Plant Ecol (2018) 219:649–663
https://doi.org/10.1007/s11258-018-0824-4

Long-term grazing impacts on vegetation diversity, composition, and exotic species presence across an aridity gradient in northern temperate grasslands

Mark P. Lyseng · Edward W. Bork · Daniel B. Hewins · Mike J. Alexander · Cameron N. Carlyle · Scott X. Chang · Walter D. Willms

Received: 12 June 2017 / Accepted: 31 March 2018 / Published online: 4 April 2018

Abstract Little is known about the specific role of exotic species on measures of grassland plant diversity, including how this may vary with climatic conditions or large mammal herbivory. This study examined vegetation responses to long-term livestock grazing, including plant richness and diversity, as well as the contribution of exotic species to these metrics, across a network of 107 northern temperate grasslands in Alberta, Canada, spanning a broad aridity gradient. Exposure to grazing modestly increased plant richness, but did not alter Shannon's diversity, Simpson's diversity, or evenness, suggesting stability in floral diversity relative to grazing. However, grazing did increase grass cover while reducing shrub cover, the latter of which was only apparent in mesic grasslands. Unlike total plant diversity, exotic species richness and cover, together with exotic plant contributions to diversity, varied jointly with grazing and aridity. While long-term grazing increased exotic species, this response was most apparent in wetter areas, and non-grazed grasslands remained more resistant to the presence of exotics. Several exotic species were positive indicators of grazing in wetter grasslands, and coincided with lower native species cover, indicating grazing may be facilitating a shift from native to exotic vegetation under these conditions. Overall, our results indicate that while long-term grazing has altered the composition and cover of certain functional groups, including favoring exotics and minimizing woody vegetation in mesic areas, overall changes to plant diversity were limited. Additionally, these findings suggest that semi-arid

---

Communicated by Sumanta Bagchi.

M. P. Lyseng
Alberta Environment and Parks, Government of Alberta,
4th Floor, 9920-108 Street, Edmonton, AB T5K 2M4,
Canada

E. W. Bork (✉) · C. N. Carlyle
Department of Agriculture, Food and Nutritional Science,
University of Alberta, 4-10E, Agriculture and Forestry,
Edmonton, AB T6G 2P5, Canada
e-mail: Edward.bork@ualberta.ca

D. B. Hewins
Biology Department, Rhode Island College, 600 Mount
Pleasant Ave, Providence, RI 02908, USA

M. J. Alexander
Alberta Environment and Parks, Government of Alberta,
2nd Floor Provincial Building, 200-5 Avenue South,
Lethbridge, AB T1J4L1, Canada

S. X. Chang
Department of Renewable Resources, University of
Alberta, 442 Earth Sciences Building, Edmonton,
AB T6G 2E3, Canada

W. D. Willms
Agriculture and Agri-Food Canada (Retired), 5403 1st
Avenue South, Lethbridge, AB T1J 4B1, Canada

northern temperate grasslands remain relatively resistant to grazing effects, including their susceptibility to exotic plant encroachment. These results improve our understanding of how ongoing grazing exposure may impact grassland diversity, including efforts to conserve native vegetation, as well as the important role of climate in altering fundamental grassland responses to grazing.

Keywords Aridity · Exotic vegetation · Long-term grazing · Native grassland · Plant diversity

Introduction

Livestock grazing impacts plant community composition, including vegetation structure and diversity (Milchunas and Lauenroth 1993; West 1993). In general, diverse assemblages of native species are a desirable characteristic of plant communities (Noss 1990), and in grasslands, diversity strengthens resilience to environmental stressors (Tilman 1997; Bai et al. 2007). Moreover, diversity is strongly associated with plant productivity, which contributes to the broader ecological goods and services of grasslands (Tilman et al. 1996). However, large-scale regional patterns of diversity are seldom examined, including the relation to ongoing land use such as livestock grazing. In this study, we use an expansive dataset from a large and agroclimatically diverse geographic region of northern temperate grasslands to examine plant diversity and compositional responses to grazing.

Plant community diversity change to ungulate herbivory can vary with environmental conditions, including regional variation in climate (Seabloom et al. 2013), the evolutionary history of grazing (Milchunas and Lauenroth 1993), as well as nutrient supply (Borer et al. 2014). More specifically, grasslands experiencing high moisture availability and a long adaptation period to large mammal herbivory tend to have greater plant diversity under moderate grazing compared to areas remaining non-grazed (Bai et al. 2001; Hart 1978; Mack and Thompson 1982). The removal of herbivory, however, has also been shown to increase native plant cover in global studies (Seabloom et al. 2015). The extent to which grassland diversity responses to long-term herbivory reflect changes in the presence and relative abundance of exotic plant species remains unclear, and requires the examination of both richness and abundance responses within these groups (Seabloom et al. 2013).

Previously documented impacts of grazing on plant community composition, including increased numbers of invasive plant species (Hobbs and Huenneke 1992), raises the possibility that grazing-induced changes in diversity are the result of the addition of exotic (i.e., non-native) species rather than changes in the composition of native flora. Given this limitation, it is important to improve our understanding of both native and exotic plant diversity change to long-term grazing, including how this may vary with environmental conditions, particularly regional climate patterns (Seabloom et al. 2013), which in grasslands often reflect aridity. This assessment will help investigate the influence of exotic species on overall grassland diversity, while assessing the susceptibility (and conversely, resistance) of grazed native plant communities to exotic plant encroachment. The latter has implications for conserving native flora, which remains an important objective in the management of many grasslands, including northern temperate regions (e.g., Burkinshaw and Bork 2009).

Resistance to exotic plant establishment has three primary elements (Lodge 1993a, b; Von Holle et al. 2003): environmental resistance (soil factors, temperature, etc.), biotic resistance (competition, availability of resources, presence of disease, etc.), and demographic resistance (volume of introduced propagules). Consistent with our understanding of niche theory, plant communities with greater diversity are considered more resistant to exotic plant entry due to greater inherent competitiveness (Elton 1958; Knops et al. 1999), and therefore should be easier to manage while conserving native flora. For example, within the wetter grasslands of SW Alberta studied here, greater densities of native bunchgrasses such as foothills rough fescue (*Festuca campestris* Rydb.) have been shown to reduce encroachment by the exotic rhizomatous grass Kentucky bluegrass (*Poa pratensis* L.) (Bork et al. 2017). Evolutionary history also plays a key role in determining invasibility (Alpert et al. 2000). Ecosystems with a long history of disturbance such as ungulate herbivory and competition may be less likely to have exotic species, with other factors known to be important including the proximity to cultivated lands and cover of existing native vegetation (Seabloom et al. 2013).

