grasslands, and upland grasslands (Michalsky and Ellis 1994). Pastures were oriented to include similar proportions of each of these vegetation types (Koper et al. 2008), but only upland grassland areas were monitored in this study, since deposition of feces by cattle is known to vary with hydrological position (Tate et al. 2003). Cattle were supplied with salt, minerals, and two anthropogenic water sources per pasture (one of which was located in upland grasslands), and were present from mid-May through mid-September. Each cattle pasture was assigned a different stocking rate, which remained consistent from year to year. Cattle stocking rates in both years were approximately 0.25, 0.40, 0.60, 0.74, 0.83, and 0.90 Animal Unit Months per hectare (AUM · ha^{-1}), when each yearling steer was considered to equal 0.75 Animal Unit Equivalents (AUE; Manske 1997). These rates were assigned as part of a long-term stocking rate study, and were intended to achieve annual utilization of forage ranging from 20% to 70%, while allowing for grazing intensity to be treated as a continuous variable (Koper et al. 2008).

In each pasture, Koper et al. (2008) established six study plots in upland grassland areas, each plot at a minimum distance of 250 metres [m] from the next (n = 54). Each study plot consisted of a 1000 m^2 Modified Whittaker plot with ten nested 0.5 m^2 quadrats (Appendix A; Stohlgren et al. 1995). On average, study plots were clustered within a 96 ha (SD = 17) area (Appendix B). Throughout, I refer to those variables that are based on data collected within a single 1000 m^2 study plot as 'patch'-scale variables, and to those that were based on observations from all plots within one ~96 ha area as ‘landscape’-scale variables.

I conducted surveys between mid-June and mid-July of 2010 and 2011, with all study plots per pasture being sampled within a single day.

Bison pasture. Since 2006, a semi-wild herd of bison has grazed within one large pasture (~18,000 ha) in the West Block of GNP (Fig. 1). Bison remain in this pasture year-round, and have access to one anthropogenic and several natural water sources, but receive no other supplements. By 2011, the herd had grown from an initial group of 73 individuals to include ~250 animals, of which 53% were female. To calculate stocking rate within the bison pasture, I assumed that one Animal Unit referred to a mature 454-kg cow or equivalent (Vallentine 1965, Holecheck et al. 2010), and derived AUE for each age and sex class of bison using estimated live animal weights to calculate metabolic weights (Kleiber 1975, NRC 1996, Kuzyk and Hudson 2007). I based estimated live animal weights of bison on body mass data collected in Elk Island National Park, where GNP’s bison herd originated (A. Handel, unpublished data). I considered bison calves to be equal to 0.44 AUE, and male and female yearlings to be equal to 0.77 and 0.70 AUE, respectively. I considered mature male and female bison (two years and older) to be equal to 1.23 and 0.94 AUE, respectively. In 2010, the stocking rate in the bison pasture was 0.10 AUM $\cdot$ ha^{-1}, increasing to 0.13 AUM $\cdot$ ha^{-1} in 2011.

I established groupings of four to six study plots in upland grassland areas throughout the bison pasture in 2010, each consisting of a Modified Whittaker plot arranged so as to be a minimum distance of 250 m from the next (*n* = 46). Study plots were clustered within eight regions that had been subject to varying degrees of grazing pressure in years preceding this study, ranging from areas that were unused to heavily used by bison (W. Olson, Parks Canada, personal communication, May 2010). On average, each of these regions encompassed approximately 61 ha (SD = 18) of upland grassland, and was a located minimum of 1.4 kilometres [km] from the next most proximate region (Appendix C). As described above, I refer to variables based on data collected within a single 1000 m^2 study plot as ‘patch’-scale variables, and to those that are based on observations from all plots within one ~61 ha region with the bison pasture (n = 8) as ‘landscape’-scale variables.

I conducted surveys between mid-June and mid-July of 2010 and 2011, with all study plots per region being sampled within two successive days.

Grazing intensity-related response variables. In the northern mixed prairie, increased grazing intensity results in increased plant removal (i.e., increased frequency of plant defoliation, decreased canopy height, decreased biomass per hectare), and decreased litter accumulation (Houston and Woodward 1966, Biondini et al. 1998, Salo et al. 2004). In all of the nested quadrats within each study plot, I monitored several structural plant community variables that were directly related to these responses. I estimated residual biomass within each quadrat using a Robel pole, by determining the height of complete and partial visual obstruction by vegetation in each cardinal direction, and averaging these values to determine 100% and 50% vegetation height-density, respectively (Robel et al. 1970, Vermeire et al. 2002). I measured canopy height using a metre stick and a piece of Styrofoam™ (20 × 50 × 2.5 cm) resting on top of the plant canopy, and litter depth at the centre of each quadrat using a metre stick. I estimated litter cover and clipped graminoid cover (i.e., the percent of the quadrat covered by graminoid species that had been defoliated by grazers) using the foliar cover class method (Daubenmire 1959). I used quadrat-scale data in models of all structural responses except clipped graminoid cover. Since values of clipped graminoid cover were mostly nil or very low at the quadrat scale, I reduced skewness in the data by summing observations from all quadrats per study plot, and basing my models on the total clipped graminoid cover observed at the plot (i.e., ‘patch’) scale.

Plant community composition data may also provide information about grazing intensity at a site over time (Lauenroth and Laycock 1989, Anderson and Briske 1995). Specifically, proportions of the plant community comprised of increaser and decreaser species change over time in relation to grazing (Dyksterhuis 1949, Smoliak et al. 1972). Furthermore, increased grazing intensity may be associated with changes in elements comprising diversity (Milchunas and Lauenroth 1993, Bai et al. 2001). I therefore visually estimated relative abundances of all vascular plant species within each quadrat using the foliar cover class method (Daubenmire 1959). I classified all plant species identified during vegetation surveys whose response to grazing was documented by the Saskatchewan Forage Council (2007) as increaser or decreaser species. I determined the relative cover of each species for each study plot (p_i), and used these data to derive the total proportion of increasers and decreasers in the plant community, as well as Simpson’s index ($D = \sum[p_i]^2$), a measure of floristic diversity, for each patch. I used Simpson’s reciprocal index ($1/D$) to scale Simpson’s index to units of species, and calculated evenness, or the relative abundance of each species (another element of diversity) for each patch using Simpson’s measure of evenness [$E_{1/D} = (1/D)/S$].

Potential proxies for grazing intensity. I considered stocking rate, the density of fecal pats at the landscape scale, the density of fecal pats at the patch scale, and an additional measure I termed Constrained Relative Use (defined below) at the patch scale as potential proxies for grazing intensity.

To determine fecal pat densities, I counted all pats present within each study plot via a walk-through survey. I walked east-west transects ≤ 2 m in width, progressing systematically from the north end of the plot to the south, until the entire plot had been surveyed. I tallied defecation events rather than individual pats, because defecation events by cattle did not typically yield perfectly discrete pats. I distinguished defecation events from one another based on the size, shape, and extent to which the observed pat(s) had broken up or decomposed (Henderson 2009, unpublished data). Given that fecal pats may take several years to decompose in semi-arid regions, and since year of deposition could not be verified, defecation events from previous years were included in counts, potentially providing an estimate of relative grazing intensity over several years (Milchunas et al. 1989). I defined the density of fecal pats at the patch scale (pats · patch^{-1}) as equal to the number of defecation events counted at each study plot, and the density of fecal pats at the landscape scale (pats · landscape^{-1}) as the sum of defecation events observed at each study plot within each 'landscape' – that is, the total number counted in all study plots clustered within a ~96-ha upland grassland area in each cattle pasture, or each ~61 ha region within the bison pasture – divided by the number of study plots sampled within that landscape.

I derived values of Constrained Relative Use at the patch scale (CRU · patch^{-1}) by summing the stocking rate in each year that a given pasture had been grazed, and multiplying the result by the ratio of observed to expected fecal pats at a given patch within that pasture:

$$\left[1 + \sum (\mathrm{AUM} \cdot \mathrm{ha}^{-1}{}_{\mathrm{year}_{1,2,3\ldots n}})\right] \times \frac{\mathrm{Observed}\,\#\,\mathrm{pats} \cdot \mathrm{patch}^{-1}}{\mathrm{Expected}\,\#\,\mathrm{pats} \cdot \mathrm{patch}^{-1}} = \mathrm{CRU} \cdot \mathrm{patch}^{-1}$$

The sum of stocking rates over several seasons, or cumulative stocking rate, could be calculated over any temporal scale of relevance to a given study; for this study, I summed stocking rates from all years that grazers had spent in their respective pastures since their most recent reintroductions to GNP. The observed number of fecal pats is the number of defecation events counted in a single study plot during the walk-through surveys (equivalent to pats · patch^{-1}). The expected number of fecal pats is the total number of defecation events counted at all study plots within a pasture, divided by the number of plots in that pasture (i.e., the number that would have been observed at a single study plot if distribution of defecation events within a given pasture had been uniform). The ratio of observed to expected fecal pats is a measure of relative use; that is, use of a given sampling plot by herbivores in relation to other plots in the same pasture (Mueggler 1965). Values less than one indicate the plot was used less than what would be expected if landscape use were uniform, and values greater than one indicate that use was greater than would be expected if landscape use were uniform. When the two terms of the equation are multiplied together, the resulting value represents relative herbivore use, adjusted for cumulative stocking rate. This value combines the information contributed by each of the other possible proxies for grazing intensity. If shown to be an effective proxy for grazing intensity, CRU · patch^{-1} would therefore have the advantage of including more information than other univariate measures based on fecal pat densities, without the need to include additional covariates in models of the effects of grazing.

I adjusted each of the aforementioned potential proxies for grazing intensity to range from zero to one based on their minimum and maximum values, so that results generated using different proxies could be compared with one another (Legendre and Legendre 1998). Before adjustment, each variable had a minimum value of zero, in control pastures. The maximum values of each variable in areas grazed by cattle were 0.90 AUM · ha^{-1}, 772 pats · ha^{-1} (calculated at the landscape scale), 1010 pats · ha^{-1} (calculated at the patch scale), and 6.90 CRU · $patch^{-1}$.

In the bison pasture, the minimum densities of fecal pats at the patch and landscape scales, and the minimum value of CRU · $patch^{-1}$ were zero, in areas that bison had not grazed since their reintroduction to GNP. Before adjustment, the minimum stocking rate in the bison pasture was 0.10 AUM · ha^{-1} and the maximum stocking rate was 0.13 AUM · ha^{-1}. When adjusted to range from zero to one, stocking rate became a binary variable. The maximum fecal pat densities I observed at the landscape and patch scales, respectively, were 788 pats · ha^{-1} and 1500 pats · ha^{-1}, and the maximum value of Constrained Relative Use was 9.39 CRU · $patch^{-1}$.

2.3.3 Statistical analyses

I used generalized linear mixed-effects models (GLMMs) in SAS statistical software (SAS Institute 2008) to model relationships between potential proxies for grazing intensity and grazing intensity-related response variables. These responses included 100% and 50% vegetation height-density, canopy height, litter depth, litter cover, clipped graminoid cover, Simpson's reciprocal index, Simpson's measure of evenness, and the proportion of increaser and decreaser species in the plant community. Using PROC GENMOD, I compared among potential distributions for each response, and identified the negative binomial distribution as the most appropriate error distribution for all variables. Next, I used PROC GLIMMIX to model relationships between grazing intensity proxies and each response variable, with maximum likelihoods estimated based on Laplace approximation (SAS Institute 2008). When modeling structural responses that were measured at the quadrat scale, I designated ‘plot’ as a random effect, to account for the spatial clustering of quadrats within study plots (Bell and Grunwald 2004). I also evaluated the importance of clustering of plots within landscapes; however, when both ‘landscape’ was included as a random variable, the standard deviation associated with covariance parameter estimates encompassed zero in models of most responses. Therefore, I considered the influence of this variable to be negligible, and I present analyses with ‘plot’ as the only random variable.

I compared the parsimony of candidate models of all plant community responses using Akaike’s Information Criterion values for small sample sizes (AIC_c; Burnham and Anderson 2002). I used a hierarchical selection process to determine the best available model for each plant community response of interest. In the first step of this process, I compared the fit of the null model to that of a model that included year of observation as the sole fixed effect. If the model including the term ‘year’ represented a substantial improvement over the null (i.e., $\Delta AIC_c > 2$; Burnham and Anderson 2002), I included this as a candidate model throughout the model selection process, and also included ‘year’ in all subsequent candidate models to control for effects of variation between the two years of the study.

In the second step of the model selection process, I evaluated the fit of four candidate models, each including one of the potential proxies for grazing intensity (AUM $\cdot$ ha^{-1}, pats $\cdot$ landscape^{-1}, pats $\cdot$ patch^{-1}, CRU $\cdot$ patch^{-1}), and year of observation if applicable. If one or more of the candidate models that included a potential proxy for grazing intensity represented a substantial improvement over the null model, the model with the highest Akaike weight (w_i) advanced to the next step. If there was substantial evidence for more than one model (i.e., a model was within two AIC$_c$ points of that with the highest Akaike weight; Burnham and Anderson 2002), each competitive model advanced.

In the third step, I evaluated whether the inclusion of a potential proxy for grazing intensity calculated at a second spatial scale improved upon the fit of the previous best model(s). For example, if a model including a landscape-scale predictor variable had the lowest AIC$_c$ value after step two, I tested to see if the inclusion of a patch-scale predictor (namely, pats · patch^{-1}) would improve the fit of that model. I did not test CRU · patch^{-1} alongside other proxies for grazing intensity, since information from the patch and landscape scales was already taken into account during the calculation of this variable.

All competitive models advanced to the fourth step wherein I tested whether the inclusion of an interaction between 'year' and the relevant proxy for grazing intensity improved the fit of the previously best model(s). If, after this step, the model with the highest Akaike weight contained one additional predictor variable and had an AIC$_c$ value within two points of a simpler model (or two additional variables and was within four points of a simpler model, etc.), the additional predictor was not considered to be informative (Arnold 2010). In such cases, I selected the simplest model that had an AIC$_c$ value within the relevant number of points of the model with the highest Akaike weight.

I first determined the most parsimonious models of plant community responses for cattle and bison separately, with each potential proxy for grazing intensity adjusted to range from zero to one based on minimum and maximum values observed under the species in question. Next, I re-adjusted each proxy to range from zero to one based on values observed under both species, and including data from areas grazed by bison and cattle in the same models, I evaluated what combination of variables represented the best fit for each grazing intensity-related response. I followed the same model selection process as above; however, I only modeled responses that the preceding analyses had shown to be related to at least one of the proxies for grazing intensity, under both species of grazer. Furthermore, I only included proxies in candidate models if they were effective at modeling at least one grazing intensity-related response for both species of grazer. To determine whether the modeled relationships between proxies and plant community responses were the same for bison and for cattle, I added a final step to test whether the inclusion of species of grazer as a fixed effect, and the interaction between ‘grazer’ and the relevant proxy for grazing intensity, improved the fit of the previously best model.

2.4 RESULTS

2.4.1 Cattle

Year of observation contributed a substantial amount of information about all response variables except plant community evenness (Table 1). Residual biomass (i.e., vegetation height-density), canopy height, litter depth, diversity, and the proportion of increasers in the plant community were all higher overall in 2011, whereas litter cover, clipped graminoid cover, and the proportion of decreasers in the plant community were higher in 2010 (Figs. 2 and 3). Despite inter-annual variability, the best models of most response variables did not include an informative interaction term between ‘year’ and the proxy for grazing intensity that was used. So, effectiveness of proxies did not vary by year, except for modeling changes in litter cover and the proportion of increasers (Table 1).

Models based on each of the potential proxies for grazing were usually a substantial improvement over the null model and the year-only model. Therefore, each was a viable proxy for grazing intensity of cattle in GNP. As each proxy increased, residual biomass, canopy height, litter depth, and litter cover decreased, while clipped graminoid cover increased (Fig. 2). Plant species diversity and the proportion of increaser species in the plant community also increased along with each proxy, while plant community evenness and the proportion of decreasers in the plant community decreased (Fig. 3). However, the relative fit of each model varied with the spatial scale of predictors, and temporal scale of responses.

Proxies for grazing intensity calculated at the landscape scale were included in the best models of each structural response, and of the proportion of increasers and decreasers in the plant community (Table 1). Stocking rate (AUM · ha^{-1}) was included in the best model of most structural responses, although the relative density of fecal pats at the landscape scale (pats · landscape^{-1}) was substantially better at modeling litter depth and litter cover. Patch-scale proxies for grazing intensity were not the most informative univariate predictors of any structural responses. However, when both year of observation and grazing intensity at the landscape scale were accounted for, the relative density of fecal pats at the patch scale (pats · patch^{-1}) contributed substantial additional information about litter cover and clipped graminoid cover (Table 1). Constrained Relative Use (CRU · patch^{-1}), a patch-scale proxy, was included in the best models of plant community diversity and evenness (Table 1).

Table 1. Log-likelihood (LL), number of parameters (*K*), change in Akaike's criterion for small sample sizes (ΔAIC$_c$), and Akaike weight (w_i) for models of plant community responses to grazing by cattle in Grasslands National Park, Saskatchewan, Canada, June–July of 2010 and 2011. Selected best models for each response are in bold.

Response variable	Model[1]	LL	*K*	ΔAIC$_c$	w_i
	--------------------Vegetation structure--------------------				
100% Vegetation height-density	**AUM·ha^{-1}, year**	-4839.78	3	0.00	0.57
	AUM·ha^{-1}, pats·patch^{-1}, year	-4839.16	4	0.80	0.38
	Pats·landscape^{-1}, year	-4842.31	3	5.06	0.05
	Year	-4846.68	2	11.78	0.00
	Pats·patch^{-1}, year	-4846.34	3	13.13	0.00
	CRU·patch^{-1}, year	-4846.66	3	13.78	0.00
	Null	-4914.96	1	146.33	0.00
50% Vegetation height-density	**AUM·ha^{-1}, year**	-5622.04	3	0.00	0.71
	AUM·ha^{-1}, pats·patch^{-1}, year	-5621.96	4	1.87	0.28
	Pats·landscape^{-1}, year	-5626.07	3	8.05	0.01
	Pats·patch^{-1}, year	-5628.67	3	13.25	0.00
	Year	-5629.90	2	13.68	0.00
	CRU·patch^{-1}, year	-5629.36	3	14.85	0.00
	Null	-5660.99	1	73.85	0.00
Canopy height	AUM·ha^{-1}, pats·patch^{-1}, year	-5610.86	4	0.00	0.58
	AUM·ha^{-1}, year	-5612.20	3	0.66	0.42
	CRU·patch^{-1}, year	-5617.35	3	13.24	0.00
	Year	-5624.90	2	24.04	0.00
	Pats·patch^{-1}, year	-5624.28	3	24.82	0.00
	Pats·landscape^{-1}, year	-5624.78	3	25.81	0.00
	Null	-5694.55	1	161.32	0.00
Litter depth	**Pats·landscape^{-1}, year**	-4847.66	3	0.00	0.69
	Pats·landscape^{-1}, pats·patch^{-1}, year	-4847.53	4	1.76	0.29
	AUM·ha^{-1}, year	-4851.01	3	6.68	0.02
	Pats·patch^{-1}, year	-4855.27	3	15.21	0.00
	CRU·patch^{-1}, year	-4859.87	3	25.21	0.00
	Year	-4863.45	2	29.55	0.00
	Null	-4882.87	1	66.38	0.00
Litter cover	**Pats·landscape^{-1}, pats·patch^{-1}, year, pp*y**	-7200.67	5	0.00	0.58
	Pats·landscape^{-1}, pats·patch^{-1}, year, pl*y	-7201.21	5	1.10	0.33
	Pats·landscape^{-1}, pats·patch^{-1}, year	-7203.63	4	3.89	0.08
	Pats·landscape^{-1}, year	-7207.77	3	10.16	0.00
	AUM·ha^{-1}, pats·patch^{-1}, year	-7207.00	4	10.64	0.00
	AUM·ha^{-1}, year	-7208.26	3	11.14	0.00
	Year	-7214.18	2	20.94	0.00
	Pats·patch^{-1}, year	-7213.91	3	22.44	0.00
	CRU·patch^{-1}, year	-7213.84	3	22.86	0.00
	Null	-7227.11	1	44.78	0.00

(Continued on next page)

Table 1, continued

Response variable	Model[1]	LL	K	ΔAIC_c	w_i
Clipped graminoid cover	**AUM·ha^{-1}, pats·patch^{-1}, year**	-213.84	4	0.00	0.94
	AUM·ha^{-1}, year	-217.76	3	5.60	0.06
	Pats·landscape^{-1}, year	-220.18	3	10.42	0.01
	Pats·patch^{-1}, year	-229.49	3	29.05	0.00
	CRU·patch^{-1}, year	-232.87	3	35.81	0.00
	Year	-257.92	2	83.71	0.00
	Null	-266.34	1	98.39	0.00
--------------------Plant community composition--------------------					
Simpson's reciprocal index	**CRU·patch^{-1}, year**	-703.98	3	0.00	0.44
	Pats·patch^{-1}, year	-704.67	3	1.38	0.22
	AUM·ha^{-1}, year	-704.73	3	1.49	0.21
	Pats·landscape^{-1}, year	-705.48	3	2.98	0.10
	Year	-708.11	2	6.05	0.02
	Null	-714.01	1	15.69	0.00
Simpson's measure of evenness	**CRU·patch^{-1}**	-652.35	3	0.00	0.37
	Pats·patch^{-1}	-652.43	3	0.16	0.34
	Null	-654.80	1	2.73	0.09
	AUM·ha^{-1}	-653.87	3	3.04	0.08
	Pats·landscape^{-1}	-653.95	3	3.19	0.08
	Year	-654.78	2	4.84	0.03
% Decreasers	**AUM·ha^{-1}, year**	-425.24	3	0.00	0.31
	Pats·patch^{-1}, year	-425.75	3	1.02	0.19
	Pats·landscape^{-1}, year	-426.07	3	1.66	0.14
	AUM·ha^{-1}, pats·patch^{-1}, year	-424.97	4	1.70	0.13
	CRU·patch^{-1}, year	-426.30	3	2.13	0.11
	Pats·landscape^{-1}, pats·patch^{-1}, year	-425.65	5	3.06	0.07
	Year	-428.06	2	3.43	0.06
	Null	-451.81	1	48.77	0.00
% Increasers	**Pats·landscape^{-1}, year, pl*y**	-405.11	4	0.00	0.43
	AUM·ha^{-1}, year, a*y	-405.47	4	0.72	0.30
	AUM·ha^{-1}, pats·patch^{-1}, year, a*y	-405.18	5	2.44	0.13
	Pats·patch^{-1}, year, pp*y	-407.60	4	4.99	0.04
	AUM·ha^{-1}, pats·patch^{-1}, year, pp*y	-406.86	5	5.79	0.02
	Pats·landscape^{-1}, pats·patch^{-1}, year, pp*y	-407.12	5	6.32	0.02
	Pats·landscape^{-1}, year	-409.40	3	6.34	0.02
	Pats·patch^{-1}, year	-409.51	3	6.55	0.02
	AUM·ha^{-1}, year	-409.83	3	7.20	0.01
	Pats·landscape^{-1}, pats·patch^{-1}, year	-409.13	4	8.04	0.01
	AUM·ha^{-1}, pats·patch^{-1}, year	-409.13	4	8.05	0.01
	Year	-411.43	3	10.41	0.00
	CRU·patch^{-1}, year	-412.55	2	10.44	0.00
	Null	-434.57	1	52.31	0.00
	Pats·landscape^{-1}, pats·patch^{-1}, year, pl*y	N/A	5	N/A	

[1] Models including the terms ‘a*y’ (AUM·ha^{-1}*year), ‘pl*y’ (pats·landscape^{-1}*year), and ‘pp*y’ (pats·patch^{-1}*year) are only shown if the interaction term(s) contributed substantial additional information about the plant community response of interest, relative to simpler models

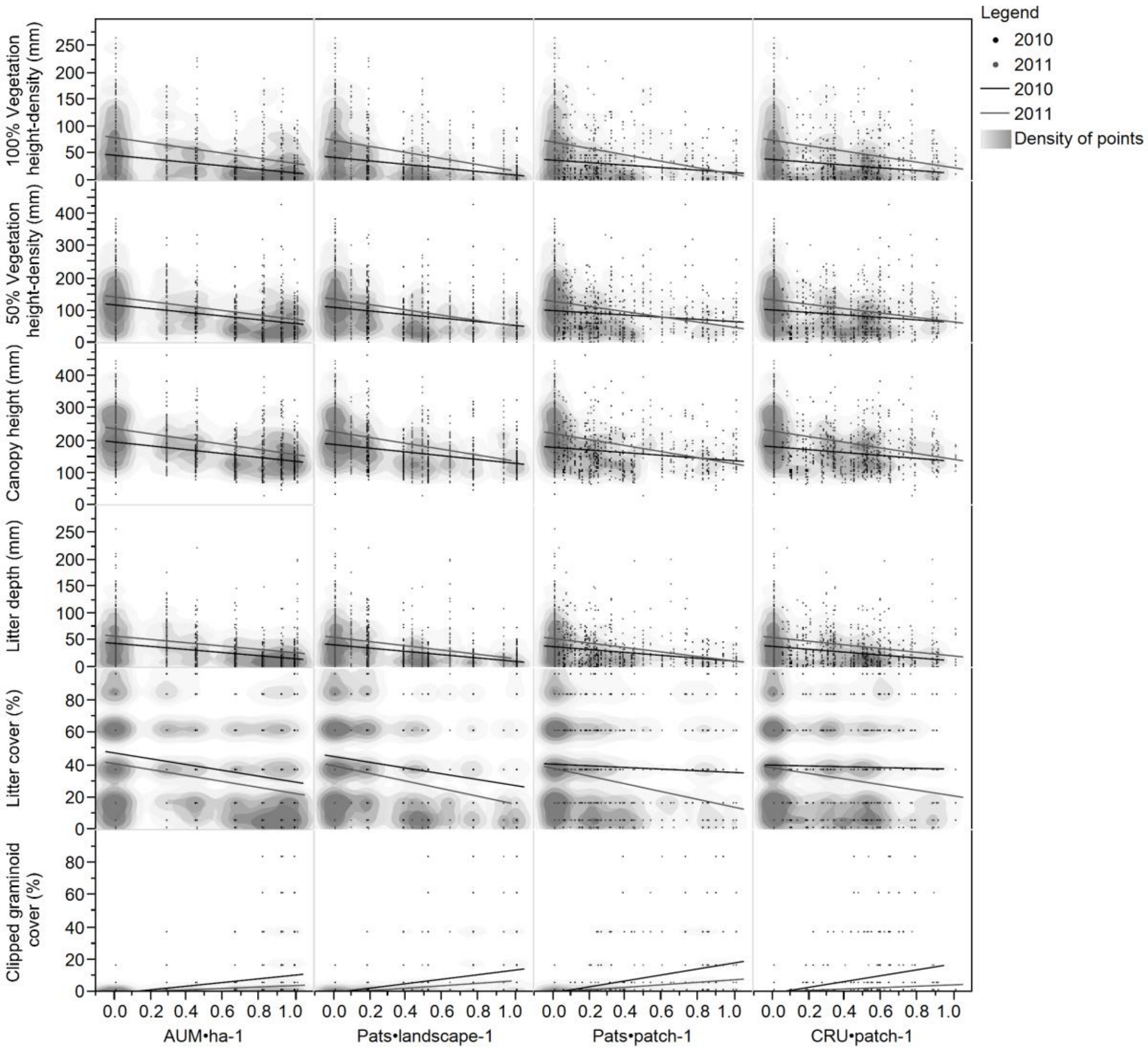

Figure 2. Changes in vegetation structure in relation to four proxies for grazing intensity of cattle in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Each proxy was adjusted to range from zero to one, based on the minimum and maximum value of each predictor variable observed within control pastures and pastures stocked with cattle. Estimated effect sizes for informative predictors of each response are listed in Appendix D.

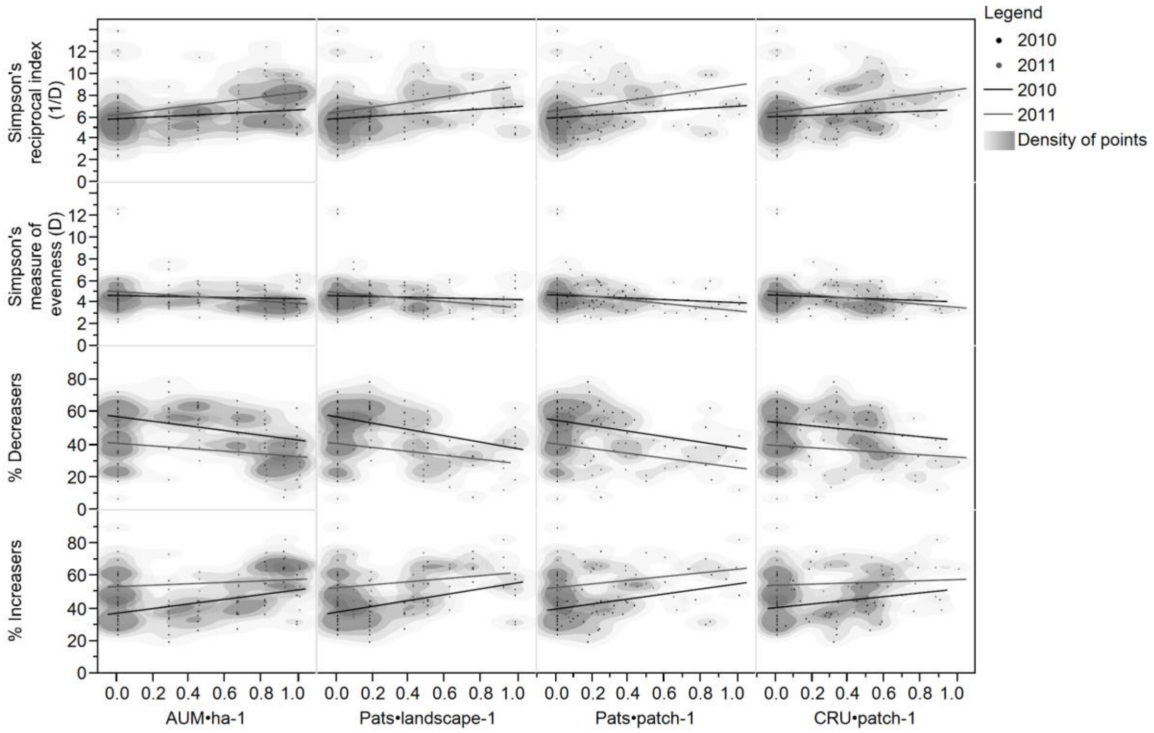

Figure 3. Changes in plant community composition in relation to four proxies for grazing intensity of cattle in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Each proxy was adjusted to range from zero to one, based on the minimum and maximum value of each predictor variable observed within control pastures and pastures stocked with cattle. Estimated effect sizes for informative predictors of each response are listed in Appendix D.

Overall, proxies based on fecal pat densities were better than stocking rate at modeling indirect, longer term effects of grazing, including reductions in litter depth and cover, and changes in the elements comprising floristic diversity (Table 1).

2.4.2 Bison

The year effect explained a substantial amount of variability associated with all response variables measured within the bison pasture, except for clipped graminoid cover (Table 2). For most structural responses to bison grazing, models that included each potential proxy for grazing intensity except AUM · ha^{-1} were a substantial improvement over the model based only on year (Table 2). Each proxy based on fecal pat densities could therefore be used to quantify grazing intensity of bison in GNP over the relatively short term, with residual biomass, canopy height, litter depth, and litter cover all declining, and clipped graminoid cover increasing with increasing grazing intensity (Fig. 4).

The best models of structural responses to bison grazing all included pats · landscape^{-1} as a fixed effect (Table 2). Patch-scale proxies for grazing intensity did not contribute substantial additional information about any plant community responses to bison grazing once grazing intensity at the landscape scale had been accounted for, and in select cases, did not contribute substantial information beyond that provided by the term ‘year’.

Only year provided substantial information about plant community composition within the bison pasture (Table 2), indicating either that none of the proxies I evaluated could model the effects of bison grazing in GNP on floristic diversity, plant community evenness, or the proportion of increasers and decreasers in the plant community, or that grazing had not yet influenced these factors.

Table 2. Log-likelihood (LL), number of parameters (K), change in Akaike's criterion for small sample sizes (ΔAIC$_c$), and Akaike weight (w_i) for models of plant community responses to grazing by bison in Grasslands National Park, Saskatchewan, Canada, June–July of 2010 and 2011. Selected best models for each response are in bold.

Response variable	Model^1	LL	K	ΔAIC$_c$	w_i
	-------------------Vegetation structure--------------------				
100% Vegetation height-density	**Pats·landscape^{-1}, year**	-4252.97	3	0.00	0.51
	Pats·landscape^{-1}, pats·patch^{-1}, year	-4252.02	4	0.12	0.48
	Pats·patch^{-1}, year	-4261.30	3	16.66	0.00
	CRU·patch^{-1}, year	-4261.75	3	17.56	0.00
	Year	-4264.15	2	20.32	0.00
	AUM·ha^{-1}, year	-4264.15	3	20.32	0.00
	Null	-4334.44	1	158.89	0.00
50% Vegetation height-density	**Pats·landscape^{-1}, year**	-4829.24	3	0.00	0.58
	Pats·landscape^{-1}, pats·patch^{-1}, year	-4828.53	4	0.63	0.42
	CRU·patch^{-1}, year	-4837.36	3	16.25	0.00
	Pats·patch^{-1}, year	-4837.53	3	16.58	0.00
	Year	-4839.99	2	19.48	0.00
	AUM·ha^{-1}, year	-4839.99	3	19.48	0.00
	Null	-4894.82	1	127.12	0.00
Canopy height	**Pats·landscape^{-1}, year**	-4845.14	3	0.00	0.72
	Pats·landscape^{-1}, pats·patch^{-1}, year	-4845.09	4	1.93	0.27
	Pats·patch^{-1}, year	-4850.40	3	10.51	0.00
	CRU·patch^{-1}, year	-4851.21	3	13.14	0.00
	Year	-4853.31	2	14.32	0.00
	AUM·ha^{-1}, year	-4853.31	3	14.32	0.00
	Null	-5014.60	1	334.87	0.00
Litter depth	**Pats·landscape^{-1}, year**	-4214.79	3	0.00	0.68
	Pats·landscape^{-1}, pats·patch^{-1}, year	-4214.51	4	1.48	0.32
	Pats·patch^{-1}, year	-4222.41	3	15.25	0.00
	CRU·patch^{-1}, year	-4222.78	3	15.99	0.00
	Year	-4228.50	2	25.40	0.00
	AUM·ha^{-1}, year	-4228.50	3	25.40	0.00
	Null	-4233.15	1	32.68	0.00
Litter cover	**Pats·landscape^{-1}, year**	-6279.23	3	0.00	0.58
	Pats·landscape^{-1}, pats·patch^{-1}, year	-6279.06	4	1.69	0.25
	Pats·patch^{-1}, year	-6281.07	3	3.69	0.09
	CRU·patch^{-1}, year	-6281.25	3	4.05	0.08
	Year	-6285.07	2	9.66	0.00
	AUM·ha^{-1}, year	-6285.07	3	9.66	0.00
	Null	-6311.78	1	61.06	0.00

(Continued on next page)

Table 2, continued

Response variable	Model[1]	LL	K	ΔAIC$_c$	w_i
Clipped graminoid cover	Pats·landscape^{-1}, pats·patch^{-1}	-87.01	3	0.00	0.49
	Pats·landscape^{-1}	-88.65	2	1.04	0.29
	Pats·patch^{-1}	-89.21	2	2.17	0.16
	CRU·patch^{-1}	-90.20	2	4.15	0.06
	Null	-100.44	1	22.44	0.00
	Year	-99.51	2	22.77	0.00
	AUM·ha^{-1}	-99.51	2	22.77	0.00
	--------------------Plant community composition--------------------				
Simpson's reciprocal index	**Year**	-597.04	2	0.00	0.23
	AUM·ha^{-1}, year	-597.04	3	0.00	0.23
	CRU·patch^{-1}, year	-596.28	3	0.71	0.16
	Pats·patch^{-1}, year	-596.48	3	1.12	0.13
	AUM·ha^{-1}, pats·patch^{-1}, year	-596.48	4	1.12	0.13
	Pats·landscape^{-1}, year	-596.98	3	2.11	0.08
	Null	-599.83	1	3.39	0.04
Simpson's measure of evenness	Pats·landscape^{-1}, year	-561.07	3	0.00	0.21
	Year	-562.23	2	0.08	0.20
	AUM·ha^{-1}, year	-562.23	3	0.08	0.20
	Pats·landscape^{-1}, pats·patch^{-1}, year	-560.19	4	0.53	0.16
	Pats·patch^{-1}, year	-562.12	3	2.09	0.07
	AUM·ha^{-1}, pats·patch^{-1}, year	-562.12	4	2.09	0.07
	CRU·patch^{-1}, year	-562.19	3	2.23	0.07
	Null	-566.23	1	5.88	0.01
% Decreasers	CRU·patch^{-1}, year	-353.70	3	0.00	0.39
	Pats·patch^{-1}, year	-354.29	3	1.18	0.21
	Year	-355.46	2	1.28	0.20
	AUM·ha^{-1}, pats·patch^{-1}, year	-354.43	4	1.45	0.19
	AUM·ha^{-1}, year	-355.62	3	1.60	0.17
	Pats·landscape^{-1}, year	-354.68	3	1.95	0.15
	Pats·landscape^{-1}, pats·patch^{-1}, year	-354.19	4	3.26	0.08
	Null	-372.11	1	32.38	0.00
% Increasers	CRU·patch^{-1}, year	-344.53	3	0.00	0.22
	Pats·patch^{-1}, year	-344.63	3	0.20	0.20
	AUM·ha^{-1}, pats·patch^{-1}, year	-344.79	4	0.53	0.17
	Year	-346.04	2	0.79	0.15
	AUM·ha^{-1}, year	-346.24	3	1.18	0.12
	Pats·landscape^{-1}, year	-345.55	3	2.04	0.08
	Pats·landscape^{-1}, pats·patch^{-1}, year	-344.48	4	2.20	0.07
	Null	-361.88	1	30.29	0.00

[1] Models including the terms ‘a*y’ (AUM·ha^{-1}*year), ‘pl*y’ (pats·landscape^{-1}*year), and ‘pp*y’ (pats·patch^{-1}*year) are only shown if the interaction term(s) contributed substantial additional information about the plant community response of interest, relative to simpler models

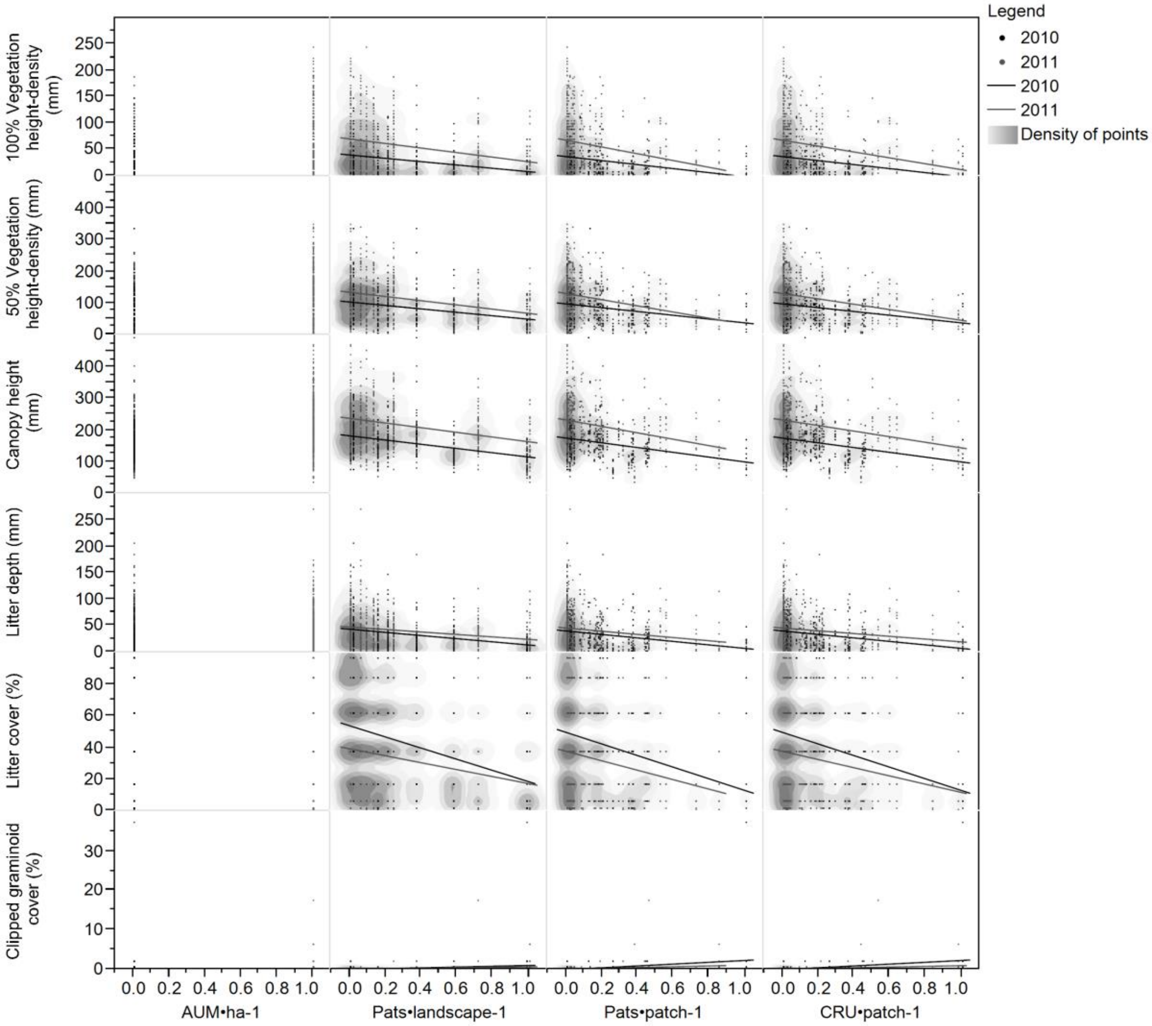

Figure 4. Changes in vegetation structure in relation to four proxies for grazing intensity of bison in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Each proxy was adjusted to range from zero to one, based on the minimum and maximum value of each predictor variable observed within the bison pasture. Estimated effect sizes for informative predictors of each response are listed in Appendix D.

2.4.3 Bison and cattle

When the structural effects of grazing by bison and cattle were modeled together, year of observation was again important for modeling all response variables, but in most cases, models including each potential proxy for grazing intensity contributed substantially more information than the year-only model (Table 3). AUM · ha^{-1} was not included in the model selection process that included both species of grazer, since this term failed to provide information about the structural effects of bison grazing, but all other proxies were effective at modeling the effects of grazing by both bison and cattle in GNP.

As each proxy based on fecal pat densities increased, residual biomass, canopy height, litter depth, and litter cover decreased under both bison and cattle (Appendices D and E). None of the best models of these structural responses included an interaction term between a proxy for grazing intensity and species of grazer (Table 3), indicating that the modeled relationships between most structural responses and their best predictors did not differ for bison and for cattle. While clipped graminoid cover increased under both species of grazer, the best model of this response included an informative interaction term between grazing intensity and species of grazer (Table 3), indicating that the magnitude of this response was different under bison and cattle. Overall, more clipped graminoids were observed in areas grazed by cattle (Appendix D).

Pats · landscape^{-1} was the proxy most frequently included in the best models of structural responses to bison and cattle grazing (Table 3). This proxy also modeled the range of grazing intensities within areas grazed by each species as being most similar to one another (Fig. 5). Models that included both pats · landscape^{-1} and pats · patch^{-1} were not selected in most cases due to their additional complexity. Alone, pats · patch^{-1} was not the best predictor for any responses, but CRU · patch^{-1} out-performed all other proxies by a substantial margin for modeling canopy height (Table 3).

Since changes in plant community composition in areas grazed by bison could not be successfully modeled using any of the available proxies for grazing intensity, the effects of bison and cattle grazing on compositional responses could not be compared.

Table 3. Log-likelihood (LL), number of parameters (K), change in Akaike's criterion for small sample sizes (ΔAIC$_c$), and Akaike weight (w_i) for models of plant community responses to grazing by bison and cattle in Grasslands National Park, Saskatchewan, Canada, June–July of 2010 and 2011. Selected best models for each response are in bold.