Similar to exotic species, there is evidence that woody species can increase in cover from ungulate herbivory (Asner et al. 2004; Archer et al. 1995; Dudwinnie 1977; Briggs et al. 2002). This is partly in response to a decline in the competitiveness of herbaceous species, but also changes in the distribution and abundance of soil nutrients. Studies examining the effect of livestock grazing on woody species are inconsistent though, with other investigations indicating grazing decreases woody species in temperate grasslands (Fitzgerald and Bailey 1984; Bork et al. 2013). From a global perspective, livestock grazing is generally thought to promote shrub encroachment (Asner et al. 2004; Eldridge et al. 2011), though few datasets have examined this phenomenon across a wide range of environmental conditions in relation to long-term livestock grazing.

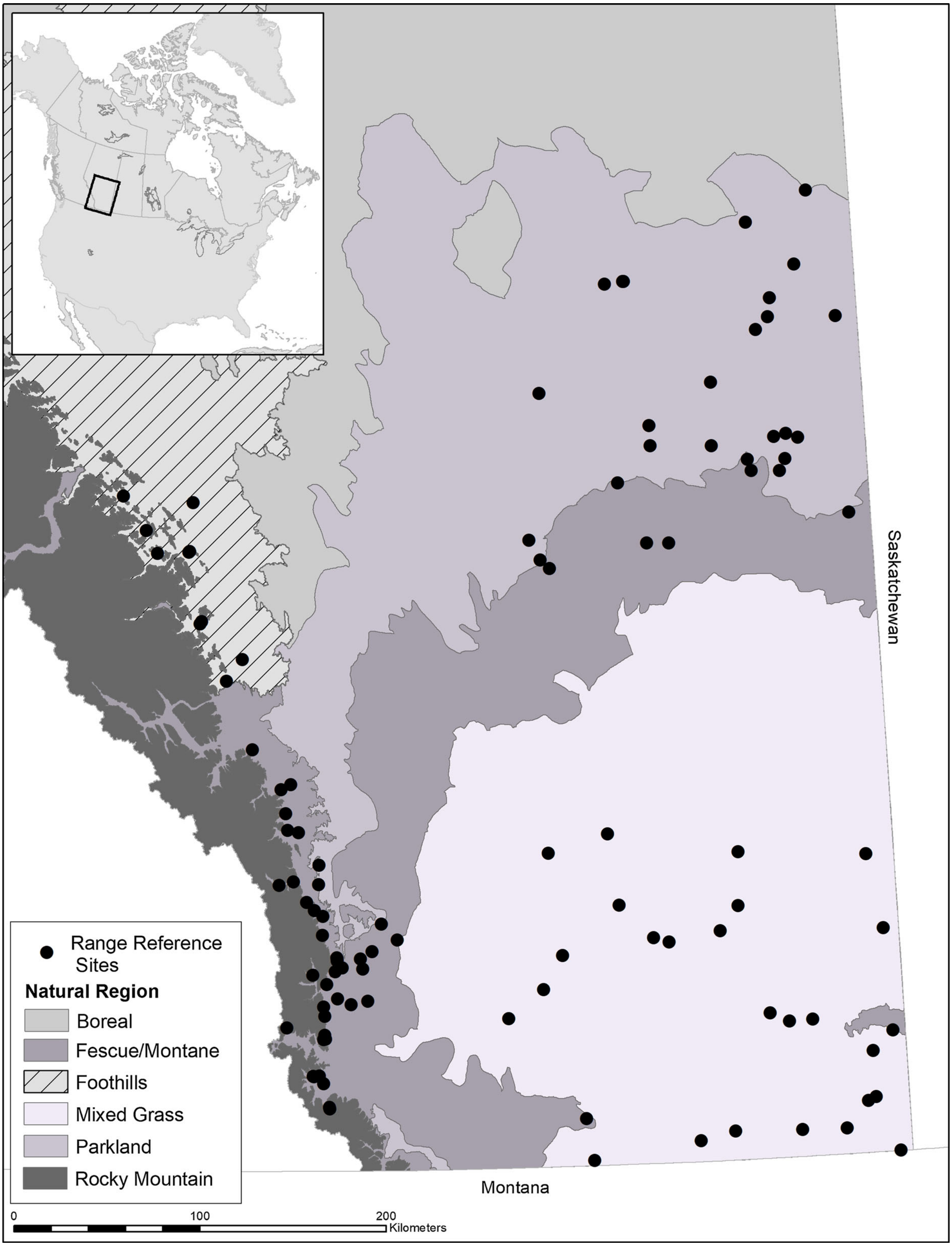
Previous studies examining the response of individual grassland communities are numerous, but often sacrifice geographic (and therefore environmental) replication in exchange for more detailed testing of specific treatments (e.g., on land use) within select locations. In general, few studies have addressed vegetation responses across a broad range of environmental conditions (but see Seabloom et al. 2013, 2015), and which allow for a robust assessment of generalized plant diversity assessment to livestock grazing. Within northern temperate environments, such analyses have recently been done for boreal forests (Mayor et al. 2012) and show plant diversity increases under moderate levels of industrial disturbance. However, Mayor et al. (2012) also found divergent patterns in the response of native and exotic plant species to disturbance; while native flora peaked under an intermediate disturbance intensity, exotic species increased linearly with disturbance. The lack of equivalent data from northern temperate grasslands is due to the limited availability of suitable study sites (i.e., sites with long-term comparisons of grazed and non-grazed conditions), the challenges associated with maintaining the infrastructure required for representative non-grazed controls, and the high costs of field sampling.

Here we utilize an existing dataset to evaluate relationships between grazing, aridity, and species diversity within a large number of northern temperate grasslands spanning a broad range of climatic conditions, and therefore associated soil and vegetation types, distributed across a large region of Alberta, Canada. We quantified the effect of long-term exposure to livestock grazing on total plant richness and diversity, exotic species presence (cover, richness, and contribution to diversity), and the cover of various vegetation components. More specifically we aimed to (1) determine if long-term grazing has a consistent and predictable impact on plant community composition (i.e., richness, evenness, and diversity) in northern temperate grasslands, including whether climatic conditions play a role in modifying the effects of grazing on grassland composition, and (2) investigate if long-term grazing influences the ‘footprint’ of exotic plants, as exhibited by the richness and abundance of exotic species, and explore the role that climate has on this relationship. Based on previous studies, and the location of the study area within an area with a long evolutionary history of grazing (Milchunas and Lauenroth 1993), we hypothesized that the presence of grazing would increase overall species diversity, including the contribution of grazing-tolerant exotic species richness, diversity, and cover. Second, we hypothesized that exotic richness, cover, and their contribution to overall diversity, will be greater in response to grazing within regions having greater resource availability (i.e., moisture).