Response variable	Model^1	LL	K	ΔAIC$_c$	w_i
100% Vegetation height-density	**Pats·landscape^{-1}, pats·patch^{-1}, year**	-9097.38	4	0.00	0.86
	Pats·landscape^{-1}, year	-9100.17	3	3.55	0.14
	Pats·patch^{-1}, year	-9112.03	3	27.27	0.00
	Year	-9114.15	2	29.51	0.00
	CRU·patch^{-1}, year	-9113.30	3	29.83	0.00
	Null	-9255.56	1	310.32	0.00
50% Vegetation height-density	**Pats·landscape^{-1}, year**	-10465.39	3	0.00	0.58
	Pats·landscape^{-1}, pats·patch^{-1}, year	-10464.72	4	0.67	0.42
	Pats·patch^{-1}, year	-10473.97	3	17.16	0.00
	CRU·patch^{-1}, year	-10474.51	3	18.24	0.00
	Year	-10477.06	2	21.33	0.00
	Null	-10559.15	1	183.50	0.00
Canopy height	**CRU·patch^{-1}, year**	-10487.97	3	0.00	1.00
	Pats·landscape^{-1}, year	-10495.80	3	15.68	0.00
	Pats·landscape^{-1}, pats·patch^{-1}, year	-10495.68	4	17.44	0.00
	Pats·patch^{-1}, year	-10496.83	3	17.74	0.00
	Year	-10498.90	2	19.86	0.00
	Null	-10713.39	1	446.83	0.00
Litter depth	**Pats·landscape^{-1}, year**	-9069.14	3	0.00	0.65
	Pats·landscape^{-1}, pats·patch^{-1}, year	-9068.76	4	1.25	0.35
	Pats·patch^{-1}, year	-9083.87	3	29.46	0.00
	CRU·patch^{-1}, year	-9090.28	3	42.27	0.00
	Year	-9098.01	2	55.73	0.00
	Null	-9120.45	1	98.59	0.00
Litter cover	Pats·landscape^{-1}, pats·patch^{-1}, year	-13488.74	4	0.00	0.62
	Pats·landscape^{-1}, year	-13490.25	3	1.01	0.38
	Pats·patch^{-1}, year	-13499.90	3	20.31	0.00
	CRU·patch^{-1}, year	-13501.19	3	22.89	0.00
	Year	-13503.03	2	24.55	0.00
	Null	-13540.35	1	97.18	0.00
Clipped graminoid cover	Pats·landscape^{-1}, year, pl*y, grazer, pl*g	-306.89	6	0.00	0.61
	Pats·landscape^{-1}, year, grazer, pl*g	-308.62	5	1.28	0.32
	Pats·landscape^{-1}, year, pl*y, grazer	-310.89	5	5.84	0.03
	Pats·landscape^{-1}, year, grazer	-312.15	4	6.20	0.03
	Pats·landscape^{-1}, year	-330.38	3	40.55	0.00
	Pats·landscape^{-1}, year, pl*y	-329.71	4	41.32	0.00
	Pats·patch^{-1}, year	-339.09	3	57.95	0.00
	CRU·patch^{-1}, year	-340.09	3	59.95	0.00
	Year	-370.16	2	117.99	0.00
	Null	-380.55	1	136.69	0.00

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Table 3, continued

[1] Models including the terms ‘a*y’ (AUM·ha^{-1}*year), ‘pl*y’ (pats·landscape^{-1}*year), ‘pp*y’ (pats·patch^{-1}*year), ‘pl*g’ (pats·landscape^{-1}*grazer), and other interaction terms between potential proxies for grazing intensity and ‘grazer’ are only shown if these interaction term(s) contributed substantial additional information about the plant community response of interest, relative to simpler models

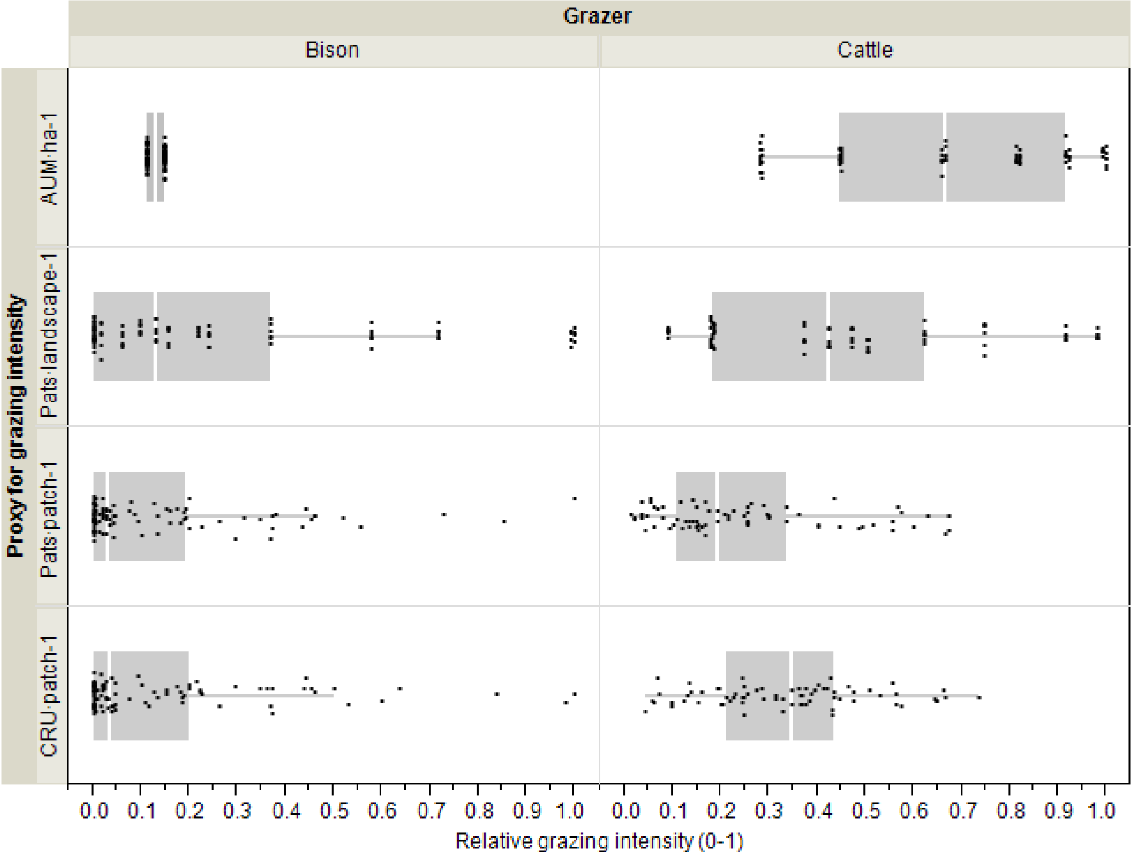

Figure 5. Boxplot with jittered points showing the range of grazing intensities of bison and cattle within study plots located in grazed areas of Grasslands National Park, Saskatchewan, Canada, June–July of 2010 and 2011, as modeled by four proxies for grazing intensity. Each proxy has been adjusted to range from zero to one, based on the minimum and maximum value of each predictor variable observed within the entire study area.

2.5 DISCUSSION

Almost all of the grazing intensity-related responses that I used to evaluate potential proxies for grazing intensity varied with year of observation. Some of this variation was likely related to inter-annual differences in precipitation; for example, canopy heights were substantially higher and there was substantially more residual biomass in 2011, the second year of this study, when precipitation was also highest. It is typical for plant community characteristics in semi-arid regions of the Great Plains to vary annually because of climatic conditions, with climate sometimes being more important than grazing intensity at determining ecological outcomes (Biondini et al. 1998, Fuhlendorf et al. 2001). This may have been the case for the proportion of increasers and decreasers in the plant community in this study; abnormally moist conditions may have allowed for the emergence of more forbs (typically increaser species). My results showed, however, that while year was an important determinant of plant community structure and composition within Grasslands National Park, grazing intensity also had a marked effect on most responses during the study period. Furthermore, the estimated effect of grazing intensity on most responses did not vary substantially with year of observation, indicating that the best proxies for grazing intensity were generally robust to differences in baseline values of response variables between years.

2.5.1 Cattle

Overall, proxies calculated at the landscape scale were best at modeling grazing intensity-related responses. This is surprising, as selective foraging by cattle is known to result in spatial variability in grazing intensity (Hart et al. 1993, Bailey et al. 1996, Barnes et al. 2008). My results could be partly due to the class of cattle used in this study; landscape use by yearlings is generally more uniform than that of cow-calf pairs (Bell 1973), especially relative to cows that have previously spent time within a given pasture (as in the study by Barnes et al. 2008; Vallentine 1990, Launchbaugh and Howery 2005). Furthermore, the yearlings used in this study may have selected to graze in the upland grassland landscapes I surveyed because these contained an abundance of palatable forage (Senft et al. 1987, Bailey et al. 1996), and then exhibited comparatively less selectivity when choosing small patches or feeding stations within those landscapes (WallisDeVries 1999), thereby minimizing the patch-scale effects of grazing.

Still, grazing intensity did vary within landscapes in this study. After the relative level of grazing intensity at the landscape scale was accounted for, finer-scale variability associated with some structural responses to grazing could be quantified using patch-scale proxies. For example, cover of defoliated graminoid species was greater in landscapes with higher stocking rates, and was also greater in patches with higher fecal pat densities within those landscapes. While the utility of patch-scale proxies for modeling most other structural responses was limited, this may have been because fecal pat densities at the patch scale were poor proxies for grazing intensity over the short term (Julander 1955, Kohler et al. 2006), and several of the structural responses I monitored changed in response to the level of grazing intensity at a patch within a single season.

If fecal pat densities within patches were indicative of relative herbivore use of that patch over time, as asserted by Milchunas et al. (1989), patch-scale proxies should have contributed substantial information about the variables I monitored that respond to grazing intensity over longer temporal scales. I did find that the relative density of fecal pats at each patch (pats · patch^{-1}) was important for modeling reductions in litter cover, an indirect effect of long-term grazing observed by Biondini et al. (1998). Patch-scale proxies were also the best predictors of floristic diversity and evenness, two other indirect effects of grazing that are expressed over time (Lauenroth and Laycock 1989, Anderson and Briske 1995). Therefore, my results support the idea that grazing intensity of cattle in GNP did vary significantly at the patch scale.

Of the two patch-scale proxies I evaluated, Constrained Relative Use (CRU · patch^{-1}) out-performed pats · patch^{-1} by a slight margin at modeling the effects of grazing on floristic diversity. While these results do not strongly recommend the use of one patch-scale proxy over the other, CRU · patch^{-1} has some advantages over pats · patch^{-1}. First, the former incorporates information from both the patch and landscape scales, so models based on this proxy retain degrees of freedom while including more information. The additional information included in CRU · patch^{-1} is ecologically relevant, given that foraging decisions made at broader scales constrain decision-making at finer spatial scales (Bailey et al. 1996). My results also affirm the importance of accounting for landscape-scale grazing intensity even when modeling structural responses that vary at the patch scale. Second, models based on actual fecal pat densities could be confounded by extraneous factors that vary among treatments or study sites, such as different rates of pat breakdown based on stocking rate (e.g., accelerated breakdown under higher stocking rates due to trampling effects), so the utility of these models for making direct comparisons among pastures that are managed differently may be limited. Such problems are reduced by basing models on CRU · patch^{-1}, since the actual number of pats counted at a patch is transformed based on the total number of pats counted in the broader landscape in the calculation of this parameter.

My results indicate that the spatial scale over which a proxy for grazing intensity is calculated can have important implications for the conclusions that may be drawn from a given study. Proxies for grazing intensity calculated over small scales can be more ecologically informative than pasture-scale proxies like stocking rate, given that the effects of grazing at small spatial scales can influence a wide range of ecosystem processes, including primary productivity, and population dynamics of native flora and fauna (Turner 1989, Adler et al. 2001, Augustine and Frank 2001). However my results also showed there to be a tradeoff wherein proxies for localized grazing intensity based on the density of fecal pats were able to model small-scale effects of grazing, but only over longer temporal scales. In contrast, the discrepancy between observed fecal pat densities and within-year grazing intensity was not as great when fecal pat densities were averaged across entire landscapes. Landscape-scale predictors were generally strong proxies for grazing intensity over the short term, and thus, either the density of fecal pats or stocking rate are simple and effective ways of quantifying grazing intensity in the uplands of large, seasonally grazed pastures in northern mixed prairie ecosystems.

2.5.2 Bison

Grazing intensity differed substantially both within and among the landscapes that I surveyed in the bison pasture. Since stocking rate (AUM · ha^{-1}) modeled grazing intensity throughout the entire ~18,000-ha pasture as being uniform within a given year, it unsurprisingly failed to explain the variability associated with responses to bison grazing. The relative density of fecal pats in landscapes nested within the bison pasture (pats · landscape^{-1}) out-performed patch-scale proxies, possibly because like cattle, bison are not as selective when choosing small patches or feeding stations once they have selected to graze within a given landscape (Wallace et al. 1995, Bailey et al. 1996). Alternatively, as I suggest above, fecal pat densities observed within patches may not have corresponded well to the actual level of grazing intensity exerted on those patches during a given season. When the density of fecal pats was calculated at the landscape scale, this variable served as a strong proxy for grazing intensity over the short term.

Unlike for cattle, none of the proxies that I evaluated were effective at modeling changes in plant community composition associated with bison grazing. This could have been because the bison pasture in this study was very large, encompassing several disjunct landscapes dominated by upland grassland plant communities, and because the average grazing intensity of bison was lower than that of cattle. The larger the area in which animals graze, the more opportunity they have to express their selective preferences at multiple scales, resulting in the effects of grazing being more heterogeneous in large pastures than in small (Hart et al. 1993). Therefore, grazing intensity at patches within the bison pasture is likely highly variable in both space and time. Furthermore, since bison in GNP are free to select among many patches dominated by their preferred forage, and since bison have been stocked at a low rate since their re-introduction to the area, cumulative grazing intensity may not have been great enough at any one location within the bison pasture to induce changes in plant community composition. However, changes in plant community composition are likely to occur eventually, given that bison elsewhere have been observed to establish grazed patches in areas of low species diversity, and to continually revisit these patches until they are converted to sites of higher diversity (Knapp et al. 1999, Towne et al. 2005). Since changes in plant community structure precede changes in composition, targeted monitoring of grazing intensity effects on plant community structure within landscapes that currently experience the highest grazing intensities will be important for detecting plant community changes in response to bison grazing in GNP.

2.5.3 Comparing grazing intensity of bison and cattle

My results show that proxies for grazing intensity based on fecal pat densities can be used to directly compare the effects of grazing by bison and cattle in GNP. Specifically, I found that pats · landscape^{-1} was the most consistent predictor of structural responses when the effects of both species were modeled simultaneously. All of the grazing intensity-related responses to this predictor variable were the same, whether the landscape in question was grazed by bison or by cattle, except for the amount of clipped graminoid cover. This single difference between the structural effects of the two species of grazer may have been because the spatial impacts of grazing varied between the two (as asserted by Freese et al. 2007), or because of the timing of surveys in the bison pasture happened to have allowed regrowth following defoliation. Even if spatial patterns of defoliation did vary based on species of grazer, fecal pat densities averaged across entire landscapes successfully modeled several direct and indirect effects of grazing by both bison and cattle. Some of these responses could have occurred within a single grazing season, while others, such as declines in litter cover, may have resulted from the cumulative effects of grazing over more than one season. Further work would be required to determine the exact temporal scale over which pats · landscape^{-1} represents grazing intensity, and whether this varies by species of grazer. Until more is known about how fecal pat densities correspond to cumulative levels of grazing intensity over time, the conservative interpretation of my results is that the density of fecal pats observed within landscapes in GNP served as a proxy for grazing intensity *within* the study period.

Bison and cattle grazed at a similar range of intensities in landscapes within GNP during the years that this study took place, despite bison being stocked at a much lower rate than the average cattle stocking rate. The distribution of grazing intensity did differ between bison and cattle, with more landscapes in the bison pasture (and more patches within those landscapes) being grazed at very low intensities, and hundreds of hectares of upland grassland not being grazed by bison at all. In contrast, the intensity of cattle grazing was distributed more evenly. However, in some areas within their pasture, bison impacted plant community structure at a similar magnitude as cattle stocked at the heaviest rates used in this study (aimed at achieving 70% forage utilization, considered a very high rate for the area). This is a critical piece of information for managers of GNP, since cattle are currently being employed as surrogates for bison to achieve certain desired ecological outcomes that are assumed not be occurring within the bison pasture, given the low stocking rate (Parks Canada 2010). By using proxies for grazing intensity based on observed densities of fecal pats, managers will be able to monitor and quantify the full range of effects that bison have within their pasture, and compare and contrast these with the effects of cattle grazing at a similar range of intensities. Given limited time and effort to dedicate to monitoring, the density of fecal pats may therefore serve as a useful proxy for clarifying how management practices and species differences affect ecological outcomes on rangelands at multiple scales.

2.6 IMPLICATIONS

My results indicate that fecal pat densities can serve as the basis for effective proxies of grazing intensity, with patch-scale proxies being best for modeling plant community changes in response to grazing intensity over time, and the average density of fecal pats observed within landscapes being better for modeling short-term responses. When several levels of stocking rate are included in a given study, stocking rate may be more useful than the density of fecal pats at the landscape scale for modeling changes in vegetation structure. However, landscape-scale fecal pat densities are very useful when there are few levels of stocking rate or pastures are very large, or when the aim of a study is to compare grazing intensity effects within pastures that are subject to different management regimes.

For modeling variability in grazing intensity within landscapes, my results indicate that it is important to first account for the relative level of grazing intensity at the landscape scale. Information from both of these spatial scales is included in the measure of Constrained Relative Use that I introduce in this study, and this may have contributed to its usefulness for modeling changes in plant community diversity in response to cattle grazing. Constrained Relative Use may also be useful for comparing grazing intensity effects over time within pastures subject to different management regimes, including pastures grazed by bison and cattle, at an ecologically relevant spatial scale; however, further study is required to verify this.

My results show that fecal pat densities can serve as valid proxies for grazing intensity, that are both practical, given the relative ease of determining fecal pat densities compared to other quantitative methods used to estimate grazing intensity, and informative, given that proxies for grazing intensity can model effects of grazing that would go undetected if analyzed using pasture-scale estimates of grazing intensity only.

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3.0 RELATIVE EFFECTS OF GRAZING BY BISON AND CATTLE ON PLANT COMMUNITY HETEROGENEITY IN NORTHERN MIXED PRAIRIE

3.1 ABSTRACT

Grazing by domestic cattle (*Bos taurus*) is sometimes considered a useful tool to promote diversity in prairie ecosystems that were historically grazed by bison (*Bison bison*). However, there is no consensus within the literature as to whether cattle function as ecological equivalents to bison. To determine whether bison and cattle grazing at a similar range of intensities have similar effects on plant communities, I monitored several response variables in 100, 0.1-hectare study plots clustered in grazed and ungrazed landscapes (n = 17) in Grasslands National Park, Saskatchewan, Canada, in June—July of 2010 and 2011. Using the relative density of fecal pats observed within each ~80 hectare landscape as a proxy for grazing intensity, I modeled the effects of grazing intensity, year, species of grazer, and interactions between these on plant community response variables using generalized linear mixed-effects models, and I quantified the spatial effects of grazing using semivariance analyses and Moran's I. In 2010, I established two experimental transects of mowed and unmowed plots (n = 40) and monitored responses in 2011 to evaluate whether the effects of grazing differed from those of nonselective defoliation. I found cattle and bison had similar but not identical effects on vegetation structure and composition after four and six years of grazing, respectively. Floristic diversity increased and evenness decreased significantly with both grazing and mowing, implying that competitive release may be important for driving plant community changes in this system. Spatial patterns of grazing were similar for bison and cattle, although bison created more discrete patches at the highest intensities of grazing. My results suggest that despite some differences in their selective preferences, the two species may have similar ecological effects.

Key words. *Bison bison*, *Bos taurus*, conservation grazing, floristic diversity, grazing intensity, keystone species, spatial heterogeneity

3.2 INTRODUCTION

North American grasslands are among the world's most threatened ecosystems, both because of their historic conversion to other land uses, and because of ongoing threats to their ecological integrity (Noss 1995, Hoekstra et al. 2005). Consequently, there is an increasingly high imperative to conserve remaining grasslands and the species they support (Samson et al. 2004). Since central North American grasslands evolved under the influence of Plains bison (*Bison bison*; Anderson 2006), grazing by large herbivores may be a critical process by which biodiversity is maintained in these ecosystems (Grumbine 1994, Fuhlendorf and Engle 2001). However, domestic cattle (*Bos taurus*) have replaced bison as the dominant grazers in North America (Holecheck et al. 2010), and some authors have suggested that, because they play a different ecological role than bison, cattle cannot be used to comprehensively restore biodiversity in the continent's grassland ecosystems (e.g., Freese et al. 2007). However, claims about ecological differences between bison and cattle have mostly not been proven, because most grazing studies have used small pastures, in isolation from the inherent variability herbivores encounter in natural ecosystems (Allred et al. 2011). Since plant community heterogeneity can influence the diversity and population dynamics of native biota, as well as other ecosystem dynamics (Hooper and Vitousek 1997, Wiens 1997, Fuhlendorf and Engle 2001), more information on the mechanisms driving changes in extensively grazed plant communities will help to clarify how grazing by either bison or cattle might be used to optimize conservation outcomes in central North American grasslands.

Evolutionary history is an important factor in explaining responses of grasslands to grazing (Milchunas et al. 1988, Cingolani et al. 2005). In ecosystems with long histories of grazing, plant species often possess traits that facilitate regrowth following defoliation (Coughenour 1985). Species with these traits that would otherwise be co-dominant or subordinate within a given plant community often increase in abundance following grazing, resulting in a more diverse plant community (Milchunas et al. 1988). Grazing disturbance can also create opportunities for the enhanced recruitment of the species-rich forb component into plant communities, and thus to increased floristic diversity (Anderson and Briske 1995, Bakker and Olff 2003, Towne et al. 2005). However, the mechanisms behind increases in diversity in grazed plant communities, and the potential influence of factors such as species of grazer, are still not entirely clear.

In some instances, the consumption of biomass by grazers results in a formerly limiting resource becoming available, leading to a temporary relaxation of competitive interactions, allowing a wide variety of species to flourish (Milchunas et al. 1988, Collins et al. 1998). If grazing by both bison and cattle results in competitive release, then grazing by both species could create the conditions necessary for subordinate species to regrow rapidly and increase in abundance. Competitive release has been shown to be a primary mechanism regulating plant community changes following defoliation in tall-grass prairie, with both grazing and mowing of plant communities inducing an increase in diversity (Collins et al. 1998). However, the importance of this mechanism in northern mixed prairie ecosystems is not well understood.

Herbivore selectivity can also play an important role in determining plant community changes (Augustine and McNaughton 1998); when the fitness or abundance of preferred plant species decline as these species are grazed, less palatable, subordinate species may increase in abundance (Anderson and Briske 1995, Hartnett at al. 1996). Although bison and cattle both primarily select to consume graminoid species, bison exhibit a stronger preference for C_4 graminoids (Plumb and Dodd 1993) and avoid forbs almost entirely, thereby allowing this species-rich component to flourish (Knapp et al. 1999). If selective defoliation of preferred species plays an important role in determining plant community changes in response to grazing, then differences in selectivity between bison and cattle may result in the two herbivores having different impacts on biodiversity, and on other ecosystem processes (Plumb and Dodd 1993).