Materials and methods

Field sites and study design

We used data from 107 grassland sites distributed throughout the south central region of Alberta, Canada (Fig. 1), covering an area of about 10 million ha. Sites were distributed across a wide range of grassland natural sub-regions, including the relatively arid Dry Mixedgrass and Mixedgrass plains, the hummocky moraine of the Central Parkland, and the distinctly hilly and topographically varied landscapes of the Foothills Fescue, Montane, and Upper Foothill natural sub-regions (Downing and Pettapiece 2006). As a result, the sites examined represent a wide range of climatic and edaphic conditions, as well as plant community composition (Table 1). All study sites were part of the Rangeland Reference Area (RRA) program established by Alberta Environment and Parks (AEP), which is an extensive network of fenced


Saskatchewan
Montana
Range Reference Sites
Natural Region
Boreal
Fescue/Montane
Foothills
Mixed Grass
Parkland
Rocky Mountain
0
100
200
Kilometers

◀**Fig. 1** Distribution of 107 rangeland reference area study sites across south central Alberta, Canada. Inset map indicates the location of the study region in North America

exclosures intended to monitor grassland responses with and without long-term grazing by livestock, predominantly cattle (Weerstra and Willoughby 1998). Exclosures had minimum dimensions of 18 m × 40 m, were occasionally larger (e.g., up to 30 × 50 m), and were at least 15 years old at the time of initial sampling, but ranged up to 62 years, and excluded cattle and feral horses using a four-strand barb wire fence approximately 1.2 m high. While not intentionally designed to eliminate use by wild ungulates (e.g., deer, moose, and elk), vegetation in the exclosures expressed minimal use by wildlife, presumably because of their small size, which is known to deter wildlife entry (Gross and Knight 2000).

A paired sampling design on the same ecosite (i.e., area of uniform growing conditions based on soil and topographic conditions) with the same level of prior disturbance at the time of exclosure establishment facilitated direct assessment of long-term livestock grazing impacts at each location. Allowable stocking rates for these grasslands ranged from 0.4 to 1.5 animal-unit-months (AUM) per ha (where an AUM is the forage required by one cow for a month) in the most arid and mesic sub-regions, respectively

Table 1 Summary of mean annual precipitation (MAP), mean annual temperature (MAT), annual heat:moisture index, and sub-region size, for each of the six different areas examined, as described by Downing and Pettapiece (2006)

Natural subregion	MAP (mm)	MAT (°C)	AHM index	Total area (ha)	% Native grassland	Dominant soil	Predominant vegetation	Production (kg ha^{-1})	Stocking rate (AUM ha^{-1})
Dry Mixedgrass (*n* = 17)	333	4.2	44.8	46,937	43	Brown Chernozem	*Hesperostipa comata* (BG), *Pascopyrum smithii* (RG), *Bouteloua gracilis* (RG)	700	0.7
Mixedgrass (*n* = 9)	394	3.9	36.3	20,072	15	Dark Brown Chernozem	*Hesperostipa curtiseta* (BG), *Pascopyrum smithii* (RG), *Elymus lanceolatus* (RG)	1000	1.0
Central Parkland (*n* = 26)	441	2.7	31.4	53,706	5	Thin Black Chernozem	*Festuca hallii* (RG), *Hesperostipa curtiseta* (BG), *Koeleria macrantha* (BG)	1800	1.2
Foothills Fescue (*n* = 7)	470	3.0	24.4	13,623	30	Black Chernozem	*Festuca campestris* (BG), *Danthonia parryi* (BG), *Festuca idahoensis* (BG)	2200	1.4
Montane (*n* = 37)	589	2.3	20.4	8768	> 90	Black Chernozem & Luvisols	*Festuca campestris* (BG), *Danthonia parryi* (BG), *Festuca idahoensis* (BG), *Poa pratensis* (RG)	2200	1.4
Upper Foothills (*n* = 11)	632	1.3	21.4	21,537	> 95	Brunisols & Luvisols	*Festuca campestris* (BG), *Deschampsia caespitose* (BG), *Poa pratensis* (RG)	2700	1.5

Also shown are the relative land areas remaining as native grassland, dominant soil and vegetation types, and typical annual production levels, as well as allowable livestock stocking rates on public lands. The number of study sites for each subregion is shown in parentheses. Species are denoted as either bunchgrasses (BG) or rhizomatous grasses (RG)

(Table 1). Grazing typically occurs during the growing season (June–October) and additional adjustments are made for variation in phenology and growing conditions. Although not quantified directly, intensities of herbage utilization within grazed grasslands outside each exclosure were light to moderate ($< 50\%$ biomass removal each growing season), consistent with grazing policy on public rangelands (Robertson et al. 1991).

Vegetation sampling and analysis

Vegetation was assessed at each location within non-grazed exclosures and adjacent grazed grassland every third year to assess comparative plant species composition over the period 2002 through 2012, thereby providing at least three, and up to four, sampling periods for each community. During each sampling event, 15 subsample quadrats (20×50 cm) were systematically located 2 m apart along permanent transects (33 m). The foliar cover of all plant species was assessed visually (to the nearest 1%) at peak vegetation growth between July and mid-August. Sampling was typically done earlier in the Mixedgrass prairie due to more advanced phenology (i.e., early July), and later in the Foothill, Montane, and Upper Foothill regions (late July through early August) due to delayed growth in elevated grasslands of those regions.

Climate data

Summary climate data were obtained for each study site. These included mean annual (30 years) precipitation (MAP), mean growing-season precipitation, mean annual (30 years) temperature (MAT), and an index of annual heat:moisture (AHM). Measures of AHM represent the aridity for each location and were calculated using the following equation: AHM = [(MAT + 10)/(MAP/1000)]. All climate metrics were derived for each site from the Climate AB 3.21 software package (http://tinyurl.com/ClimateAB), based on the methodology described by Mbogga et al. (2010) and Alberta Environment (2005). As all climate metrics were found to be highly correlated with one another ($|r| > 0.81$), we elected to use AHM for further analysis, as AHM simultaneously accounts for changes in moisture and temperature, and ultimately represents fundamental moisture limitations for plant growth. Values of AHM ranged from 14 to 53, and varied among natural sub-regions (see Table 1).

Data analysis

Individual plant species cover values for the subsampled quadrats were first averaged separately into grazed and non-grazed treatments for each year of sampling. Individual species values for grazed and non-grazed communities were then further averaged to derive single values for each plant species for the duration of time over which data were collected (2002–2012), thereby providing a long-term estimate of ‘average’ composition for each plant community (i.e., the experimental unit; $n = 214$). All species in the resulting dataset were further characterized by growth form (grass, forb or woody), rhizomatous or bunchgrass habit in the case of grasses, longevity (perennial or annual/biennial), and origin (exotic or native/endemic). All plant nomenclature followed Moss and Packer (1983) and Budd et al. (1987), including longevity and origin.

To assess overall plant diversity change to grazing and agroclimatic conditions, richness was determined as the total number of vascular species found in each community throughout the period during which vegetation data were collected. In addition, mean plant cover values were used to determine Simpson’s and Shannon’s diversity, as richness alone can be a poor determinant of grassland diversity change (Seabloom et al. 2013). The inverse Simpson’s index was calculated as follows: $\lambda = [1/(\Sigma(P_i)^2)]$, where P_i is the proportional cover of each plant species in relation to total cover. Shannon’s diversity was calculated using the formula: $H' = -\sum [P_i \times \log P_i]$, where P_i is the proportional abundance of each plant species relative to total plant cover. Both indices were assessed because they emphasize unique aspects of vegetation diversity, with the Simpson’s index emphasizing dominant species in the community and the Shannon’s index weighting all species equally (Kent and Coker 1992). Plant species evenness was calculated for each community as $E = H'/\log(\text{Richness})$. Finally, the relative contribution of exotic plant species to total richness and Shannon’s diversity were quantified by summing the proportion of all exotic species for each metric, as a percentage of total richness/diversity.

Measures of diversity and richness (both total and exotic plant species), together with the various cover components (described above), were evaluated using a Mixed Model analysis of variance (ANOVA) using SAS software (SAS Institute Inc., Cary, NC, USA), with two grazing (long-term grazed and non-grazed) treatments and AHM as fixed factors. The interaction of grazing × AHM was also tested. Blocked study locations were considered random in the analysis. All diversity metrics and cover data were checked for normality and equal variances prior to analysis, with no transformation required. Where grazing × AHM interactions occurred, emphasis during interpretation was on isolating grazing effects in relation to climate by separately modeling the grazed and non-grazed treatments against AHM, with regression used to obtain model coefficients. Where only AHM effects were evident, regressions were performed on data from both grazing treatments.

An indicator species analysis (ISA) was also completed for the vegetation composition data within each of the Mixedgrass (Dry Mixedgrass and Mixedgrass combined), Parkland, and Foothills/Montane (Upper Foothills, Foothills Fescue, and Montane combined) regions using PC Ord software (MJM Software Design, Gleneden Beach, Oregon, USA). An ISA is useful for detecting the response of individual plant species within a communal dataset to specific environmental conditions (Dufrêne and Legendre 1997), which in this study included the long-term presence and absence of grazing. More specifically, we were interested in identifying those species, both native and exotic in origin, responding either positively or negatively to grazing. ISA values ranged from 0 (no indication) to 100 (perfect indication between a species and the grazing treatment) and are derived from calculations of proportional abundance of a species within a treatment group, relative to the abundance of that species across all groups (McCune and Grace 2002). A Monte Carlo simulation, run 4999 times, was used to determine the probability that the maximum observed indicator value for a species differed from chance as obtained by randomly reassigned sample units. Data from the various natural sub-regions were aggregated to primary grassland biomes for this assessment, thereby increasing regional sample sizes, and allowing for generalized assessments of intra-specific responses within arid, semi-arid, and mesic environments. Significant indicator species scores were identified at an $\alpha \leq 0.05$.

Results

Vegetation cover responses

Total plant cover did not vary with grazing ($F_{1,105} = 0.46$; $P = 0.50$) or grazing × AHM ($F_{1,105} = 0.02$; $P = 0.90$), suggesting grazing did not alter the aggregate abundance of vegetation. Similar responses were observed for perennial plant cover in relation to grazing ($F_{1,105} = 0.31$; $P = 0.58$) and grazing × AHM ($F_{1,105} = 0.01$; $P = 0.93$). However, both the total cover of vegetation and that of perennial plants, were associated with the AHM index, in which cover declined under increasing AHM values (Table 2). Annual plant cover was also not affected by grazing ($F_{1,105} = 1.67$; $P = 0.19$), nor by the interaction of grazing × AHM ($F_{1,105} = 0.12$; $P = 0.73$), and was also unrelated to AHM ($F_{1,105} = 1.12$; $P = 0.29$).

Among growth forms, forb cover was not affected by grazing ($F_{1,105} = 0.82$; $P = 0.37$; Fig. 2), nor by its interaction with AHM ($F_{1,105} = 0.07$; $P = 0.79$). However, forb cover generally declined with increasing aridity as represented by high AHM values (Table 2). Live grass cover was impacted by grazing ($F_{1,105} = 5.18$; $P = 0.02$), being greater in the presence of livestock grazing (Fig. 2), with no further interaction with AHM ($F_{1,105} = 2.94$; $P = 0.09$). No differences were evident in the specific cover of rhizomatous grasses in relation to grazing ($F_{1,105} = 0.61$; $P = 0.44$), nor in combination with AHM ($F_{1,105} = 1.31$; $P = 0.26$). Bunchgrasses were similarly unaffected by grazing ($F_{1,105} = 3.15$; $P = 0.08$) or the interaction of grazing × AHM ($F_{1,105} = 1.13$; $P = 0.29$). Long-term exposure to grazing reduced woody cover in mesic sites rather than arid sites across the study area (grazing × AHM interaction: $F_{1,105} = 4.53$; $P = 0.04$; see Fig. 3).