Finally, when grazers interact with natural variability they produce a pattern of disturbance that is variable in space and time (Bailey et al. 1996). Since the impacts of both foraging and non-foraging behaviours are spatially heterogeneous, more niches may be present within grazed landscapes, allowing for the co-existence of more plant species, and resulting in higher levels of species diversity (Adler et al. 2001, Fuhlendorf and Engle 2001, Bakker and Olff 2003, Fuhlendorf et al. 2006). The spatial pattern of landscape use by a given species of grazer is dependent on the expression of a hierarchy of selective behaviours (Bailey et al. 1996), which are in turn influenced by the morphology, social behaviour, physiology, and environmental tolerance of the herbivore in question (Damhoureyeh and Hartnett 1997, Launchbaugh and Howery 2005, Smith et al. 2010). Differences in these factors between bison and cattle may cause the two species to make divergent decisions at several spatial and temporal scales, resulting in the two species having distinct patterns of disturbance throughout landscapes. Non-foraging behaviours, including wallowing and the deposition of dung and urine, may also generate spatial patterns in soil and vegetation characteristics (Augustine and Frank 2001, McMillan et al. 2011). In turn, these small-scale disturbances may create the conditions required for subordinate and/or transient plant species to enter the plant community (Trager et al. 2004). Since bison and cattle differ in their expression of these behaviours, spatial patterns of heterogeneity generated by each species of grazer may differ even further. However, the ecological implications of bison and cattle expressing their foraging and non-foraging behaviours at multiple scales have not been documented, because most comparative experiments have been conducted in small pastures (e.g., less than 50 hectares; Plumb and Dodd 1993, Towne et al. 2005), thereby eliminating the complexity and variation inherent to large natural landscapes (Fuhlendorf et al. 2010).

The presence of both bison and cattle grazing within large pastures in different parts of Grasslands National Park (GNP), located in southern Saskatchewan, Canada, provided a unique opportunity to examine the ecology of northern mixed prairie as influenced by its native herbivore compared to domestic grazing animals. I compared effects of cattle and bison grazing on floristic diversity, plant community composition, and vegetation structure and patchiness. To determine whether the changes in floristic diversity that I observed were the result of a competitive release following defoliation, I used experimental mowing treatments to simulate nonselective grazing, and compared responses with those observed under selective grazing by each species of grazer. To clarify whether differences in the selective preferences of bison and cattle resulted in different plant community responses, I also examined the proportion of individual plant species, and groups of species in plant communities that were grazed by each herbivore. Finally, I assessed the importance of spatial heterogeneity for driving plant community changes using spatially explicit analyses to examine whether the average size and discreteness of patches with relatively uniform vegetation structure differed under bison and cattle.

3.3 METHODS

3.3.1 Study area

This study was conducted in Grasslands National Park (GNP), located in southern Saskatchewan, Canada (49°15’ N, 107°00’ W; Fig. 1). The area’s climate is classified as a cool, semi-arid type (Singh et al. 1983). Over the long-term, monthly average temperatures ranged from -12.4° C in January to 18.3° C in July, and the area received an average of 348 mm of annual total precipitation (Environment Canada 2011*a*). On average, approximately 70% of annual precipitation is received as summer rainfall (between April and September; Environment Canada 2011*a*). The majority of this precipitation is typically received during the spring, followed by a late summer drought (Coupland 1950). During the study period, summer rainfall in the area was higher than the long-term average (14% and 22% above average in 2010 and 2011, respectively; Environment Canada 2011*b*).

The topography in GNP is rough to rolling, supporting a wide range of landscapes with variable drainage conditions, soil types, and plant communities characteristic of northern mixed prairie (Coupland 1950). Within the study area, vegetation was composed of a mixture of mid-height cool-season grasses, warm-season shortgrasses, forbs, and shrubs. Common grasses included northern and western wheatgrass (*Elymus lanceolatus*

[Scribn. & J. G. Sm.] Gould, *Pascopyrum smithii* [Rydb.] Barkworth & D. R. Dewey), needle-and-thread and western porcupine grass (both needlegrasses; *Hesperostipa* spp. [Elias] Barkworth), June grass (*Koeleria macrantha* Schult.), and blue grama (*Bouteloua gracilis* [Kunth] Lag. ex Griffiths). Dominant forbs included moss phlox (*Phlox hoodii* Richardson), pasture sage (*Artemisia frigida* Willd.), scarlet mallow (*Sphaeralcea coccinea* [Nutt.] Rydb.), and milk vetches (*Astragalus spp.* L.). Silver sage (*Artemisia cana* Pursh.) and winterfat (*Krascheninnikovia lanata* [Pursh] A. Meeuse & A. Smit) were the most common shrubs. Cacti, lichens, and lesser spikemoss (*Selaginella densa* Rydb.) made up a significant part of the plant community in drier locations. Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.), an exotic invasive, was present in some plots; however, I avoided selecting study sites in areas dominated by this species, as these areas often represented former cropland or otherwise highly disturbed communities that were substantially different in structure and composition than surrounding native plant communities.

3.3.2 Study design

The East Block of GNP contained six cattle pastures (~300 hectares [ha] each) that were seasonally grazed by Angus and Hereford yearling steers from 2008 to 2011, and three adjacent pastures that served as ungrazed controls (*n* = 9; Fig. 1). Livestock had not grazed these areas for approximately 15 years prior to the re-introduction of cattle in 2008 (Koper et al. 2008). Each cattle pasture contained a natural water source, and at least the following three major vegetation types: riparian shrublands, valley grasslands, and upland grasslands (Michalsky and Ellis 1994). Pastures were oriented to include similar proportions of each of these vegetation types (Koper et al. 2008), but only upland grassland areas were monitored in this study. Cattle were supplied with salt, minerals, and two anthropogenic water sources per pasture (one of which was located in upland grasslands), and were present from mid-May through mid-September. Stocking rates of grazed pastures were approximately 0.25, 0.40, 0.60, 0.74, 0.83, and 0.90 Animal Unit Months per hectare (AUM · ha^{-1}) in both years of this study.

Since 2006, a semi-wild herd of bison has grazed within one large pasture (~18,000 ha) in the West Block of GNP (Fig. 1). Bison remain in their pasture year-round, and have access to one anthropogenic and several natural water sources, but receive no other supplements. By 2011, the herd had grown from an initial group of 73 individuals to include ~250 animals, of which 53% were female. The stocking rate in the bison pasture was estimated as 0.10 AUM · ha^{-1} in 2010 and 0.13 AUM · ha^{-1} in 2011, based on herd demographics and body mass data collected in Elk Island National Park, where the GNP bison herd originated (A. Handel, unpublished data).

In each cattle pasture, Koper et al. (2008) established six study plots in upland grassland areas, each plot at a minimum distance of 250 meters [m] from the next (n = 54). Each study plot consisted of a 1000-m^2 Modified Whittaker plot with ten nested 0.5-m^2 quadrats (Appendix A; Stohlgren et al. 1995). I established similar groupings of four to six study plots in upland grassland areas throughout the bison pasture, each plot at a minimum distance of 250 m from the next (n = 46). These study plots were clustered within eight regions that had been subject to varying degrees of grazing pressure in years preceding this study, ranging from areas that were unused to heavily used by bison (W. Olson, Parks Canada, personal communication, May 2010). Throughout, I refer to each area dominated by upland grassland vegetation within which groups of study plots were clustered as a ‘landscape’. Within cattle pastures, these landscapes encompassed an average of 96 ha (SD = 17; Appendix B) and were separated by fences, while landscapes within the bison pasture encompassed an average of 61 ha (SD = 18; Appendix C), and were separated by distance (each being located a minimum of 1.4 kilometres [km] from the next landscape).

I conducted surveys of vegetation structure and composition between mid-June and mid-July of 2010 and 2011, with all study plots per landscape being sampled within two successive days.

Mowed plots. In 2010, I established one 40-m experimental transect in ungrazed areas in each of the East and West Blocks of GNP. Along these transects, I mechanically mowed 10, 2-m × 2-m plots to a height of ~5 centimetres [cm], removing clipped vegetation and some of the existing plant litter, and I left 10 alternating 2-m × 2-m plots unmowed. I repeated the mowing treatment once every two weeks from May through July 2010.

In 2011, I surveyed plant community composition in mowed and unmowed plots (n = 40), using a 0.5-m^2 quadrat placed in the centre of each. I sampled all plots per transect within a single day.

Spatially explicit sampling. In 2011, I sampled vegetation structure in 14 additional 0.5-m^2 quadrats, arranged in and around each Modified Whittaker plot. The new quadrats were arranged at distances ranging from 1 m to ~100 m from the existing quadrats, to allow for the examination of autocorrelation of vegetation structure between paired plots at increasing distance classes (Appendices G and H).

Vegetation surveys. I sampled vegetation structure in all of the quadrats that were located in and around each study plot. I estimated residual biomass using a Robel pole by determining the height of complete and partial visual obstruction by vegetation in each cardinal direction, and averaging these values to determine 100% and 50% vegetation height-density, respectively (Robel et al. 1970, Vermeire et al. 2002). I also used a Robel pole to estimate the height of the tallest plant within each quadrat, and a metre stick to measure the actual height of the tallest plant rooted within each quadrat, providing me with two measures of vegetation height per quadrat. I measured canopy height within each quadrat using a metre stick and a piece of Styrofoam™ (20 × 50 × 2.5 cm) resting on top of the plant canopy, and litter depth at the centre of each quadrat using a metre stick. I estimated percent cover of litter, bare ground, and lesser spikemoss using the foliar cover class method (Daubenmire 1959).

I identified all vascular plant species present within each study plot via a walk-through survey, wherein I walked east-west transects ≤ 1 m in width, progressing systematically from the north end of the plot to the south, until the entire plot had been surveyed. In the ten original quadrats nested within each study plot, and at quadrats nested within experimental transects, I visually estimated relative abundances of each plant species using a foliar coverage class method (Daubenmire 1959).

Fecal pat counts. I counted all fecal pats present within each study plot via a walk-through survey. I calculated the average number of fecal pats observed at plots within a given landscape, or ‘pats · landscape^{-1}’, adjusted values of this variable to range from zero to one based on the minimum and maximum fecal pat densities observed (Legendre and Legendre 1998), and used the adjusted values as a proxy for grazing intensity to model plant community responses (see Chapter 2).

3.3.3 Statistical analyses

Floristic diversity is one element of plant community heterogeneity, and is itself a function of species richness (S; the number of species in a given area) and evenness (E; the relative abundance of each species). When examining changes in species richness itself, I calculated S as the total number of species identified in each study plot during the walk-through survey, as this most accurately represented the number of species present per 1000 m^2. For calculating floristic diversity, however, I considered S to be equal to the total number of species identified in quadrats within each study plot, because relative cover of each species was not available from the walk-through survey. For each study plot, I calculated E using Simpson's measure of evenness [$E_{1/D} = (1/D)/S$], and I derived two measures of floristic diversity: the Shannon-Wiener index ($H' = -\sum[p_i][\log_2 p_i]$), and Simpson's index ($D = \sum[p_i]^2$). These two indices were chosen because they differ in their sensitivity to rare species (Peet 1974). Both require an estimate of the relative cover of each species in the plant community (p_i), which I determined by dividing the midpoint of the coverage class assigned to species i by the summed midpoints for all flowering plant species identified in each quadrat per study plot (i.e., omitting the cover of litter, bare ground, and *Selaginella densa*, a non-flowering plant). I scaled both indices to units of species using the Shannon-Wiener function ($2^{H'}$), and Simpson's reciprocal index ($1/D$), respectively, so values of each could be easily compared. For data collected from experimental transects, I calculated all of the aforementioned variables at the quadrat scale.

Another element of plant community heterogeneity is variability in the type of species that are present. I classified all plant species that were identified during vegetation surveys based on their lifeform (shrub, forb, or graminoid) and photosynthetic pathway (C_3 or C_4; as per Wang et al. 2006). I derived the total proportion of forbs and C3 and C4 graminoids in the plant community based on the sum of the relative cover of each species per group ($\sum p_i$). I also calculated the proportion of the plant community comprised of shrubs, but this was always negligible, and thus was not included in subsequent analyses.

Grazing intensity effects. I used generalized linear mixed-effects models (GLMMs) to model relationships between relative grazing intensity (pats · landscape^{-1}), designated as a fixed effect, and each of the response variables I collected. I used PROC GENMOD in SAS statistical software (SAS Institute 2008) to identify the appropriate error distribution for each response variable, and found the negative binomial distribution to be the best-fitting distribution for all responses. Next, I used PROC GLIMMIX to determine results of GLMMs, with maximum likelihoods being estimated based on Laplace approximation (SAS Institute 2008). When modeling structural responses, I designated 'plot' as a random effect, to account for the spatial clustering of quadrats within study plots (Bell and Grunwald 2004). I also evaluated the importance of clustering of plots within landscapes; however, when 'landscape' was included as a random variable, the standard error associated with covariance parameter estimates encompassed zero in models of most responses, indicating that the parameter estimate for this random variable was not different from zero. Therefore, the influence of this variable was negligible, and I present analyses with 'plot' as the only random variable.

I used a hierarchical selection process to determine the best available model for each plant community response of interest, by comparing the parsimony of candidate models using Akaike's Information Criterion (AIC_c) values for small sample sizes (Burnham and Anderson 2002). In the first step of the model selection process, I compared the fit of the null model to that of a model that included year of observation as the sole fixed effect, since annual variation in climate can override the effects of grazing in northern mixed prairie ecosystems (Biondini et al. 1998). If the model including the term 'year' represented a substantial improvement over the null (i.e., $\Delta AIC_c > 2$; Burnham and Anderson 2002, Arnold 2010), I included this as a candidate model throughout the model selection process, and also included 'year' in all subsequent candidate models to control for effects of variation between the two years of the study.

In subsequent steps of the model selection process, I systematically evaluated whether models including different combinations of predictor variables represented a substantial improvement over the best model from the previous step, for each response. The process I followed for evaluating the relative importance of year, grazing intensity, species of grazer, and interactions between these predictor variables is illustrated in Appendix F. I first evaluated whether 'year' had substantial explanatory power. Second, I evaluated the importance of grazing intensity for modeling plant community responses. Since plant community changes in response to grazing could be non-linear (as per Milchunas et al. 1988), during this step I also evaluated the importance of the polynomial term 'pats · landscape^{-1}* pats · landscape^{-1}' for modeling changes in floristic diversity and plant community composition. In the next step, I evaluated the importance of species of grazer, and the interaction between 'grazer' and 'grazing intensity'. I subsequently checked for informative interactions between 'grazing intensity' and 'year', confirmed that my model selection process was not path-dependent by testing the best model from this step against simpler models (i.e., models that did not include ‘grazing intensity’ as a predictor variable), and selected the most parsimonious model of each response.

I selected the model with the highest Akaike weight (w_i) as the best model of each response variable, unless this model contained one additional predictor variable and had an AIC$_c$ value within two points of a simpler model (or contained two additional variables and was within four points, and so on). In this case, I did not consider the additional variable(s) to be informative (Arnold 2010), and selected the simplest model that had an AIC$_c$ value within the appropriate number of points of the model with the highest weight.

Mowing effects. I used a two-factor analysis of variance (ANOVA) to model differences in the elements of floristic diversity between mowed and unmowed plots in the East and West Blocks of GNP. I modeled my data using SAS statistical software (SAS Institute 2008), including ‘treatment’ and ‘block’ as main effects, and the interaction between these two factors in each model. First, I used PROC GLM to calculate residuals; I plotted these against predicted values using PROC GPLOT, and generated histograms using PROC UNIVARIATE, which confirmed that the assumptions of ANOVA were met. Next, I used PROC ANOVA to evaluate the effects of treatment, block, and the interaction of these terms on species richness, diversity, and plant community evenness, using an alpha value of 0.05.

Spatial effects of grazing. The third element of plant community heterogeneity that I evaluated was spatial patchiness. Previous studies indicate that grazing by both bison and cattle could create discrete patches less than 15 m in diameter (Knapp et al. 1999, WallisDeVries et al. 1999), and that small patches might be embedded within larger patches (e.g., > 25 m in diameter) generated by selection for and avoidance of certain plant communities by each herbivore (Knapp et al. 1999, Augustine and Frank 2001). To quantify spatial patterns over spatial scales within which these previous findings indicated that grazing-induced patchiness might occur, I conducted geostatistical analyses for observations of vegetation structure in paired quadrats that were a minimum of 1 m and a maximum of 50 m from one another. For these analyses, I classified grazing intensity as ‘none’, ‘low’, ‘medium’, or ‘high’ based on values of ‘pats · landscape^{-1}’ that ranged from zero to one. Zero values corresponded to no grazing (with two landscapes within the bison pasture, and three landscapes within control pastures falling within this class); values between 0.01 and 0.30 corresponded to low grazing (with four landscapes within the bison pasture, and two landscapes within cattle pastures falling within this class); values between 0.31 and 0.60 corresponded to medium grazing (with no landscapes within the bison pasture, and two landscapes within cattle pastures falling within this class); and, values between 0.61 and 1.00 corresponded to high grazing intensity (with two landscapes within the bison pasture, and two landscapes within cattle pastures falling within this class).

I conducted semivariance analyses using the geoR package in the statistical program R (Diggle and Ribeiro Jr. 2007) to examine patterns of spatial dependence in 100% and 50% vegetation height-density, canopy height, litter depth, and the percent cover of litter and bare ground. First, I evaluated whether my data met the assumptions of least squares estimation, and performed a square root transformation of all of the aforementioned response variables, so that they better met the assumption of normality as evidenced by diagnostic plots. I then constructed semivariograms of each response, by plotting semivariance (a measure of spatial dependence, or autocorrelation; Legendre and Fortin 1989) against physical separation between paired quadrats. I specified lag distances between 1 m and 50 m that increased in an exponential pattern to ensure that there were sufficient paired points in each distance class. There were never fewer than 40 paired observations in a given distance class; therefore, the rule of thumb for the number of observations suggested by Rossi et al. (1992) was satisfied. I fitted random, linear, exponential, and spherical models to semivariograms of each structural response, and selected the model that minimized the sum of squares based on least squares estimation (Augustine and Frank 2001). I derived key parameters from the best model for each response variable, including the average size of patches within which the response of interest was relatively homogeneous (indicated by ‘range’, or the lag distance at which the asymptote of the fitted curve is reached), and the magnitude of spatial dependence [MSD]. As values of MSD approach 1.0, a greater proportion of the sample variance is spatially structured over the distance examined (Robertson and Gross 1994); that is, more of the variation in the response variable may be predicted by the geographical separation between data points.

I also calculated Moran’s *I*, a quantitative measure of spatial autocorrelation (Legendre and Fortin 1989) for 100% vegetation height-density using the ape package in the statistical program R (Paradis et al. 2004). Values of Moran’s *I* range from -1.0 to 1.0, indicating complete dissimilarity and complete correlation between paired observations, respectively. Zero values indicate that distance does not explain any variation in the data at the scale examined (Legendre and Fortin 1989). I assessed the significance of autocorrelation at lag distances from 1 m to 50 m using an alpha value of 0.05. I constructed correlograms for 100% vegetation height-density that plot Moran's *I* against lag distance, and used these to evaluate changes in spatial patterning of residual biomass in landscapes grazed at varying intensities by bison and by cattle. These analyses complemented the semivariance analyses described above, because while semivariance analysis tends to identify only the coarsest spatial patterns that are evident over the geographic range that is examined (in this case, over 50 m; Meisel and Turner 1998), Moran's *I* indicates whether there was significant autocorrelation in residual biomass at each individual lag distance. Therefore, if small grazed patches in GNP were embedded within larger patches with relatively homogeneous vegetation structure as other authors have observed (e.g., Knapp et al. 1999, Augustine and Frank 2001), then I could detect patches at both spatial scales by using both of these geostatistical techniques.

3.4 RESULTS

3.4.1 Effects of grazing and mowing on floristic diversity

Species richness within study plots varied based on year of observation, and whether plots were located in the West or East Blocks of Grasslands National Park, which were grazed by bison and cattle, respectively (Table 4). In 2010, I identified 149 plant species in the West Block, with an average of 48 of those species being present in each 1000-m^2 study plot. In the same block in the subsequent year, I identified a total of 153 species, with 55 species being observed in each plot, on average. I identified more species in the East Block in both years – 173 species in 2010, and 165 species in 2011 – of which an average of 46 and 50 species were present in a given study plot in each year, respectively. Overall, species richness was higher in 2011, and was not substantially influenced by grazing intensity (Fig. 6).

When the relative cover of plant species was taken into account, higher levels of grazing intensity were associated with higher diversity and lower plant community evenness (Fig. 6). Of the two measures of floristic diversity, values of the Shannon-Wiener function were higher than values of Simpson's reciprocal index, but the positive effect of grazing intensity and the effect of year were slightly greater on the latter measure (Table 4). Like species richness, diversity was higher in 2011 than in 2010 (Fig. 6), but plant community evenness was unaffected by year of observation (Appendix I). None of these responses differed substantially based on species of grazer, and models were not improved by the inclusion of a polynomial term (Appendix I), so diversity increased linearly as grazing intensity of both bison and cattle increased. While the difference was not substantial, diversity did not respond as strongly to grazing intensity in areas grazed by bison in 2011 compared with areas grazed by cattle (Fig. 6).

Table 4. Estimates, standard errors (β ± SE), and 90% confidence intervals for predictor variables included in the selected best models of the elements comprising floristic diversity within 1000-m^2 plots located in ungrazed landscapes, and in landscapes grazed by bison and cattle at a range of intensities in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Pats·landscape^{-1} (i.e., the relative density of fecal pats per ~80 ha landscape, adjusted to range from 0-1) serves as a proxy for grazing intensity. Details of the model selection process that yielded these best models may be found in Appendix I.