Results of the indicator analysis revealed distinct plant species shifts in response to grazing (Table 3), which varied further by broad geographic regions. More specifically, mesic grasslands of the Foothills/Montane showed the largest number of plant species responding to long-term grazing presence. Several native species, such as *Festuca campestris, Geum*

Table 2 Overview of significant relationships between the annual heat moisture (AHM) index across study sites, and various plant community response metrics

Dependent response	Relationship	Adj. R^2	P value
Cover (%)			
Total vegetation[a]	$Y = 144.5 - 1.86x$	0.49	< 0.0001
Forb	$Y = 59.6 - 1.05x$	0.33	< 0.0001
Diversity			
Plant richness (#/1.5 m^2)	$Y = 51.7 - 0.56x$	0.22	< 0.0001
Inverse Simpson's	$Y = 12.41 - 017x$	0.15	< 0.0001

Response metrics were not impacted by the interaction of grazing × AHM ($P > 0.05$). AHM values ranged from 14.4 to 50.1 among the 107 study sites, with increasing values indicative of greater aridity

[a] The relationship for perennial cover was similar to that of total cover

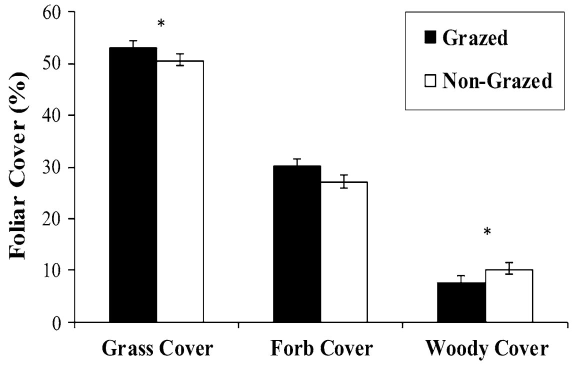


Fig. 2 Comparative response of grass, forb, and shrub cover (± 1 SE) in relation to long-term grazing exposure across 107 northern temperate grassland study sites in Alberta, Canada. Within a growth form, an * indicates differences at $P < 0.05$

aleppicum, Epilobium angustifolium, and *Juniperus horizontalis*, had a negative response to grazing. Conversely, many exotic plant species, such as *Trifolium repens, Trifolium pratense, Taraxacum officinale, Ranunculus acris, Poa pratensis,* and *Phleum pratense,* all increased with exposure to grazing in the Foothills/Montane area.

Species diversity change to grazing

Species richness was greater in areas exposed to livestock grazing ($F_{1,105} = 4.28$; $P = 0.04$), with grazed areas having an average of 3.1 more plant species than non-grazed areas (36.7 species per 1.5 m^2 sampled, and 33.6 species per 1.5 m^2 ± 1.0 SE, respectively). No grazing effects were evident on Shannon's diversity ($F_{1,105} = 0.05$; $P = 0.48$), inverse Simpson diversity ($F_{1,105} = 1.67$; $P = 0.20$), nor species evenness ($F_{1,105} = 0.02$; $P = 0.89$). Additionally, none of these overall diversity metrics were effected by a grazing × AHM interaction ($F_{1,105} \leq 1.22$; $P \geq 0.27$). Finally, both species richness and inverse Simpson diversity declined in relation to increasing AHM (i.e., greater aridity) across study sites (Table 2). However, neither Shannon's diversity nor evenness were related to AHM ($F_{1,105} \leq 2.23$; $P \geq 0.14$).

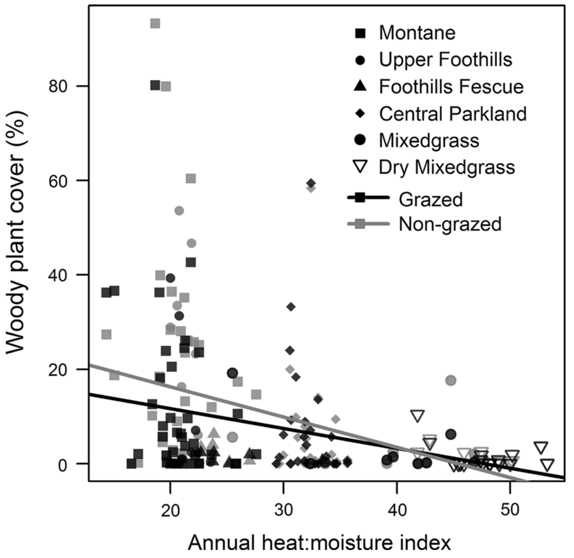


Fig. 3 Relationship of woody cover to annual heat:moisture index (AHM) across 107 study sites, for each of the long-term grazed and non-grazed study sites. Grazed: $Y = 20.1 - 0.42x$ (Adj. $R^2 = 0.095$, $P < 0.001$); Non-grazed: $Y = 29.1 - 0.64x$ (Adj. $R^2 = 0.14$, $P < 0.0001$)

Table 3 Results of the indicator species analysis relating individual plant species cover responses to the long-term presence or absence of grazing in each of three grassland regions of Alberta, Canada

Indicator plant species[a]	Sites[b]	Growth form	Grazing response[c]	Observed	Random	SD	P value
Mixedgrass (175 species) (n = 26)							
Elymus lanceolatus	25	Perennial rhizomatous grass	−	70.4	56.7	6.45	0.033
Gaillardia aristata	5	Perennial forb	+	18.9	10.3	3.90	0.044
Plantago patagonica	13	Perennial forb	+	35.3	23.9	5.66	0.047
Parkland (200 species) (n = 26)							
Agrostis scabra	18	Perennial bunchgrass	+	52.5	33.6	6.97	0.017
Androsace septentrionalis	17	Annual forb	+	49.7	36.1	6.33	0.036
Antennaria aprica	10	Perennial forb	+	31.4	19.7	5.60	0.041
Heterotheca villosa	7	Perennial forb	+	22.4	12.4	4.37	0.028
Silene nocturna (E)	8	Perennial forb	+	31.4	17.1	4.91	0.014
Sisyrinchium montanum	10	Perennial forb	+	39.8	19.3	5.28	0.003
Foothills/Montane (329 species) (n = 55)							
Epilobium angustifolium	18	Perennial forb	−	27.6	17.3	3.80	0.018
Festuca campestris	44	Perennial bunchgrass	−	50.8	41.3	3.44	0.015
Geum aleppicum	16	Perennial forb	−	24.7	16.3	3.61	0.029
Juniperus horizontalis	7	Creeping shrub	−	10.9	6.2	2.10	0.035
Koeleria macrantha	42	Perennial bunchgrass	+	50.1	37.9	4.64	0.017
Muhlenbergia richardsonis	15	Perennial bunchgrass	+	25.6	11.3	2.96	< 0.001
Phleum pratense (E)	35	Perennial rhizomatous grass	+	48.4	29.9	4.49	0.002
Poa pratensis (E)	55	Perennial rhizomatous grass	+	59.5	51.3	3.18	0.020
Potentilla gracilis	35	Perennial forb	+	57.4	43.3	4.30	0.007
Ranunculus acris (E)	6	Perennial forb	+	10.8	7.2	2.43	0.048
Sisyrinchium montanum	18	Perennial forb	+	25.1	15.7	3.25	0.014
Taraxacum officinale (E)	49	Perennial forb	+	70.2	45.8	4.86	< 0.001
Trifolium pratense (E)	11	Perennial forb	+	20.0	8.6	2.79	< 0.001
Trifolium repens (E)	16	Perennial forb	+	27.2	11.2	2.92	< 0.001

Only those species are shown where the Observed IV differs from the Random IV (at $P < 0.05$) based on 999 permutations. Values in parentheses are the total number of plant species documented

[a] Exotic plant species are denoted with (E)

[b] Value indicates the frequency of sites containing a given indicator species

[c] A (+) indicates an increase in cover when exposed to grazing (outside of exclosure) and a (−) indicates a decrease in cover under grazing

Exotic species responses to grazing

Exotic species richness was effected by the interaction of grazing × AHM ($F_{1,105} = 7.80$; $P < 0.01$). In the absence of grazing, exotic richness did not vary with AHM, while exposure to grazing generally increased the likelihood of exotic species presence, particularly in low AHM (mesic) environments (Fig. 4). Similar to richness, the proportion of Shannon's diversity comprising exotic plant species was effected by the interaction of grazing × AHM ($F_{1,105} = 3.64$; $P = 0.05$). While non-grazed areas exhibited a small increase in the presence of exotic species with declining AHM, this increase was more pronounced in the presence of long-term grazing (Fig. 4).

Finally, total cover of exotic plant species was effected by the interaction of grazing × AHM ($F_{1,105} = 9.09$; $P < 0.001$). Elevated levels of exotic plant cover were most evident in grasslands with low AHM, and were particularly apparent in the presence

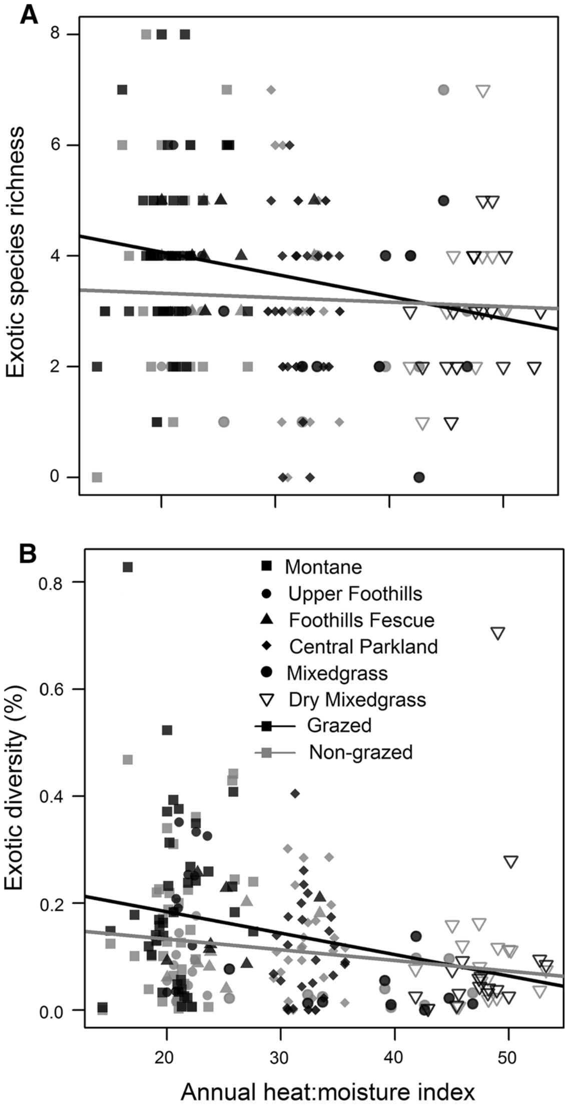


Fig. 4 Relationship of **a** exotic plant richness and **b** the proportion of Shannon's diversity comprising exotic plant species, to annual heat:moisture index (AHM) values across 107 study sites, for each of the long-term grazed and non-grazed study sites. Exotic richness Grazed: $Y = 4.87 - 0.04x$ (Adj. $R^2 = 0.078$, $P = 0.002$); Exotic richness Non-grazed: $Y = 3.49 - 0.008x$ (Adj. $R^2 = 0.007$, $P = 0.62$); Proportion exotic diversity Grazed: $Y = 0.264 - 0.004x$ (Adj. $R^2 = 0.072$, $P = 0.003$); Proportion exotic diversity Non-grazed: $Y = 0.173 - 0.002x$ (Adj. $R^2 = 0.035$; $P = 0.03$)

of grazing than without (Fig. 5). Total native cover demonstrated a reciprocal grazing × AHM response ($F_{1,105} = 4.22$; $P = 0.04$) to that of exotic cover; native cover was greater in non-grazed exclosures than adjacent grazed areas, but these differences were again more apparent in moist (low AHM) environments (Fig. 5).