Response	Variable(s) in best model	β ± SE	(90% CI)
Richness	Year	-0.11 ± 0.02	(-0.15, -0.07)
	Grazer	0.06 ± 0.04	(0.00, 0.12)
Shannon-Wiener function	Pats·landscape^{-1}	0.16 ± 0.07	(0.05, 0.27)
	Year	-0.14 ± 0.02	(-0.17, -0.10)
Simpson's reciprocal index	Pats·landscape^{-1}	0.20 ± 0.08	(0.07, 0.33)
	Year	-0.16 ± 0.02	(-0.21, -0.12)
Simpson's measure of evenness	Pats·landscape^{-1}	-0.16 ± 0.07	(-0.27, -0.05)

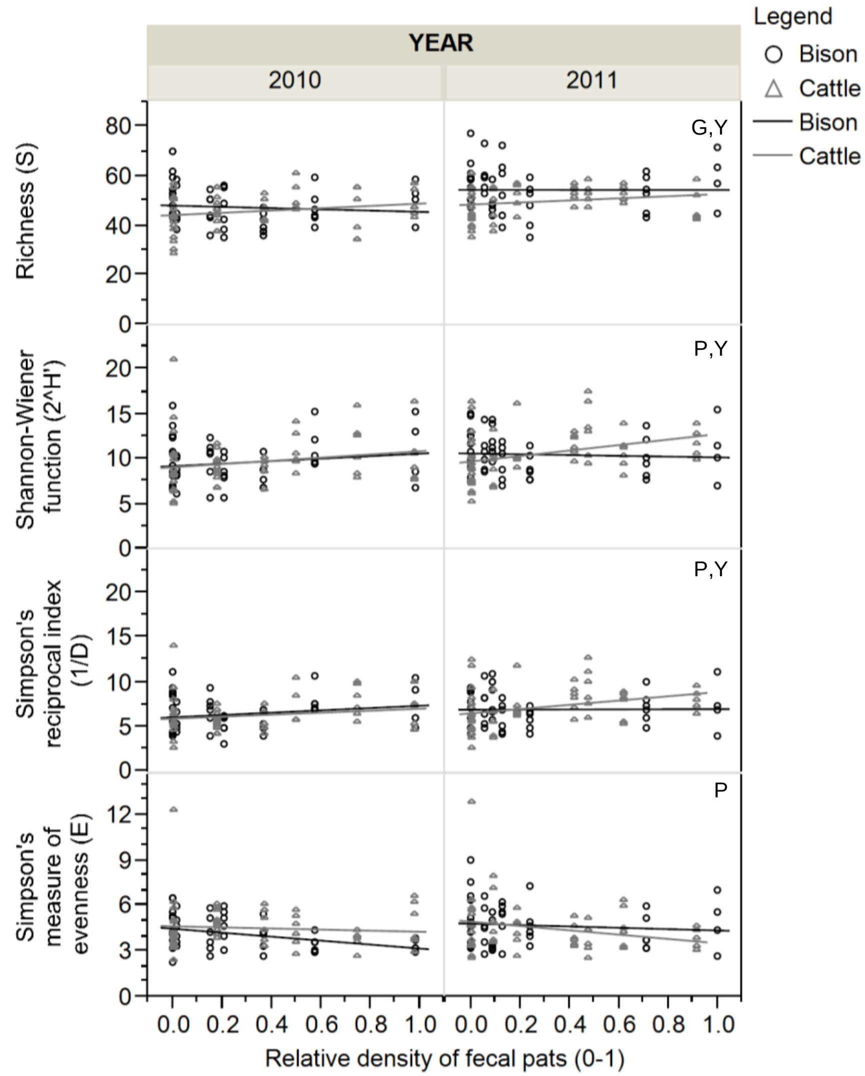

Figure 6. Change in the elements comprising floristic diversity within 1000-m^2 plots as a function of grazing intensity (i.e., relative density of fecal pats per ~80 ha landscape, adjusted to range from 0-1), year of observation, and species of grazer, in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Important predictors of each response are denoted by letters: G = species of grazer; P = pats·landscape^{-1} (i.e., grazing intensity); Y = year of observation. Bold letters denote interactions between predictor variables. Estimated effect sizes for predictors of each response are listed in Table 4.

Mowing effects. Species richness in experimentally mowed transects was not significantly affected by treatment ($F_{1,36} = 1.18$, $p = 0.2844$), block, or the interaction of the two terms; individual quadrats contained an average of 12 species, regardless of whether they were mowed or unmowed (Table 5). However, when the relative cover of each species was accounted for, the resulting measures of floristic diversity did differ between mowed and unmowed plots (Table 5). Mowing had a significant positive effect on the Shannon-Wiener function ($F_{1,36} = 9.92$, $p = 0.0033$), and on Simpson's reciprocal index ($F_{1,36} = 9.35$, $p = 0.0042$), and had a significant negative effect on plant community evenness ($F_{1,36} = 6.17$, $p = 0.0178$).

Table 5. Mean and standard deviation (SD) of plant community response variables within 0.5-m^2 quadrats in plots that were unmowed, or mowed periodically throughout June-August 2010, in the East and West blocks of Grasslands National Park, Saskatchewan, Canada, June of 2011.

Response	Block	Treatment			
		Unmowed		Mowed	
		Mean	SD	Mean	SD
Richness (S)	East	12.80	2.30	12.70	2.36
	West	11.30	1.95	12.80	1.40
Shannon-Wiener function ($2^{H'}$)	East	5.07	1.58	6.60	1.82
	West	4.73	1.56	6.52	1.69
Simpson's reciprocal index (1/D)	East	3.67	1.50	4.98	1.63
	West	3.44	1.24	5.09	1.71
Simpson's measure of evenness ($E_{1/D}$)	East	3.93	1.33	2.71	0.64
	West	3.66	1.28	2.94	1.49

3.4.1 Effects of grazing on plant community composition

The proportion of forbs in the plant community increased from the first to the second year of this study (Table 6), comprising 19 percent of the plant community in 2010, and 23 percent in 2011. Despite an apparently positive relationship between grazing intensity and the prevalence of forb species, especially in areas grazed by bison (Fig. 7), neither grazing intensity nor species of grazer were found to contribute substantially more information than ‘year’ for modeling this response (Appendix I). Species of grazer did contribute additional information about the proportion of pasture sage in the plant community (Table 6), with more of this plant species being observed in the West Block of GNP (i.e., within the bison pasture; Fig. 8).

The proportion of C_3 graminoids in the plant community declined with grazing intensity of both bison and cattle (Table 6; Fig. 7). This response was mostly driven by a decline in the abundance of needlegrasses at higher intensities of grazing (Fig. 8), as wheatgrasses and plains reed grass (*Calamagrostis montanensis* [Scribn.] Vasey) were not affected by grazing intensity (Table 6). The response of June grass to grazing intensity was non-linear, and varied by species of grazer (Table 6), increasing initially, but declining under the highest intensities of cattle grazing (Fig. 8). Needleleaf sedge (*Carex duriuscula* C. A. Mey.) was also best described by both polynomial and interaction terms (Table 6), but in this case, the abundance of sedge initially declined under bison grazing, and increased under the highest intensities of grazing by both species of grazer (Fig. 8). Nothing improved on the null model for describing the proportion of western wheatgrass in the plant community (Appendix J).

Table 6. Estimates, standard errors (β ± SE), and 90% confidence intervals for predictor variables included in the selected best models of plant community composition within 1000-m2 plots located in ungrazed landscapes, and in landscapes grazed by bison and cattle at a range of intensities in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Pats·landscape-1 (i.e., the relative density of fecal pats per ~80 ha landscape, adjusted to range from 0-1) serves as a proxy for grazing intensity. Details of the model selection process that yielded these best models are in Appendices I and J.

Response	Variable(s) in best model[1]	β ± SE (90% CI)
% Forbs	Year	-0.18 ± 0.03 (-0.23, -0.13)
% *Artemisia frigida*	Year	-0.37 ± 0.08 (-0.51, -0.23)
	Grazer	0.45 ± 0.15 (0.20, 0.69)
% C_3 graminoids	Pats·landscape^{-1}	-0.11 ± 0.05 (-0.19, -0.02)
% *Calamagrostis montanensis*	Year	-0.75 ± 0.09 (-0.89, -0.61)
% *Carex diurscula*	Pats·landscape^{-1}	-0.13 ± 0.61 (-1.14, 0.87)
	P*P	1.19 ± 0.60 (0.19, 2.19)
	Year	1.14 ± 0.10 (0.97, 1.31)
	Grazer	0.70 ± 0.16 (0.44, 0.96)
	Pats·landscape^{-1}*grazer	-1.06 ± 0.34 (-1.63, -0.49)
% *Elymus lanceolatus*	Null	-
% *Hesperostipa spp.*	Pats·landscape^{-1}	-0.54 ± 0.20 (-0.87, -0.22)
	Year	0.57 ± 0.05 (0.50, 0.65)
% *Koeleria macrantha*	Pats·landscape^{-1}	0.57 ± 0.53 (-0.30, 1.45)
	P*P	-1.26 ± 0.53 (-2.15, -0.38)
	Year	-0.64 ± 0.08 (-0.78, -0.50)
	Pats·landscape^{-1}*year	0.47 ± 0.19 (0.16, 0.78)
	Grazer	-0.63 ± 0.15 (-0.87, -0.38)
	Pats·landscape^{-1}*grazer	1.38 ± 0.34 (0.81, 1.95)
% *Pascopyrum smithii*	Null	-
% C_4 graminoids	Pats·landscape^{-1}	-0.88 ± 0.72 (-2.07, 0.32)
	P*P	1.87 ± 0.67 (0.75, 2.99)
	Year	0.15 ± 0.07 (0.03, 0.27)
	Grazer	0.37 ± 0.20 (0.04, 0.70)
	Pats·landscape^{-1}*grazer	-1.67 ± 0.45 (-2.43, -0.92)
% *Bouteloua gracilis*	Pats·landscape^{-1}	-0.75 ± 0.70 (-1.91, 0.42)
	P*P	1.84 ± 0.70 (0.69, 3.00)
	Grazer	0.60 ± 0.18 (0.30, 0.89)
	Pats·landscape^{-1}*grazer	-1.87 ± 0.42 (-2.56, -1.18)

[1] "P*P" denotes the polynomial term "pats·landscape-1*pats·landscape-1"

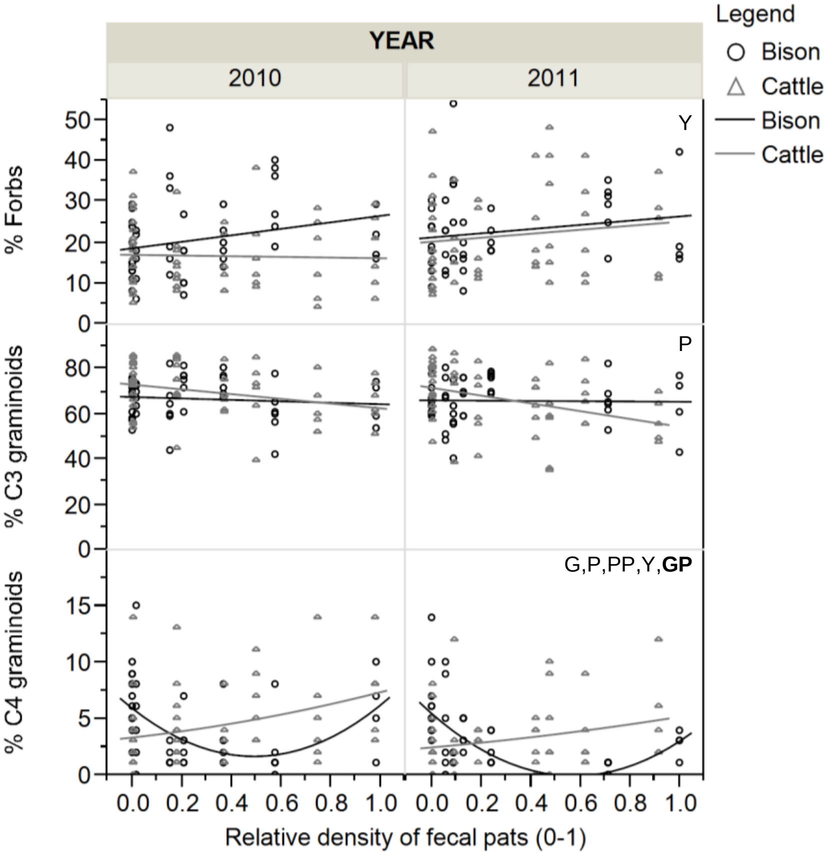

Figure 7. Change in the proportion of forbs, C3 graminoids, and C4 graminoids in the plant community within 1000-m^2 plots as a function of grazing intensity (i.e., relative density of fecal pats per ~80 ha landscape, adjusted to range from 0-1), year of observation, and species of grazer, in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Important predictor variables are denoted by letters: G = species of grazer; P = pats·landscape^{-1} (i.e., grazing intensity); Y = year of observation. Bold letters denote interactions between these predictor variables. Estimated effect sizes for predictors of each response are listed in Table 6.

The effect of grazing on the proportion of C_4 graminoids in the plant community differed based on species of grazer, as did the effect of grazing on blue grama (the most prevalent C_4 species in the plant community; Table 6).While the proportions of both blue grama and C_4 species in general increased with increasing grazing intensities of cattle, these species initially declined under low intensities of bison grazing, and increased at the highest intensities in a non-linear fashion (Fig. 8). The proportion of C_4 graminoids in the plant community also decreased from 2010 to 2011 (Table 6).

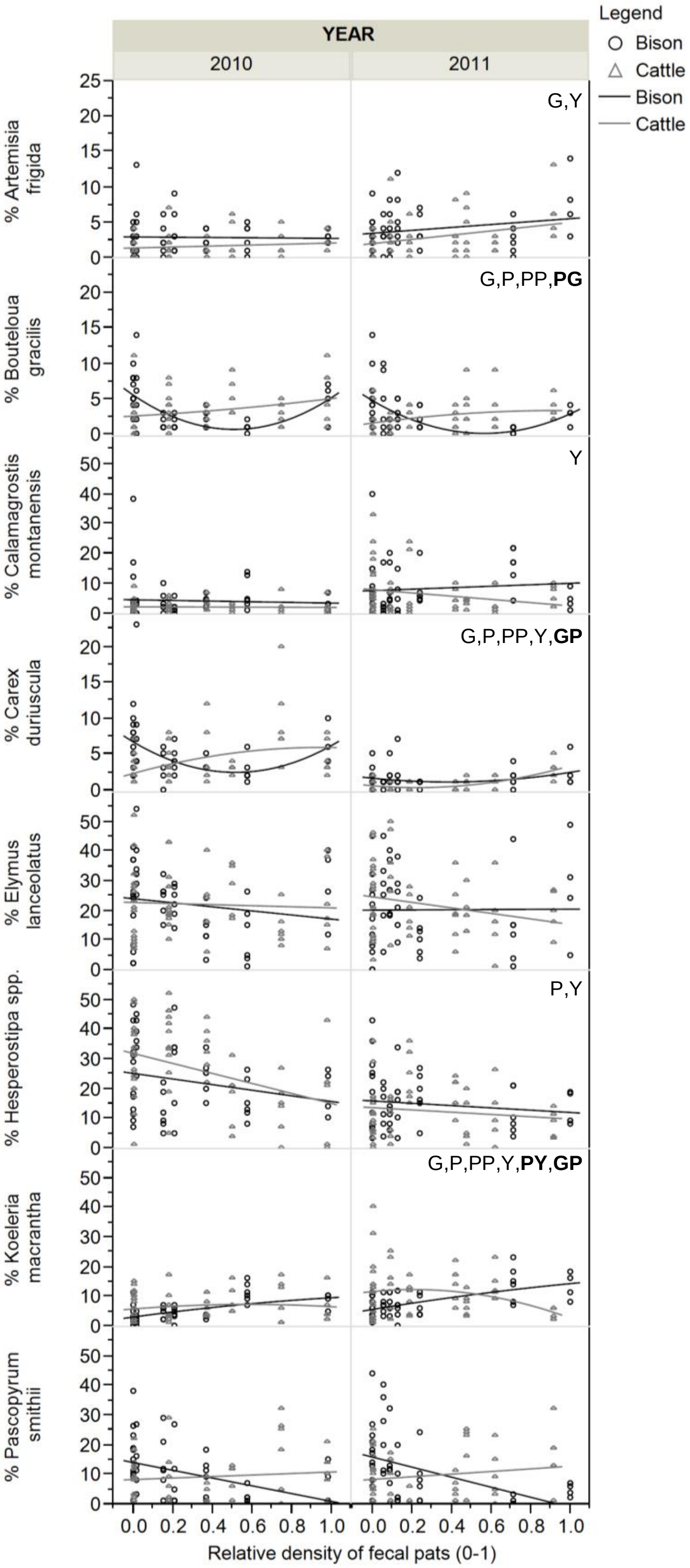

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Figure 8. Change in the proportions of individual species in the plant community within 1000-m^2 plots as a function of grazing intensity (i.e., relative density of fecal pats per ~80 ha landscape, adjusted to range from 0-1), year of observation, and species of grazer, in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Important predictor variables are denoted by letters: G = species of grazer; P = pats·landscape^{-1} (i.e., grazing intensity); Y = year of observation. Bold letters denote interactions between these predictor variables. Estimated effect sizes for predictors of each response are listed in Table 6.

3.4.1 Effects of grazing on vegetation structure and patchiness

Grazing intensity explained a substantial amount of the variation associated with vegetation structure (Appendix K). Residual biomass (i.e., 100% and 50% vegetation height density), vegetation height (measured with Robel pole and metre stick), canopy height, and litter depth all declined as grazing intensity increased (Table 7; Fig. 9), as did litter cover, while the cover of bare ground and lesser spikemoss increased (Fig 10). Lesser spikemoss is a lycophyte (i.e., a non-flowering plant) that nonetheless was an important part of the plant community, covering an average of 28 percent of each quadrat, and approximately 49 percent of each quadrat in the most highly grazed landscape. Year of observation also had an important effect on most structural response variables, except on the cover of bare ground and lesser spikemoss (Appendix K), with residual biomass, maximum vegetation height, canopy height and litter depth all being greater in 2011 than in 2010 (Table 7).

The relationship between grazing intensity and the height of the tallest plant measured within each quadrat using a metre stick differed based on species of grazer (Table 7), with bison having a greater negative effect on vegetation height (Fig. 9). The effect of grazing on bare ground cover also varied with species of grazer (Table 7), with bare ground increasing more under cattle than under bison grazing (Fig. 10).

Table 7. Estimates, standard errors (β ± SE), and 90% confidence intervals for predictors of vegetation structure within 0.5-m^2 quadrats located in ungrazed landscapes, and in landscapes grazed by bison and cattle at a range of intensities in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Pats·landscape^{-1} (i.e., the relative density of fecal pats per ~80 ha landscape, adjusted to range from 0-1) serves as a proxy for grazing intensity. Details of the model selection process that yielded these best models may be found in Appendix K.

Response	Variable(s) in best model	β ± SE	(90% CI)
100% Vegetation height-density	Pats·landscape^{-1}	-1.19 ± 0.21	(-1.54, -0.84)
	Year	-0.75 ± 0.04	(-0.81, -0.68)
50% Vegetation height-density	Pats·landscape^{-1}	-0.56 ± 0.11	(-0.75, -0.38)
	Year	-0.24 ± 0.02	(-0.27, -0.21)
Tallest plant (Robel pole)	Pats·landscape^{-1}	-0.14 ± 0.04	(-0.21, -0.06)
	Year	-0.29 ± 0.01	(-0.31, -0.27)
Tallest plant (metre stick)	Pats·landscape^{-1}	0.02 ± 0.22	(-0.33, 0.38)
	Year	-0.17 ± 0.02	(-0.20, -0.14)
	Grazer	0.10 ± 0.00	(-Infty, infty)
	Pats·landscape^{-1}*grazer	-0.27 ± 0.14	(-0.50, -0.04)
Canopy height	Pats·landscape^{-1}	-0.16 ± 0.06	(-0.26, -0.06)
	Year	-0.22 ± 0.01	(-0.24, -0.20)
Litter depth	Pats·landscape^{-1}	-1.02 ± 0.12	(-1.21, -0.82)
	Year	-0.24 ± 0.04	(-0.31, -0.18)
Litter cover	Pats·landscape^{-1}	-0.80 ± 0.15	(-1.04, -0.55)
	Year	0.29 ± 0.03	(0.24, 0.34)
Bare ground cover	Pats·landscape^{-1}	3.48 ± 0.46	(2.73, 4.23)
	Grazer	0.12 ± 0.29	(-0.37, 0.61)
	Pats·landscape^{-1}*grazer	-1.80 ± 0.68	(-2.92, -0.67)
Selaginella densa cover	Pats·landscape^{-1}	0.50 ± 0.18	(0.21, 0.79)

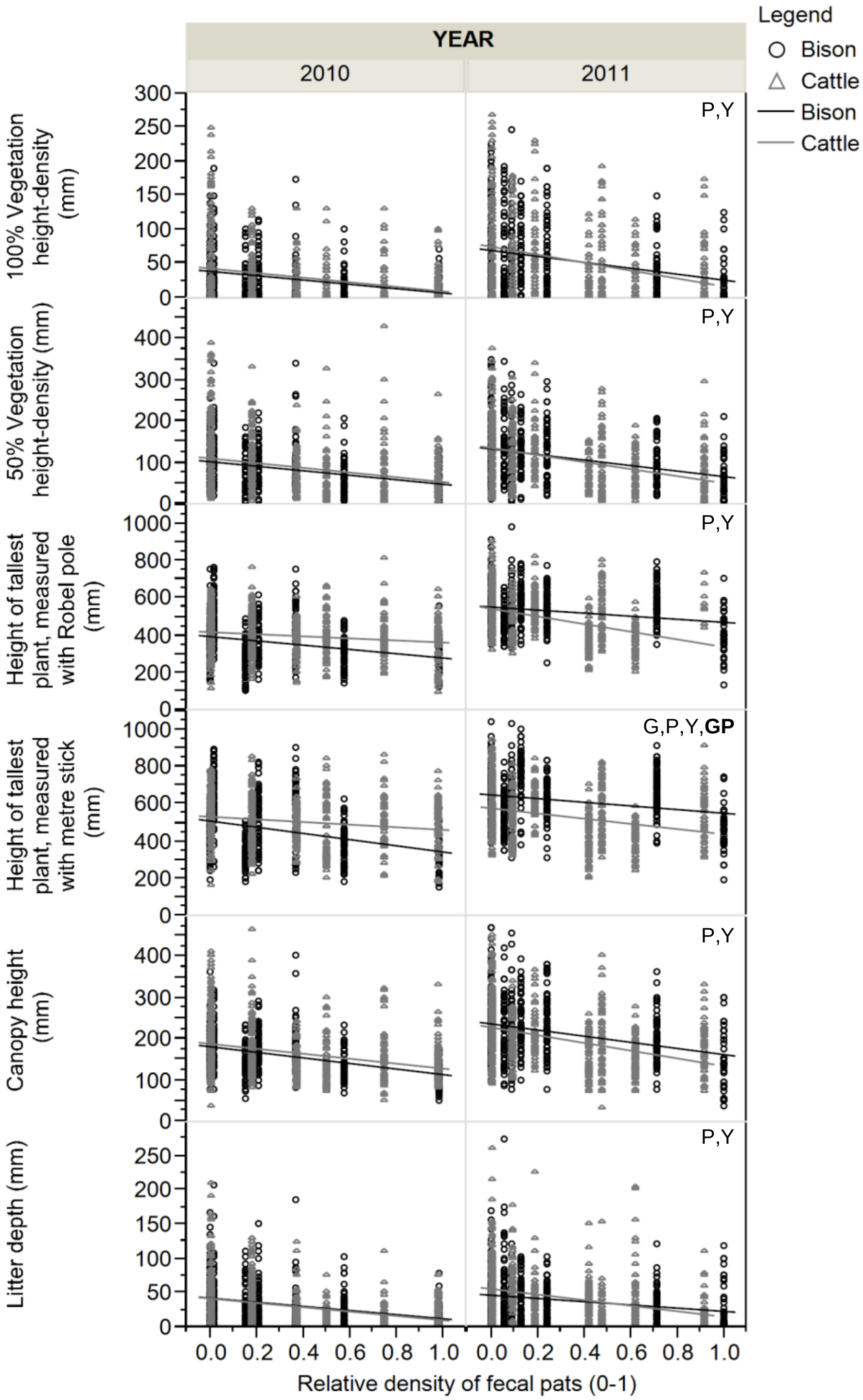

Figure 9. Change in vegetation structure within 0.5-m^2 quadrats as a function of grazing intensity (i.e., relative density of fecal pats per ~80 ha landscape, adjusted to range from 0-1), year of observation, and species of grazer, in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Important predictor variables are denoted by letters: G = species of grazer; P = pats·landscape^{-1} (i.e., grazing intensity); Y = year of observation. Bold letters denote interactions between these predictor variables. Estimated effect sizes for predictors of each response are listed in Table 7.

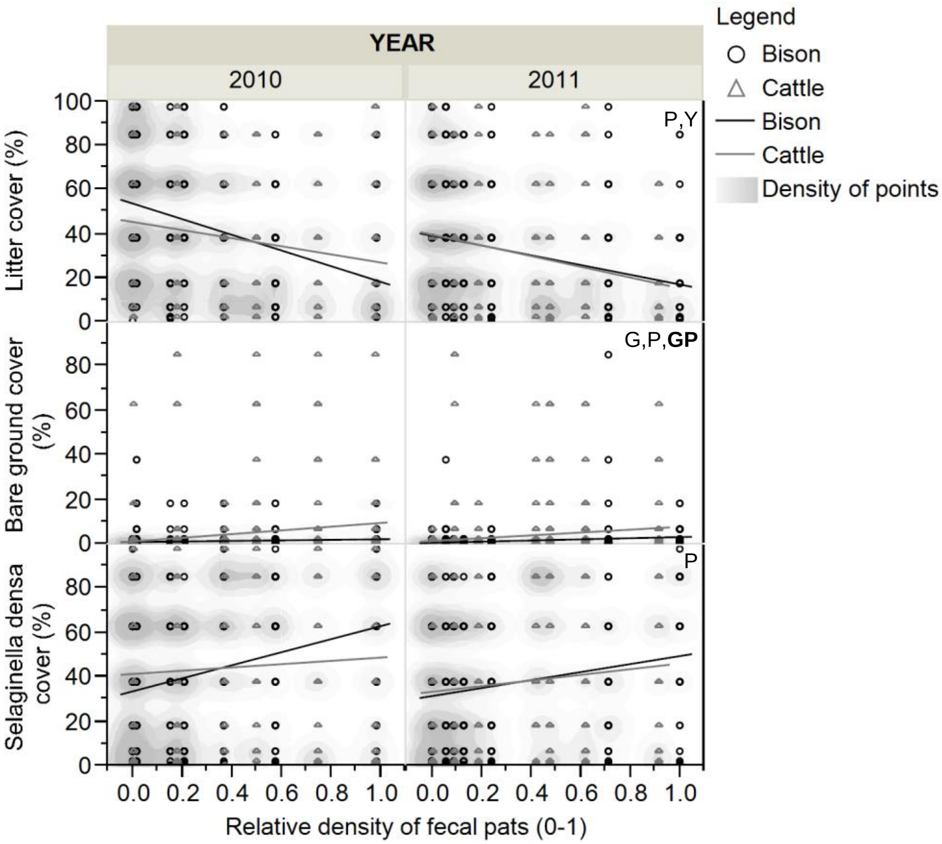

Figure 10. Change in the percent cover of litter, bare ground, and *Selaginella densa* within 0.5-m^2 quadrats as a function of grazing intensity (i.e., relative density of fecal pats per ~80 ha landscape, adjusted to range from 0-1), year of observation, and species of grazer, in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Important predictor variables are denoted by letters: G = species of grazer; P = pats·landscape^{-1} (i.e., grazing intensity); Y = year of observation. Bold letters denote interactions between these predictor variables. Estimated effect sizes for predictors of each response are listed in Table 7.

Spatial effects of grazing. All of the structural responses for which I constructed semivariograms exhibited spatial dependence (i.e., autocorrelation), with varying degrees of patchiness evident in both ungrazed and grazed landscapes (Table 8). In ungrazed areas of the West Block (i.e., within the bison pasture), patches within which vegetation structure was relatively homogeneous were mostly ~28 m in diameter (Fig. 11), and a high proportion of the variance associated with most responses was explained by the physical distance between quadrats (average MSD = 0.67; Table 8). Litter depth within ungrazed areas of the bison pasture was an exception, with the asymptote of the curve that was fitted to the semivariogram for this response variable being reached at ~4 m (Fig. 11), and lag distance explaining less of the variation in this response (MSD = 0.22; Table 8). In contrast to observations in ungrazed landscapes within the bison pasture, ungrazed pastures in the East Block exhibited finer grained patchiness, exhibiting autocorrelation over an average of ~9 m (Fig. 11), with spatially-dependent responses having an average MSD of 0.70 (Table 8). In control pastures, bare ground was the only response that did not exhibit spatial dependence (Table 8).

In grazed landscapes, the total variance associated with most variables was less than in ungrazed landscapes, except for that of bare ground cover, which increased along with grazing intensity (Fig. 11). In areas grazed by bison at low intensities, small patches (~5 m in diameter) with relatively homogeneous residual biomass (50% vegetation height-density), canopy height, and litter cover were evident (average MSD = 0.59; Table 8). In cattle pastures grazed at low intensities, patches were mostly not as evident and/or were larger in size than in neighbouring ungrazed pastures (Fig. 11, Table 8). However, cattle grazing at medium intensities did generate smaller spatial patterns; specifically, I detected very discrete (average MSD = 0.91), ~3-m diameter patches within which residual biomass was homogeneous in moderately grazed cattle pastures (Table 8).

While patches of relatively homogeneous vegetation tended to be smaller and more discrete in lightly and moderately grazed landscapes relative to ungrazed landscapes, spatial patterns of vegetation structure were mostly not evident at high grazing intensities, with random or linear models frequently being the best-fitting (Table

8). Still, under high intensities of bison grazing, small, ~5-m diameter patches of bare ground were detected (Table 8).

Table 8. Selected best model, range, and magnitude of spatial dependence (MSD) of vegetation structure within 0.5-m^2 quadrats located in ungrazed landscapes, and in landscapes grazed by bison and cattle at low, medium, and high intensities in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011.

Grazing intensity	Response	Grazer					
		Bison			Cattle		
		Model[1]	Range[2] (m)	MSD[3]	Model[1]	Range[2] (m)	MSD[3]
None	100% vegetation height-density	E	25.00	0.82	E	9.99	0.82
	50% vegetation height density	S	32.33	0.77	E	7.46	0.78
	Canopy height	E	23.39	0.70	S	4.85	0.74
	Litter depth	S	4.17	0.22	E	13.13	0.55
	Litter cover	S	34.21	0.50	S	9.27	0.61
	Bare ground cover	S	24.77	0.87	R	0.00	0.00
Low	100% vegetation height-density	S	38.43	0.48	E	13.28	0.58
	50% vegetation height density	S	6.01	0.71	E	31.15	0.55
	Canopy height	S	3.77	0.44	L	Infty	0.01
	Litter depth	E	11.07	0.30	S	10.71	0.12
	Litter cover	E	5.08	0.62	L	Infty	0.00
	Bare ground cover	S	10.01	0.59	E	32.25	0.78
Medium	100% vegetation height-density	N/A	N/A	N/A	S	3.33	0.86
	50% vegetation height density	N/A	N/A	N/A	S	2.50	0.95
	Canopy height	N/A	N/A	N/A	E	14.64	0.33
	Litter depth	N/A	N/A	N/A	S	49.80	0.54
	Litter cover	N/A	N/A	N/A	S	5.42	0.37
	Bare ground cover	N/A	N/A	N/A	S	37.09	0.66
High	100% vegetation height-density	L	Infty	0.01	E	16.74	0.40
	50% vegetation height density	R	0.00	0.00	L	Infty	0.02
	Canopy height	L	Infty	0.03	R	0.00	0.00
	Litter depth	E	58.18	0.33	E	26.75	0.22
	Litter cover	S	49.39	0.31	S	3.62	0.30
	Bare ground cover	S	4.78	0.42	L	Infty	0.03

[1] Candidate models included random (R), linear (L), exponential (E), and spherical (S)

[2] Refers to the distance at which the asymptote of fitted model is reached; represents the geographic scale of dependence, beyond which data spatially independent

[3] Indicates the proportion of estimated total sample variation explained by structural variance; as index approaches 1.0, a greater proportion of the total sample variance is spatially dependent over the distance examined

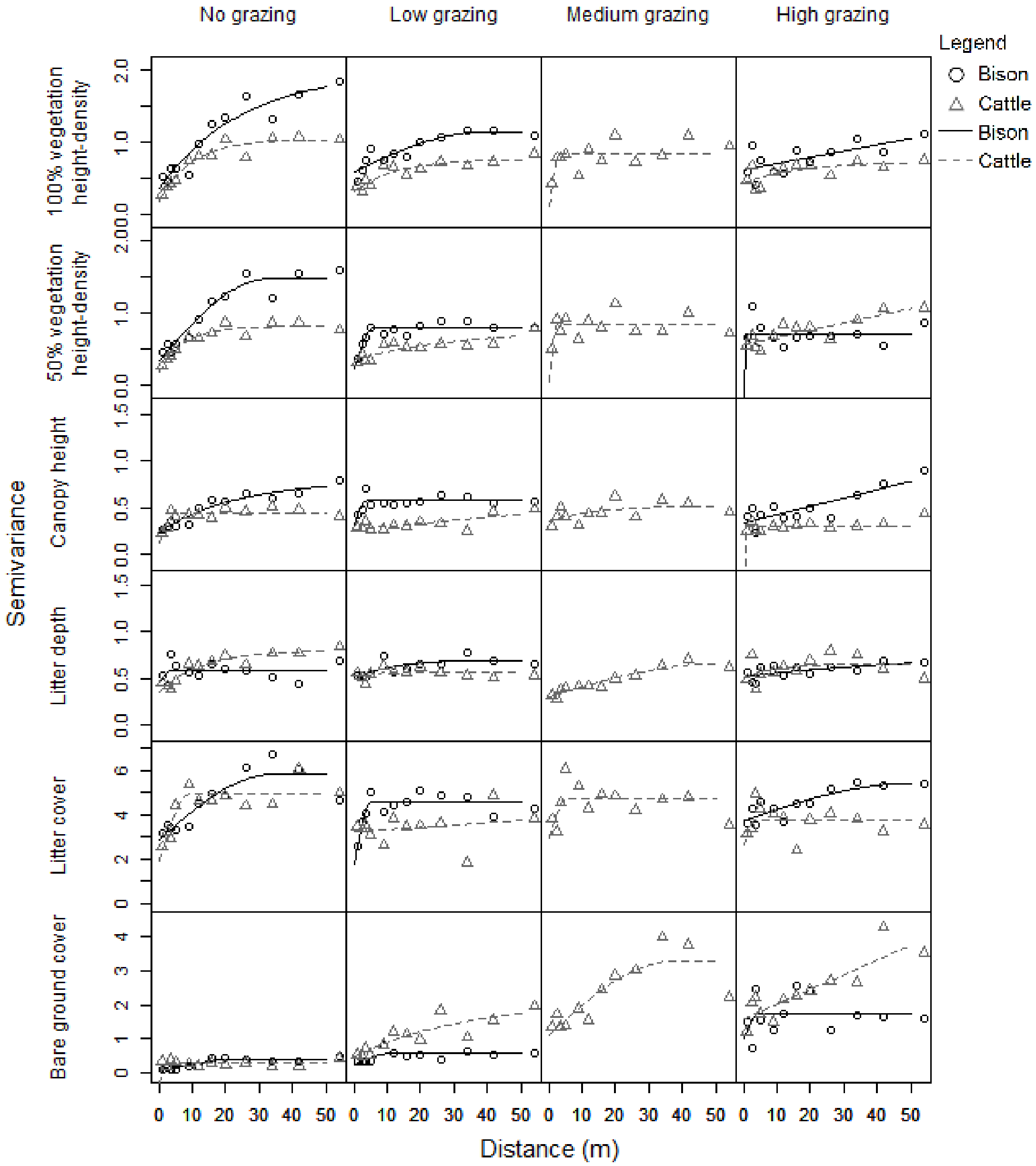

Figure 11. Semivariograms showing best fitting models of spatial heterogeneity of vegetation structure in ungrazed landscapes and landscapes grazed by bison and cattle at low, medium, and high intensities within Grasslands National Park, Saskatchewan, Canada, June-July of 2011. The selected best model, range, and magnitude of spatial dependence (MSD) of each response are listed in Table 8. Random and linear models indicate that there was no spatial dependence over the scale examined, whereas exponential and spherical models indicate that patchiness was evident, with the distance at which the asymptote is reached representing the geographic scale of dependence, beyond which data are spatially independent.

Semivariograms of bare ground cover and other structural responses, including residual biomass, show that semivariance varied widely at short lag distances under bison grazing, and in some cases, under cattle grazing also (Fig. 11). Values of Moran's *I* for 100% vegetation height-density reveal that distinct, small-scale patchiness was present at the highest grazing intensities (Fig. 12). Specifically, while autocorrelation declined gradually in ungrazed landscapes, residual biomass in landscapes grazed at high intensities was correlated at distances up to 1 m, not as correlated or no longer exhibiting any spatial dependence at distances up to 3 m (i.e., $p > 0.05$ at this distance class in areas grazed by bison), and more similar again at lag distances between 4 m and 8 m (Fig. 12). At low grazing intensities, spatial dependence dropped off at distances of 4-8 m in areas grazed by bison, and 8-12 m in areas grazed by cattle (Fig. 12). These results indicate that bison created smaller patches that were more differentiated from the surrounding vegetation at the highest intensities of grazing than did cattle.

Overall, my results show that increasing grazing intensity of both bison and cattle reduced the average patch size within which vegetation structure was relatively homogeneous.

Figure 12. Correlograms showing values of Moran's I for vegetation height-density at increasing lag distances in ungrazed landscapes and landscapes grazed by bison and cattle at low, medium, and high intensities within Grasslands National Park, Saskatchewan, Canada, June-July of 2011. Distance classes are (1) 0-1 m; (2) 1-2 m; (3) 2-3 m; (4) 3-4 m; (5) 4-8 m; (6) 8-12 m; (7) 12-16 m; (8) 16-20 m; (9) 20-30 m; and (10) 30-50 m.

3.5 DISCUSSION

Both grazing and mowing were associated with substantially higher floristic diversity and lower plant community evenness than in ungrazed plant communities within Grasslands National Park. Since both selective and nonselective defoliation resulted in similar diversity responses, my results were consistent with those that would be expected if competitive release were a primary mechanism driving changes in floristic diversity (Collins et al. 1998). This suggests that the growth of subordinate plant species in ungrazed northern mixed prairie ecosystems can be limited by the availability of above-ground resources (Milchunas et al. 1988). For example, if light was limiting plant growth in ungrazed plant communities, the reductions in canopy height and vegetation height-density that I observed under higher intensities of grazing would have increased the availability of this resource. Similarly, mechanical defoliation would have increased the availability of light, since the mowing treatment involved the removal of both growing and senescent biomass from experimental plots.

Floristic diversity increased with grazing intensity of both bison and cattle in GNP, in accordance with the results reported by Towne et al. (2005) in a tall-grass prairie ecosystem; however, while these authors found bison to have a greater effect than cattle on diversity after 10 years of grazing, I found no substantial differences between the effects of cattle and bison grazing after four and six years of grazing, respectively. Differences in selective preferences have been suggested as the mechanism behind higher increases in diversity under bison grazing, since bison mostly do not consume forb species, whereas cattle seek these out for inclusion in their diets (Knapp et al. 1999, Plumb and Dodd 1993). While there was an apparent increase in the proportion of forb species in areas grazed at higher intensities by bison in GNP, grazing intensity did not explain this response. Other differences in selective preferences have also been identified for bison and cattle in northern mixed prairie; bison have been observed to take advantage of seasonal variability in forage quality by including higher proportions of C_4 species in their diets than cattle (Peden et al. 1974, Plumb and Dodd 1993). However, these did not result in substantial differences in plant community composition in this study. The plant community changes that I observed are better explained by the physiological and morphological traits of the different plant species than differences in selective preferences between bison and cattle. Specifically, as tall, palatable C_3 graminoid species were defoliated at increasing intensities, blue grama, a short-statured, grazing-tolerant species, and the most prevalent C_4 in the plant community, increased in abundance, as has been reported in several grazing intensity studies conducted in northern mixed prairie ecosystems (e.g., Houston and Woodward 1966, Smoliak et al. 1972, Hart et al. 1993, Willms et al. 2002). Other subordinate graminoids, including June grass and needleleaf sedge, also flourished when grazers reduced the relative cover of taller, more dominant C_3 species, especially needlegrasses.

Grazing by bison and cattle also corresponded to similar changes in vegetation structure. All variables were related to grazing intensity as expected (given that grazers consume more biomass as grazing intensity increases); residual biomass, canopy heights, and heights of tallest plants all decreased with increasing intensities of grazing. Bare ground increased with grazing intensity, as reported in other arid and semi-arid rangelands (e.g., Jones 2000, Augustine et al. 2012), but interestingly, the increase was greater under cattle grazing than under bison grazing. One possible explanation is differences in plant community composition in areas grazed at high intensities by bison and by cattle. Specifically, Derner and Whitman (2012) found that bunchgrass-dominated northern mixed prairie plant communities had smaller plant interspaces than plant communities dominated by rhizomatous species (e.g., western wheatgrass) in a northern mixed prairie. If western wheatgrass or other rhizomatous species were more prevalent in plant communities that were grazed by cattle at high intensities, the total cover occupied by plant interspaces (and thus total bare ground cover) may have been greater than in landscapes grazed by bison at high intensities, if these were dominated by bunchgrasses. Differences in plant community composition between the East and West Blocks of GNP may also explain why vegetation height responded differently to bison and cattle grazing, while all other changes in vegetation structure were similar.

Spatial analyses revealed that there were inherent differences between plant communities in the West and East Blocks of GNP. In the ungrazed areas of the West Block, semivariance associated with most structural variables was higher, and patchiness was coarser, than in control pastures located in the East Block of GNP. These differences in the inherent variability of vegetation structure in ungrazed landscapes could reflect differences in topography, soil type, and/or plant community composition between the two blocks. Differences in the plant community characteristics of ungrazed landscapes could also reflect the fact that there were no true controls in the West Block, only landscapes that had not been grazed by bison since their re-introduction to GNP. Plant community composition in these landscapes did not always resemble that of long-term ungrazed controls in the East Block, as evidenced by the different intercepts in models of some responses (e.g., the proportion of C_4 graminoids in the plant community). The reason(s) for certain landscapes being ungrazed by bison may have been multifold, but recent research in GNP suggests that landscape use by bison is influenced by terrain, the spatial orientation of natural and anthropogenic elements (e.g., fences), and by plant community composition (Babin et al. 2011). While these factors complicate the interpretation of my results, the effects of grazing on most response variables were still detectable.

Although it can be difficult to determine to what degree herbivores influence the spatial structure of ecosystems when inherent heterogeneity is high (Augustine and Frank 2001), grazers clearly influenced the spatial patterns of several structural response variables in GNP. Small-scale (~5-m diameter) patches with distinctly different amounts of residual biomass and litter, and lower canopy heights, than surrounding areas were evident in landscapes that were grazed by bison at low intensities. Similar responses were not detected at low intensities of cattle grazing, but this could have been due to the fact that vegetation structure was inherently patchy at small spatial scales in the East Block (e.g., responses exhibited strong spatial dependence over distances of ~5-13 m), which low intensities of grazing did not override. Cattle grazing at medium intensities, however, generated discrete ~3-m diameter patches within which the amount of residual biomass was relatively uniform. Variability of structural responses at small lag distances increased with grazing intensity; at high intensities, the peaks and troughs evident in the correlograms of vegetation height-density show that grazing by bison and cattle both generated ~1- to 2-m diameter patches in a repeating pattern across the landscape, with patchiness being slightly more pronounced in areas grazed by bison, since vegetation structure alternated between being significantly correlated and not significantly correlated at increasing lag distances. This could reflect the fact that bison continually revisit the same grazing patches after they have been established (Knapp et al. 1999), resulting in more pronounced differences between vegetation structure inside and outside of grazed patches. While no published studies have explicitly compared patterns of spatial heterogeneity in areas grazed by bison and by cattle, it is speculated that the size and arrangement of grazing patches may differ between these two species of grazer (e.g., Freese et al. 2007). However, except that bison grazing at high intensities seemed to generate more discrete small-scale patches, I found the patchiness of most response variables in areas of GNP grazed by cattle to be similar to the patterns observed in areas grazed by bison.

Spatial patterns of bare ground cover, however, did differ between landscapes grazed by cattle and landscapes grazed by bison in this study. The variability in bare ground cover increased dramatically with increasing intensities of cattle grazing, but observations were correlated over long distances (~32 m and 37 m at low and medium grazing intensities, respectively). In contrast, bison grazing was associated with smaller patches of bare ground (~10 m and 5 m at low and high grazing intensities, respectively). These differences may have been related to the fact that bison create discrete patches that are a few metres to many metres in diameter by wallowing (Trager et al. 2004, McMillan et al. 2011), while cattle do not wallow. There were active wallows in some of my study plots within the bison pasture, which could have partly driven these results. However, since bison generated more discrete patches of residual biomass at smaller spatial scales than cattle, it may be the case that the impacts of bison grazing are generally more concentrated, and the impacts of cattle grazing are generally more diffuse. However, Augustine et al. (2012) found that cattle grazing in a semi-arid rangeland increased bare soil primarily at scales less than one metre. Since one metre was the minimum lag distance over which I could assess autocorrelation, my results neither confirm nor refute that this was the case in GNP. Since the amount and orientation of bare ground cover can have important implications for hydrologic functioning and soil erosion (Ludwig et al. 2005), seedling establishment (Aguilera and Lauenroth 1995), and wildlife habitat (Derner et al. 2009), further study on the mechanisms driving the different effects of grazing by bison and cattle on this structural response is warranted. In particular, future studies should investigate the spatial patterns of bare ground at scales less than one metre.

Grazing-induced increases in biodiversity have sometimes been attributed to increases in spatial heterogeneity, as variability in vegetation structure may allow for the coexistence of more species (Fuhlendorf et al. 2001, Bakker and Olff 2003, Lundholm 2009). In particular, it has been suggested that bison generate a mosaic of lightly to heavily disturbed patches across a given landscape, leading to increases in both patch and taxonomic diversity (Knapp et al. 1999, Trager et al. 2004, Towne et al. 2005). However, I did not detect substantial differences in the spatial pattern of vegetation structure generated by each species of grazer, nor in the relationship between grazing intensity of each herbivore and floristic diversity. While it is possible that the patchiness of vegetation structure in grazed landscapes within GNP allowed for the co-existence of more species than would otherwise be present, competitive release within mowed plots led to a similar diversity response. Therefore, competitive release seems to have been the primary mechanism driving plant community changes in my study system.