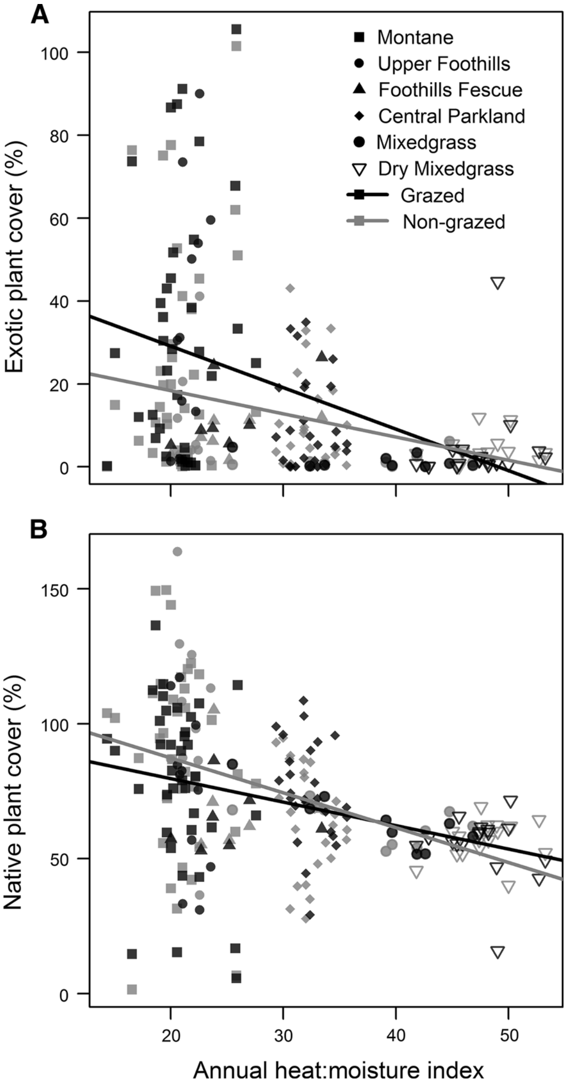


Fig. 5 Relationship of **a** exotic plant cover and **b** native plant cover, to annual heat:moisture index (AHM) values across 107 study sites, for each of the long-term grazed and non-grazed study sites. Exotic cover Grazed: $Y = 49.1 - 1.00x$ (Adj. $R^2 = 0.162$, $P < 0.001$); Exotic cover Non-grazed: $29.6 - 0.56x$ (Adj. $R^2 = 0.082$, $P = 0.002$); Native cover Grazing: $Y = 97.1 - 0.87x$ (Adj. $R^2 = 0.123$, $P < 0.0001$); Native cover Non-grazed: $Y = 113.1 - 1.29x$ (Adj. $R^2 = 0.194$; $P < 0.0001$)

Discussion

Diversity change to long-term grazing

In relation to our first hypothesis, we detected a modest increase (i.e., ~ 9%) in plant richness across study sites in relation to grazing, with no further response in other diversity metrics, including Shannon's and Simpson diversity, nor evenness. Instead, all diversity metrics and the cover of different growth forms were more dependent on climatic conditions, with increasing aridity leading to direct reductions in richness and diversity. The increased richness observed under grazing was consistent with theory suggesting moderate grazing favors a larger number of plant species (Milchunas et al. 1988), including western Canada (Bai et al. 2001). Mid-seral ecological conditions are thought to result in a combination of grazing-tolerant and grazing-intolerant plant species (Grime 1973). While grazing did manifest in plant compositional changes within our study, including the abundance of exotic and native plant species (discussed below), it translated into limited detectable diversity increases (i.e., richness) under grazing within these temperate grasslands. Collectively, these findings suggest that any vegetation change occurring under long-term grazing are likely the result of both species addition, represented here by exotic plants, as well as species replacement (i.e., the loss and/or decline of natives), which together would reduce the sensitivity of total diversity change to grazing treatment. The limited overall diversity change in our study may also reflect relatively low grazing intensities, as allowable livestock stocking rates on public land in our study area are conservative, and typically allow for only 25% utilization of available herbage during any one growing season (Adams et al. 2013). This may have limited grazing-induced changes in plant diversity, which in turn, could have remained below detectable levels for most diversity metrics assessed, even despite some changes in the identity and abundance of different plant species under grazing.

Finally, we point out that our study region coincides with an area known to have a long evolutionary history of grazing by herbivores (Milchunas and Lauenroth 1993), including large herds of bison (Morgan 1980). It is therefore possible that the non-grazed treatments examined here, specifically the use of small exclosures wherein most large herbivore grazing was removed, may represent a marked deviation from the historical disturbance regime. This, in turn, could limit the utility of exclosed areas for evaluating plant diversity, including when scaling up to the landscape level (Stohlgren et al. 1999). For example, it is possible that vegetation composition within our study exclosures may have been influenced by propagule pressure originating from immediately adjacent grazed areas (Valdivia and Simonetti 2007), in essence limiting any differences in diversity expression between grazing treatments.

Despite the limited diversity change to grazing, the cover of some vegetation components did vary in response to long-term grazing exposure. In particular, live grass cover increased in the presence of grazing, a response that was consistent across all study sites, and suggests that the maintenance of grass vigor may rely on at least some ongoing defoliation. While previous studies have found a key role of herbivory in maintaining plant productivity (e.g., Sims and Singh 1978), these effects were limited to higher rainfall environments (e.g., > 500 mm annual precipitation) where litter accumulation can negatively impact plant growth in non-grazed areas through reduced light availability, water interception, and slower decomposition (e.g., Bardgett and Wardle 2003). Notably, the only sites that had favorable moisture conditions within our study region were the high rainfall environments of the Montane and Upper Foothills, which represented almost half of our study sites. Despite this, our increase in grass cover, which remained rather modest at 5%, was more widely applicable across a range of moisture conditions, potentially due to the long-term nature of our grazing-exclusion treatments, which could have allowed litter to accumulate for extended periods, even in arid regions.

We also found an interaction of grazing with climate on shrub cover across our study area. Within arid regions, grasslands subject to grazing tended to have more shrubs, consistent with the notion that grazing, particularly by cattle, may reduce competition from herbaceous vegetation on shrubs and thereby facilitate an increase in shrub cover (Asner et al. 2004; Eldridge et al. 2011). However, the opposite pattern was evident in high moisture environments of our study region, where favorable moisture led to greater shrub cover, but largely within non-grazed exclosures. While allowable livestock stocking rates on all study sites were relatively low, variable topography in the

Montane and Upper Foothill regions can markedly impact observed patterns of grassland use by livestock, with greater use in lowlands (Willms 1988; Kaufmann et al. 2013) wherein exclosures are often located. Additionally, areas in the Upper Foothills are known to have experienced shrub encroachment and an associated decline in ungulate carrying capacity (Burkinshaw and Bork 2009), and over time under stable livestock stocking rates, this may increase localized grazing intensity on remaining grasslands to the point of impacting shrubs. Should this be the case, livestock grazing may be an unintended mechanism responsible for helping control shrub abundance (and encroachment) within mesic grasslands, particularly in the absence of other means of shrub control such as fire. Finally, while native ungulates had access to the exclosures, we are unable to rule out the possibility that the small size of fenced areas may have deterred wildlife from browsing within them (Gross and Knight 2000), thereby further contributing to woody encroachment.

Grazing impacts on exotic species

Increasing attention is being paid to understanding and managing exotic species, particularly with species migration becoming more common globally (van Kleunen et al. 2015). Regionally, the conservation of native plant communities will depend on an understanding of how the presence of exotic vegetation contributes to diversity change under grazing. Consistent with our second hypothesis, we found that exotic species richness, exotic cover, and the contribution of exotic species to Shannon's diversity, all increased with exposure to long-term grazing, but only under certain climatic conditions. More specifically, the presence of exotic plant species within these northern temperate grasslands increased as water became less of a limiting factor for plant growth, such as within the Montane and Upper Foothill regions. These findings are consistent with Seabloom et al. (2013) and suggest the combination of moist conditions and ongoing disturbance from livestock and other large herbivores may favor the establishment and propagation of exotic plant species in these grasslands. Within grazed areas of the Upper Foothills (the area with the lowest AHM index; Table 1), exotic species comprised up to 34% of total cover, but remained at 8% cover in non-grazed areas. While some legacy effects of grazing prior to exclosure establishment may have existed within these grasslands, unpublished data from these sites indicate that in the years following exclosure establishment non-grazed grasslands were dominated by native vegetation, but in some instances have since become co-dominated by exotic species, including *Poa pratensis*. The latter has occurred even in the absence of grazing, and appeared to coincide with periods of elevated precipitation (Government of Alberta 2017).