Since the importance of competitive release in determining plant community response differs along gradients of environmental moisture (Milchunas et al. 1988), and since GNP received higher than average precipitation during the study period, it is not clear whether this is always the primary mechanism driving responses to grazing in northern mixed prairie plant communities. These ecosystems can fall under either a sub-humid or a semi-arid classification depending on prevailing climatic conditions (Scott and Suffling 2000), and while defoliation results in competitive release in moist, tall-grass prairie ecosystems (Collins et al. 1998), this is not the case in more arid short-grass ecosystems, since interspecific competition in the latter is primarily for soil resources (Milchunas et al. 1988). Therefore, in a year when lower than average precipitation was received, grazing could alter competitive interactions in northern mixed prairie in a different way than I observed, for example, shifting from competition for above-ground to below-ground resources (Milchunas et al. 1988). Differences in herbivore selectivity might also become more evident when conditions are drier; in this study, grazing intensity did not provide substantial information about the proportion of the plant community comprised of forbs, which may have been partly because higher than average rainfall was received during the study period, and this allowed forbs, including rare species that only germinate when environmental conditions are hospitable enough, to flourish throughout the entire study area. Since it is typical for plant community characteristics in semi-arid regions of the Great Plains to vary annually because of climatic conditions, with grazing intensity sometimes having only a minor influence relative to weather variables (Biondini et al. 1998, Fuhlendorf et al. 2001, Gillen and Sims 2006), further study is required to understand the mechanisms driving plant community changes in northern mixed prairie ecosystems in response to grazing over the long term.

3.6 IMPLICATIONS

My results indicate that bison and cattle have similar effects on floristic diversity in northern mixed prairie ecosystems. Furthermore, I found that increases in diversity were driven in part by competitive release, since mowing also increased diversity, and since purported differences in selectivity between the two herbivores did not result in the two having disparate effects on plant community composition. Cattle and bison grazing at comparable intensities usually had similar effects on vegetation structure, including on spatial patterns of variability in most structural responses. However, since there were some differences in patchiness caused by bison and cattle grazing, and since the magnitude and spatial arrangement of patchiness can have important ecological implications, further monitoring is required to clarify the relative ecological effects of each grazer, and the utility of each for meeting specific conservation management goals.

3.7 ACKNOWLEDGEMENTS

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4.0 MANAGEMENT IMPLICATIONS AND CONCLUSIONS

Attempts to restore the ecological role of bison to the Great Plains have been called a prerequisite to the comprehensive restoration of biodiversity in North American grasslands (Freese et al. 2007). However, rigorous scientific study of the ecological differences between bison and cattle is challenging, and although differences between the two species are often stated in both lay and scientific literature, most of these have not been explicitly proved or disproved via empirical study (Fuhlendorf et al. 2010).

The presence of both bison and cattle within Grasslands National Park (GNP) provides a unique opportunity to monitor the effects of each herbivore's grazing within complex natural landscapes. GNP's management plan recognizes grazing as a critical ecological process, and indicates that bison are the preferred herbivore for the restoration of this natural disturbance, with domestic cattle being used to achieve desired outcomes when the use of bison is not feasible (Parks Canada 2010). Understanding the differences and similarities between the ecological effects of grazing by bison and cattle will therefore be important for informing current and future management in GNP.

The results of my study provide some practical insights for how best to monitor and compare the effects of grazing by bison and cattle within GNP. In Chapter 2, I demonstrate the usefulness of the relative density of fecal pats as a proxy for grazing intensity of both bison and cattle. While densities of fecal pats do not always correspond with the most grazed areas of a given pasture within a single season (Kohler et al. 2006), I show that they can be effective for modeling both short- and long-term effects of grazing if calculated over appropriate scales. Additionally, I found that changes in plant community composition in response to grazing may best be detected at relatively fine spatial scales (1000 m^2), and I introduce a new proxy for this purpose, which I term Constrained Relative Use. I showed Constrained Relative Use to be effective for modeling fine-scale responses to cattle grazing among pastures that were stocked at a wide range of rates.

In Chapter 3, I concluded that bison and cattle had very similar effects on floristic diversity, plant community composition, and vegetation structure during my study period, including on the spatial variability of structural response variables. However, inherent differences between the West and East Blocks of GNP, and unusually high precipitation during the years that my study took place mean that my results are not conclusive. Additionally, the differences I observed in spatial patterns of disturbance under each species of grazer warrant further investigation, especially to clarify the relative effects of bison and cattle on vegetation structure at very fine spatial scales (e.g., lag distances less than one metre). Grazed pastures should, therefore, be monitored over the long term in order to detect important ecological changes in response to grazing by these two herbivores. When grazers are deployed within extensive pastures, some proxy for grazing intensity will need to be used. While my results suggest that patch-scale predictors based on the density of fecal pats are suitable for detecting the cumulative effects of grazing, other methods for quantifying grazing intensity, such as location data from GPS collars, could also be useful. However, location data indicates that herbivores have spent time in a given area, but in and of itself, provides no information regarding how much time they spent grazing; therefore, location data also needs to be validated before being used as a proxy for grazing intensity (Turner et al. 2000).

Once grazed sites have been identified within a given pasture, I suggest that these could be selectively monitored (e.g., based on the level of grazing intensity at that site, on the presence of plant species or cultural resources of interest, etc.), using spatially explicit approaches[1].When heterogeneity occurs at different levels of resolution in the form of patches or mosaics, as is the case for the effects of grazing, the recommended approach is to collect data from a grid of contiguous quadrats (Dutilleul 1993). Such an approach would help to clarify whether localized disturbances, such as wallowing and other behavioural differences, result in higher levels of species diversity or other ecological differences in areas grazed by bison relative to areas grazed by cattle, and would maximize the amount of information from monitoring relative to the cost. Spatial patterns in vegetation structure, growth, production, species composition, and nutrient dynamics caused by grazing play crucial roles in ecosystem functioning (Franklin 2005). Therefore, spatially explicit monitoring may provide important information about the long-term effects of grazing in GNP, and how these align with management goals.

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[1] See Dutilleul (1993) for an introduction to spatially explicit sampling and statistics, and Stokes et al. (2009) for discussion of a selective monitoring approach aimed at detecting the effects of spatially heterogeneous disturbances

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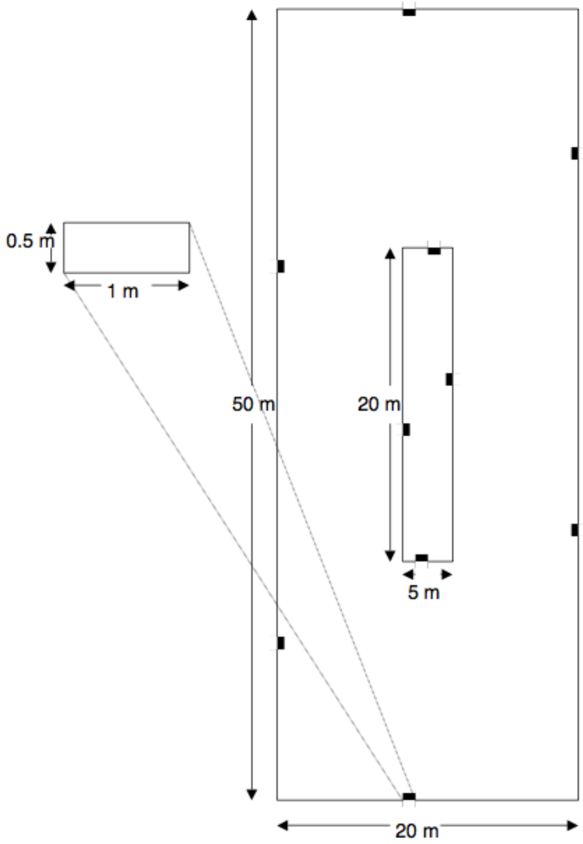
APPENDIX A

Layout of Modified Whittaker plots used in this study.

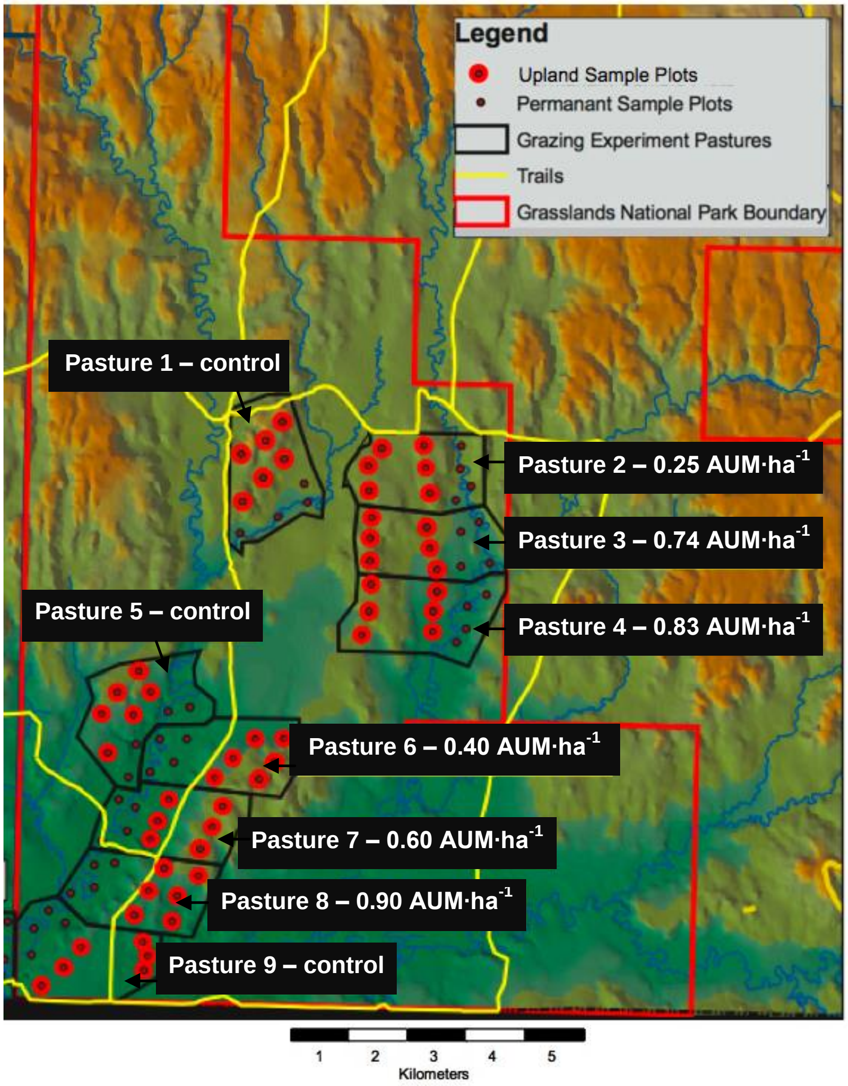


APPENDIX B

Location and stocking rates of pastures and study plots in the East Block of Grasslands National Park, Saskatchewan, Canada.

Note that only plots located in upland grassland areas ('Upland Sample Plots') were used in this study.

Map courtesy of Grasslands National Park.

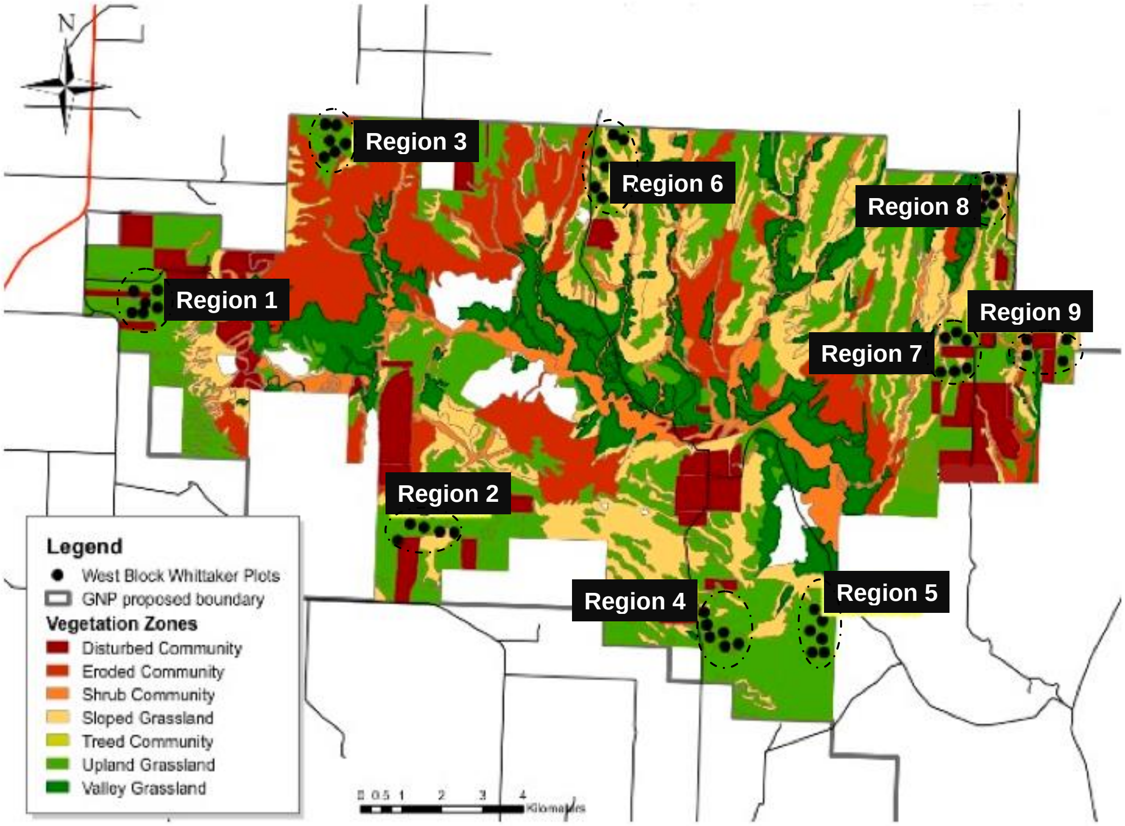


APPENDIX C

Location of regions (i.e., ‘landscapes’, indicated with dotted lines) within which Modified Whittaker plots were clustered, in relation to vegetation zones in the West Block of Grasslands National Park, Saskatchewan, Canada.

Study plots located in ‘Region 1’ are located outside of the bison pasture. Note, however, that data from these plots were not included in analyses in this study, as these plant communities were deemed to have experienced too much disturbance (namely, invasion by *Agropyron cristatum*) to be comparable to other upland grassland plant communities within the study area.

Map courtesy of Grasslands National Park.



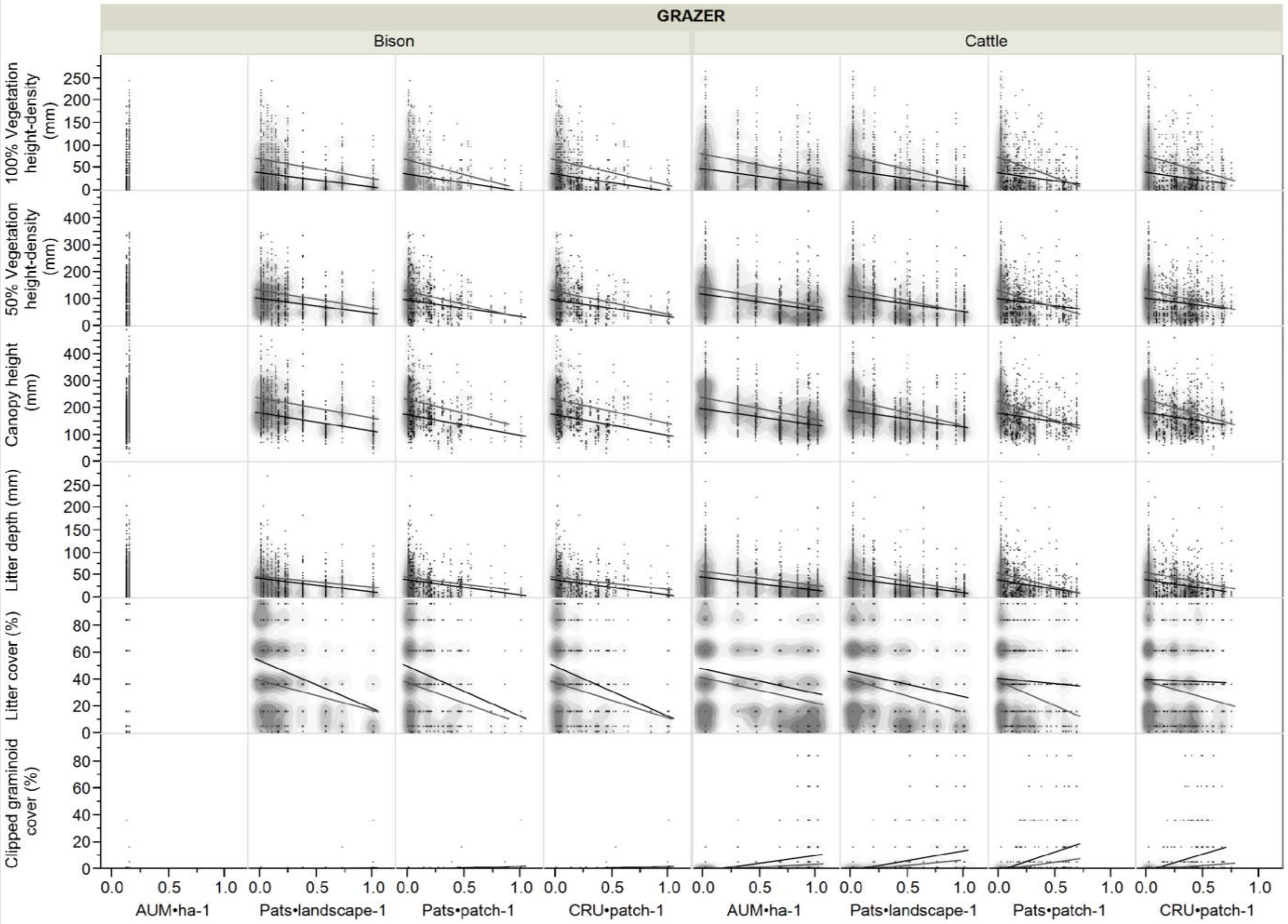
APPENDIX D

Appendix D. Estimates, standard errors (β ± SE), and 90% confidence intervals for parameters included in the selected best models of the effects of grazing by cattle, by bison, and by both species of grazer on plant community responses in Grasslands National Park, Saskatchewan, Canada, June-July 201of 2010 and 2011.

Response	Cattle		Bison		Bison + Cattle	
	Parameter(s) in best model	β ± SE (90% CI)	Parameter(s) in best model	β ± SE (90% CI)	Parameter(s) in best model	β ± SE (90% CI)
--------------------Plant community structure--------------------						
100% Vegetation height-density	AUM·ha^{-1}	-1.28 ± 0.32 (-1.81, -0.75)	Pats·landscape^{-1}	-1.43 ± 0.28 (-1.90, -0.96)	Pats·landscape^{-1}	-1.73 ± 0.31 (-2.24, -1.22)
	Year	-0.80 ± 0.06 (-0.90, -0.71)	Year	-0.73 ± 0.05 (-0.82, -0.64)	Pats·patch^{-1}	1.02 ± 0.43 (0.31, 1.73)
					Year	-0.76 ± 0.04 (-0.82, -0.69)
50% Vegetation height-density	AUM·ha^{-1}	-0.69 ± 0.16 (-0.96, -0.42)	Pats·landscape^{-1}	-0.78 ± 0.15 (-1.03, -0.52)	Pats·landscape^{-1}	-0.56 ± 0.11 (-0.75, -0.38)
	Year	-0.23 ± 0.03 (-0.28, -0.18)	Year	-0.28 ± 0.03 (-0.32, -0.23)	Year	-0.24 ± 0.02 (-0.27, -0.21)
Canopy height	AUM·ha^{-1}	-0.38 ± 0.07 (-0.49, -0.27)	Pats·landscape^{-1}	-0.34 ± 0.07 (-0.46, -0.22)	CRU·patch^{-1}	-0.32 ± 0.07 (-0.43, -0.21)
	Year	-0.18 ± 0.01 (-0.20, -0.15)	Year	-0.28 ± 0.01 (-0.30, -0.25)	Year	-0.23 ± 0.01 (-0.25, -0.22)
Litter depth	Pats·landscape^{-1}	-1.07 ± 0.17 (-1.36, -0.79)	Pats·landscape^{-1}	-0.90 ± 0.15 (-1.14, -0.65)	Pats·landscape^{-1}	-1.02 ± 0.12 (-1.21, -0.82)
	Year	-0.31 ± 0.05 (0.40, 0.22)	Year	-0.16 ± 0.06 (-0.26, -0.07)	Year	-0.24 ± 0.04 (-0.31, -0.18)
Litter cover	Pats·landscape^{-1}	-1.33 ± 0.29 (-1.80, -0.86)	Pats·landscape^{-1}	-0.85 ± 0.22 (-1.21, -0.48)	Pats·landscape^{-1}	-0.80 ± 0.15 (-1.04, -0.55)
	Pats·patch^{-1}	0.51 ± 0.33 (-0.02, 1.05)	Year	0.34 ± 0.04 (0.26, 0.41)	Year	0.29 ± 0.03 (0.24, 0.34)
	Year	0.15 ± 0.06 (0.06, 0.25)				
	Pats·patch^{-1}*year	0.40 ± 0.16 (0.13, 0.67)				
Clipped graminoid cover	AUM·ha^{-1}	3.33 ± 0.56 (2.38, 4.28)	Pats·landscape^{-1}	2.83 ± 0.47 (2.04, 3.62)	Pats·landscape^{-1}	4.72 ± 0.42 (4.02, 5.41)
	Pats·patch^{-1}	1.74 ± 0.62 (0.71, 2.78)			Year	0.71 ± 0.18 (0.42, 1.01)
	Year	0.86 ± 0.21 (0.51, 1.21)			Grazer	-0.90 ± 0.36 (-1.50, -0.30)
					Pats·landscape^{-1}*grazer	-1.75 ± 0.65 (-2.83, -0.66)
--------------------Plant community composition--------------------						
Simpson's reciprocal index	CRU·patch^{-1}	0.35 ± 0.12 (0.15, 0.55)	Year	-0.08 ± 0.03 (-0.14, -0.03)	-	
	Year	-0.12 ± 0.04 (-0.18, -0.06)				
Simpson's measure of evenness	CRU·patch^{-1}	-0.24 ± 0.11 (-0.43, -0.06)	Year	-0.12 ± 0.04 (-0.19, -0.05)	-	
% Decreasers	AUM·ha^{-1}	-0.30 ± 0.12 (-0.50, -0.09)	Year	0.21 ± 0.03 (0.15, 0.26)	-	
	Year	0.33 ± 0.03 (0.27, 0.38)				
% Increasers	Pats·landscape^{-1}	0.07 ± 0.11 (-0.11, 0.25)	Year	-0.18 ± 0.03 (-0.23, -0.13)	-	
	Year	-0.35 ± 0.04 (-0.42, -0.28)				
	Pats·landscape^{-1}*year	0.27 ± 0.09 (0.12, 0.41)				

APPENDIX E

Changes in vegetation structure in relation to four proxies for grazing intensity of bison and cattle in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Each proxy was adjusted to range from zero to one, based on the minimum and maximum value of each predictor variable observed within the entire study area.



APPENDIX F

Appendix F. Flow chart showing step-wise process for selecting among candidate models of plant community responses to grazing by bison and cattle in Grasslands National Park, Saskatchewan, Canada, June–July of 2010 and 2011. Models were considered to contain informative predictor variables and advanced to the next step if they had the lowest AIC$_c$ value, or were within 2 points of the model with the lowest AIC$_c$ value. New models introduced at each step are in black font, while models that advanced from previous steps (if found to be informative) are in grey. The polynomial term 'pats·landscape^{-1}*pats·landscape^{-1}', denoted here as 'P*P', were included in candidate models of responses related to floristic diversity and plant community composition, but not vegetation structure. 'P*G' denotes the interaction term 'pats·landscape^{-1}*grazer', and 'P*Y' denotes 'pats·landscape^{-1}*year'.

Step 1: Is year of observation informative?

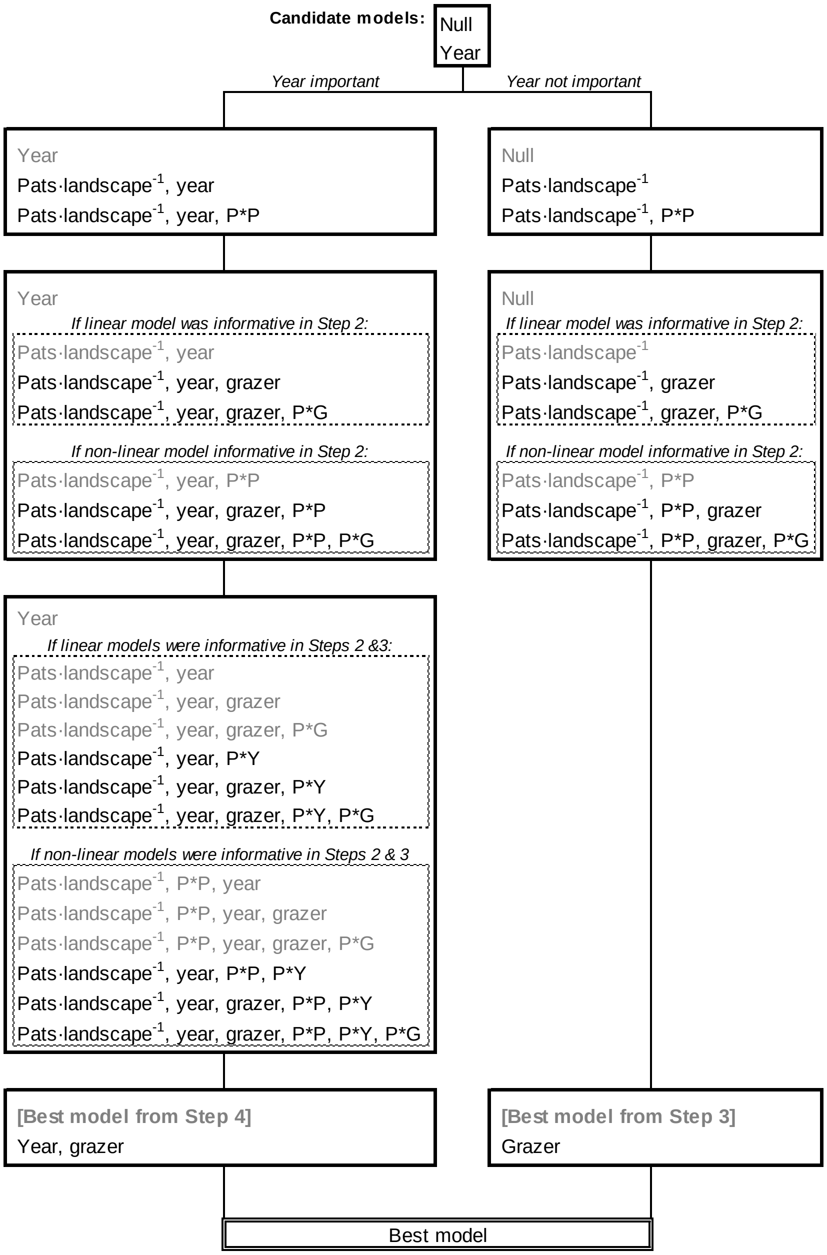
Step 2: Is grazing intensity informative, and is the response linear or nonlinear?

Step 3: Is species of grazer, and/or the interaction of grazer and grazing intensity informative?

Step 4: Did the effect of grazing intensity vary substantially by year?

Step 5: Is grazing intensity still informative once species of grazer is accounted for?

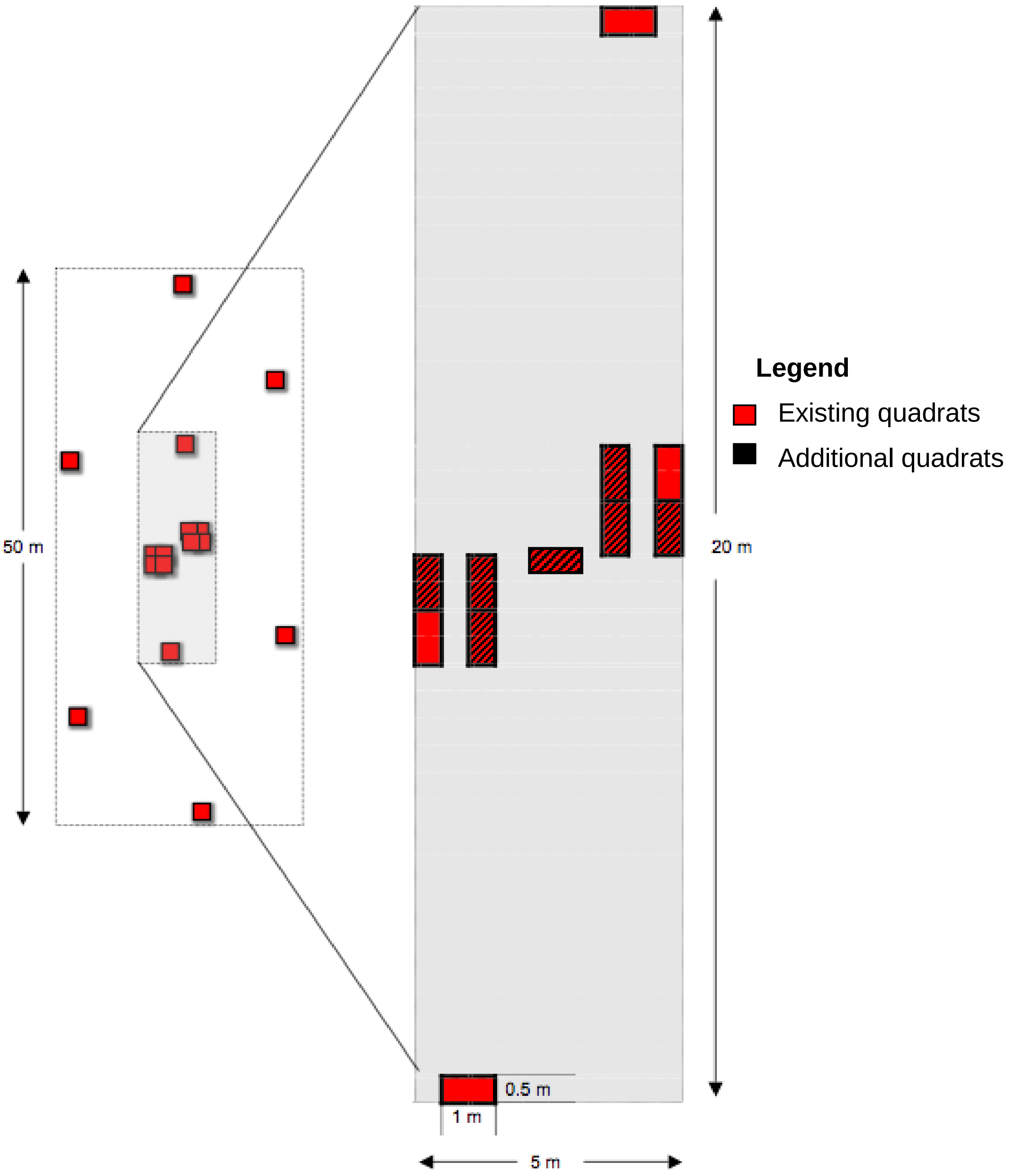
Step 6: Which model is best? (i.e., has the lowest AICc value, or contains one less predictor variable and ΔAICc ≤ 2)



APPENDIX G

Location of seven quadrats added to each sampling plot in 2011 to generate small-scale data for the spatially explicit analyses used in this study.

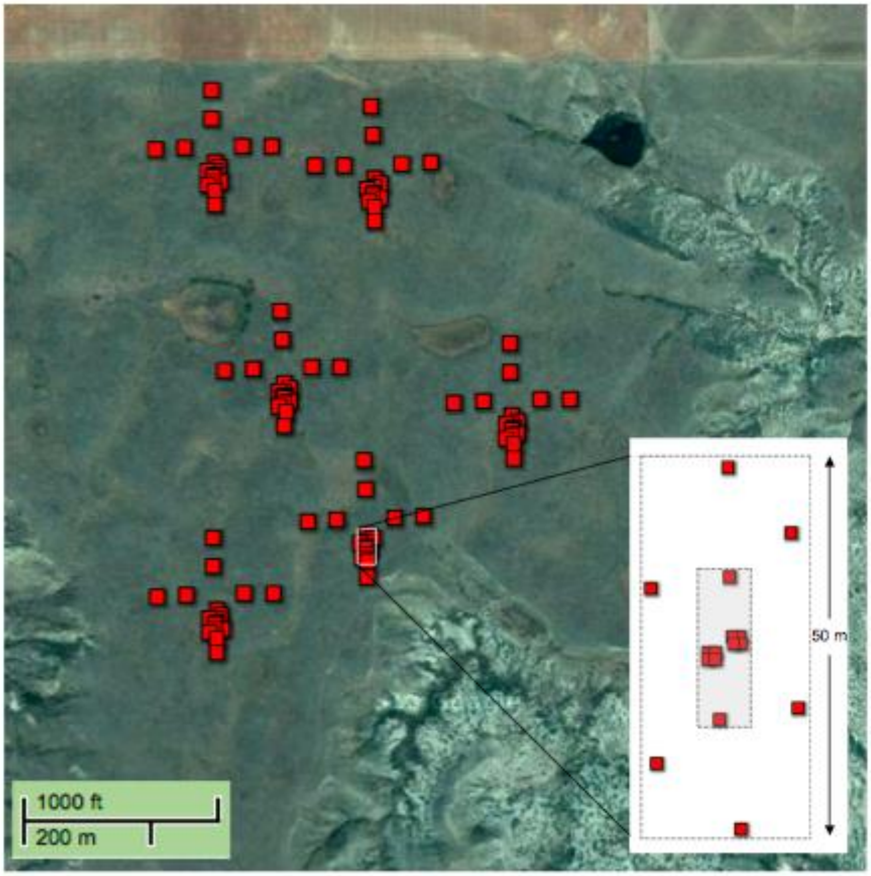
The minimum distance between the centres of paired quadrats was 1 metre,



APPENDIX H

Location of seven quadrats surrounding each study plot, added in 2011 to generate data at intermediate to large distance classes for the spatially explicit analyses used in this study. Plots indicated below were located in the north-west corner of the bison pasture in Grasslands National Park, Saskatchewan, Canada.

Note that quadrats were placed at 50 m and 100 m from the centre of the songbird point count plots established by Koper et al. (2008), or from 25 m north of each Modified Whittaker plot. Therefore, the quadrat placed at 50 m south was located in the exact centre of the Modified Whittaker plot, generating additional paired quadrats at small spatial scales (Appendix G).



APPENDIX I

Appendix I. Log-likelihood (LL), number of parameters (*K*), change in Akaike's criterion for small sample sizes (ΔAIC_c), and Akaike weight (w_i) for models of floristic diversity and plant community composition in landscapes grazed by bison or cattle in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Selected best models for each response are in bold.

Response variable	Model[1]	LL	*K*	ΔAIC_c	w_i
Richness	**Year, grazer**	-682.17	3	0.00	0.39
	Pats·landscape^{-1}, year, grazer	-681.71	4	1.22	0.21
	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-680.76	5	1.46	0.19
	Year	-684.24	2	2.05	0.14
	Pats·landscape^{-1}, year	-683.99	3	3.64	0.06
	Null	-689.40	1	10.29	0.00
Shannon-Wiener function	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-1348.15	5	0.00	0.44
	Pats·landscape^{-1}, year	-1350.48	3	0.39	0.36
	Pats·landscape^{-1}, year, grazer	-1350.44	4	2.44	0.13
	Year	-1353.16	2	3.63	0.07
	Null	-1372.16	1	39.56	0.00
Simpson's reciprocal index	**Pats·landscape^{-1}, year**	-1305.63	3	0.00	0.53
	Pats·landscape^{-1}, year, grazer	-1305.54	4	1.95	0.20
	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-1304.49	5	2.00	0.20
	Year	-1308.71	2	4.06	0.07
	Null	-1326.15	1	36.86	0.00
Simpson's measure of evenness	**Pats·landscape^{-1}**	-1193.08	2	0.00	0.48
	Pats·landscape^{-1}, grazer	-1192.54	3	1.02	0.29
	Pats·landscape^{-1}, grazer, pats·landscape^{-1}*grazer	-1192.51	4	3.09	0.10
	Null	-1195.81	1	3.39	0.09
	Year	-1195.81	2	5.47	0.03
% Forbs	**Year**	-662.14	2	0.00	0.47
	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-659.37	5	0.83	0.31
	Pats·landscape^{-1}, year	-661.81	3	1.44	0.23
	Null	-678.50	1	30.63	0.00
	Pats·landscape^{-1}, year, grazer	DNC	4	DNC	
% C3 graminoids	Pats·landscape^{-1}, grazer, pats·landscape^{-1}*grazer	-733.40	4	0.00	0.38
	Pats·landscape^{-1}	-735.68	2	0.33	0.32
	Pats·landscape^{-1}, grazer	-735.16	3	1.41	0.19
	Null	-737.73	1	2.35	0.12
	Year	-746.75	2	22.47	0.00
% C4 graminoids	**Pats·landscape^{-1}, P*P, year, grazer, pats·landscape^{-1}*grazer**	-445.14	6	0.00	1.00
	Pats·landscape^{-1}, P*P, year	-453.14	4	11.68	0.00
	Pats·landscape^{-1}, P*P, year, grazer	-452.95	5	13.45	0.00
	Year	-457.90	2	16.96	0.00
	Pats·landscape^{-1}, year	-457.51	3	18.29	0.00
	Null	-460.89	1	20.86	0.00

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[1] Models including the interaction term 'pats·landscape^{-1}*year' are only shown if this term contributed substantial additional information about the plant community response of interest, relative to simpler models

APPENDIX J

Appendix J. Log-likelihood (LL), number of parameters (K), change in Akaike's criterion for small sample sizes (ΔAIC_c), and Akaike weight (w_i) for models of plant community composition in landscapes grazed by bison or cattle in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Selected best models for each response are in bold.

Response variable	Model[1]	LL	K	ΔAIC_c	w_i
% *Artemisia frigida*	Pats·landscape^{-1}, year, grazer	-401.50	4	0.00	0.52
	Year, grazer	-403.33	3	1.53	0.24
	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-401.26	5	1.68	0.23
	Pats·landscape^{-1}, year	-407.97	3	10.82	0.00
	Year	-409.09	2	10.96	0.00
	Null	-417.00	1	24.70	0.00
% *Bouteloua gracilis*	**Pats·landscape^{-1}, P*P, grazer, pats·landscape^{-1}*grazer**	-405.96	5	0.00	1.00
	Year	-416.13	2	13.96	0.00
	Pats·landscape^{-1}, P*P, grazer	-414.01	4	13.97	0.00
	Null	-418.11	1	15.84	0.00
	Pats·landscape^{-1}	-417.97	2	17.66	0.00
% *Calamagrostis montanensis*	Year, grazer	-515.36	3	0.00	0.45
	Year	-517.17	2	1.52	0.21
	Pats·landscape^{-1}, year, grazer	-515.25	4	1.90	0.18
	Pats·landscape^{-1}, year	-517.11	3	3.49	0.08
	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-514.99	5	3.54	0.08
	Null	-545.70	1	56.49	0.00
% *Carex diurscula*	**Pats·landscape^{-1}, P*P, year, grazer, pats·landscape^{-1}*grazer**	-362.54	6	0.00	0.97
	Pats·landscape^{-1}, P*P, year, grazer	-367.08	5	6.90	0.03
	Pats·landscape^{-1}, P*P, year	-371.60	4	13.80	0.00
	Pats·landscape^{-1}, year	-373.75	3	15.97	0.00
	Year	-375.73	2	17.81	0.00
	Null	-426.28	1	116.83	0.00
% *Elymus lanceolatus*	Pats·landscape^{-1}	-729.02	2	0.00	0.29
	Pats·landscape^{-1}, grazer, pats·landscape^{-1}*grazer	-727.07	4	0.32	0.25
	Year	-729.24	2	0.43	0.24
	Pats·landscape^{-1}, grazer	-728.78	3	1.62	0.13
	Null	-731.25	1	2.38	0.09
% *Hesperostipa spp.*	**Pats·landscape^{-1}, year**	-721.91	3	0.00	0.64
	Pats·landscape^{-1}, year, grazer	-721.89	4	2.09	0.22
	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-721.72	5	3.88	0.09
	Year	-725.64	2	5.35	0.04
	Null	-769.00	1	89.99	0.00
% *Koeleria macrantha*	**Pats·landscape^{-1}, P*P, year, pats·landscape^{-1}*year, grazer, pats·landscape^{-1}*grazer**	-557.27	7	0.00	0.87
	Pats·landscape^{-1}, P*P, year, grazer, pats·landscape^{-1}*grazer	-560.24	6	3.76	0.13
	Pats·landscape^{-1}, P*P, year, grazer	-566.77	5	14.65	0.00
	Pats·landscape^{-1}, P*P, year	-568.64	4	16.23	0.00
	Pats·landscape^{-1}, year	-570.97	3	18.77	0.00
	Year	-572.07	2	18.87	0.00
	Null	-596.85	1	66.34	0.00
% *Pascopyrum smithii*	Pats·landscape^{-1}, grazer, pats·landscape^{-1}*grazer	-601.69	4	0.00	0.79
	Null	-606.96	1	4.22	0.10
	Pats·landscape^{-1}	-606.75	2	5.88	0.04
	Year	-606.77	2	5.92	0.04
	Pats·landscape^{-1}, grazer	-606.05	3	6.58	0.03

[1] Models including the interaction term 'pats·landscape^{-1}*year' are only shown if this term contributed substantial additional information about the plant community response of interest, relative to simpler models

APPENDIX K

Appendix K. Log-likelihood (LL), number of parameters (K), change in Akaike's criterion for small sample sizes (ΔAIC_c), and Akaike weight (w_i) for models of floristic diversity and plant community composition in landscapes grazed by bison or cattle in Grasslands National Park, Saskatchewan, Canada, June-July of 2010 and 2011. Selected best models for each response are in bold.

Response variable	Model^{1}	LL	K	ΔAIC_c	w_i
100% Vegetation height-density	**Pats·landscape^{-1}, year**	-9100.17	3	0.00	0.62
	Pats·landscape^{-1}, year, grazer	-9100.09	4	1.87	0.24
	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-9099.62	5	2.94	0.14
	Year	-9114.15	2	25.96	0.00
	Null	-9255.56	1	306.77	0.00
50% Vegetation height-density	**Pats·landscape^{-1}, year**	-10465.39	3	0.00	0.54
	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-10464.13	5	1.50	0.26
	Pats·landscape^{-1}, year, grazer	-10465.37	4	1.98	0.20
	Year	-10477.06	2	21.33	0.00
	Null	-10559.15	1	183.50	0.00
Tallest plant (Robel pole)	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-11925.03	5	0.00	0.48
	Pats·landscape^{-1}, year	-11927.34	3	0.59	0.36
	Pats·landscape^{-1}, year, grazer	-11927.22	4	2.35	0.15
	Year	-11931.31	2	6.50	0.02
	Null	-12188.73	1	517.32	0.00
Tallest plant (metre stick)	**Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer**	-12516.12	5	0.00	0.88
	Pats·landscape^{-1}, year	-12520.81	3	5.35	0.06
	Pats·landscape^{-1}, year, grazer	-12520.36	4	6.48	0.03
	Year	-12522.52	2	6.77	0.03
	Null	-12623.64	1	206.99	0.00
Canopy height	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-10492.04	5	0.00	0.79
	Pats·landscape^{-1}, year	-10495.80	3	3.49	0.14
	Pats·landscape^{-1}, year, grazer	-10495.62	4	5.14	0.06
	Year	-10498.90	2	7.67	0.02
	Null	-10713.39	1	434.64	0.00
Litter depth	**Pats·landscape^{-1}, year**	-9069.14	3	0.00	0.62
	Pats·landscape^{-1}, year, grazer	-9069.11	4	1.95	0.23
	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-9068.54	5	2.82	0.15
	Year	-9098.01	2	55.73	0.00
	Null	-9120.45	1	98.59	0.00
Litter cover	**Pats·landscape^{-1}, year**	-13490.25	3	0.00	0.64
	Pats·landscape^{-1}, year, grazer	-13490.13	4	1.77	0.26
	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	-13490.13	5	3.79	0.10
	Year	-13503.03	2	23.54	0.00
	Null	-13540.35	1	96.17	0.00
Bare ground cover	**Pats·landscape^{-1}, grazer, pats·landscape^{-1}*grazer**	-5593.21	4	0.00	0.85
	Pats·landscape^{-1}, grazer	-5596.49	3	4.54	0.09
	Pats·landscape^{-1}	-5597.85	2	5.25	0.06
	Year	-5619.27	2	48.09	0.00
	Null	-5621.02	1	49.57	0.00
Selaginella densa cover	**Pats·landscape^{-1}**	-13632.02	2	0.00	0.90
	Pats·landscape^{-1}, grazer	-13633.43	3	4.83	0.08
	Null	-13636.66	1	7.28	0.02
	Year	-13674.89	2	87.76	0.00
	Pats·landscape^{-1}, year, grazer, pats·landscape^{-1}*grazer	DNC	4	DNC	

[1] Models including the interaction term 'pats·landscape^{-1}*year' are only shown if this term contributed substantial additional information about the plant community response of interest, relative to simpler models