While the ultimate cause of the increase in exotic species remains unclear, a number of factors may play a role. As noted earlier, increased grazing pressure in a landscape of declining grassland in SW Alberta may lead to higher localized grazing intensities by both cattle (Willms 1988; Kaufmann et al. 2013), and where present, feral horses (Girard et al. 2013). Together, this incremental use may favor the invasion of exotic plant species that possess superior defoliation tolerance, which includes *Poa pratensis*, *Phleum pratense*, *Taraxacum officinale*, and various *Trifolium* spp., all of which were indicators of long-term grazing in our study and are known to respond positively to grazing (Willms et al. 1985; Bork et al. 2012).

Increases in exotic vegetation have been found in relation to disturbance intensity within the adjacent boreal forest of northern Alberta (Mayor et al. 2012). Unfortunately, the lack of localized grassland utilization data for individual sites in our study precludes the assessment of varied grazing intensity on exotic species. The inclusion of livestock utilization measurements during future monitoring could help further elucidate the role of grazing intensity on diversity change, including exotic species. Additionally, we note that exotic vegetation establishment in the relatively small and fragmented area of grasslands remaining in SW Alberta is likely to be aided by many other disturbances, including oil and gas extraction and transport, commercial forestry, urban–industrial sprawl, nearby cultivation, and widespread recreational activities. Proximity to other disturbances, including cultivation, is known to be a factor responsible for increasing exotic species presence in grasslands (Seabloom et al. 2013). In contrast, many of the grasslands in the Mixedgrass Prairie are situated in a region with high levels of intact prairie, with as much as 43% of the Dry Mixedgrass Prairie remaining non-cultivated (Adams et al. 2013). Reduced cultivation in turn, is likely an important factor responsible for limiting the overall presence and abundance of exotic plant species in that region.

Our results also provide clarity on the inherent resistance of non-grazed grasslands to exotic species invasion. Within our study both exotic richness and diversity remained consistent across all climatic regions in the absence of grazing ($\sim$ 10% of vegetation, see Fig. 4), suggesting relatively high resistance to the entry of new exotic plant species. Unlike richness, however, exotic plant cover increased under greater moisture in the absence of grazing (Fig. 5), a pattern that presumably reflects enhanced growth of already established exotic plant species under favorable growing conditions. Competition from the existing native plant community therefore appeared to be less important in resisting exotic plant growth within mesic areas, and is consistent with previous studies in the region (Lamb and Cahill 2008). Notably, the inverse pattern evident in native and exotic vegetation cover in relation to grazing, and regardless of climatic regime, suggests that the grazing-induced condition of native vegetation may play an important role in regulating exotic species abundance, presumably via changes in interspecific competition (Lamb and Cahill 2008). In general, there is evidence that some exotic species are less competitive in environmentally stressed conditions, such as those with low moisture and nutrient availabilities (Nernberg and Dale 1997; MacDougall and Turkington 2005). These conclusions are partly corroborated here by findings that study sites with moderate to high aridity (i.e., the Parkland and Mixedgrass Prairie) generally had a lower relative presence of exotic vegetation, both with and without long-term grazing.

Finally, it is important to review the potential implications of increased exotic plant richness and abundance on ecosystem function. While exotic species may pose a risk of reducing native plant cover (i.e., displacement) under chronic grazing (Willms et al. 1985), and in particular by aggressive noxious weed species (e.g., *Ranunculus acris* in Table 3), exotic species may remain important in providing ground cover, stabilizing soil, and ultimately producing biomass for forage and/or habitat cover for livestock and wildlife. Thus, the mere presence of exotic species alone may not be as great a concern as the type and abundance of particular exotic species, and warrants closer examination.

Conclusion

This study reports on the long-term effects of grazing on grassland diversity, composition, and exotic plant presence, across a widely dispersed network of 107 study sites representing a range of agroclimatic conditions. Long-term grazing led to minor increases in plant richness, but not diversity or evenness, within these northern temperate grasslands, and were accompanied by modest changes in vegetation composition and cover. Long-term grazing generally increased grass cover and reduced woody species cover, the latter in high moisture environments, suggesting a role of grazing in maintaining grassland presence and productivity. Unlike overall diversity metrics, exotic species richness, cover, and their contribution to diversity, all increased markedly with exposure to grazing, but only under greater levels of moisture (i.e., reduced aridity). In contrast, non-grazed grasslands had relatively high resistance to exotic plant presence, as did arid grazed grasslands, suggesting both grazing and resource availability are important factors that combine to alter exotic species abundance in northern temperate grasslands. Further research is needed to determine whether and how exotic plant species are impacting ecological goods and services, such as faunal diversity, watershed function, or carbon storage, before this information is likely to affect management.

Acknowledgements Funding for this project was provided by a Strategic Grant from the Alberta Livestock and Meat Agency, with additional support from Alberta Environment and Parks. We are grateful to the numerous AEP staff, specifically Kevin France, Craig Demaere, Jennifer Richman, Laura Blonski, Tennille Kupsch, Terri France, Darlene Moisey, Barry Adams, Tanner Broadbent, and Mike Willoughby, for allowing access to the Rangeland Reference Areas and helping with data collection. We also thank the following individuals for technical field assistance: Mark Donner, Ian Brusselars, Donald Schoderbek, and Leah Rodvang, and special thanks to Sarah Green for assisting with the graphics.

References

Adams BW, Richman J, Poulin-Klein L, France K, Moisey D, McNeil RL (2013) Rangeland plant communities for the dry mixedgrass natural subregion of Alberta, second approximation. Pub. T/040. Rangeland Management Branch Policy Division, Alberta Environment and Sustainable Resource Development, Lethbridge, p 135

Alberta Environment (2005) Alberta climate model (ACM) to provide climate estimates (1961–1990) for any location in Alberta from its geographic coordinates. Alberta Environment, Edmonton, AB, Publ. No. T/749. ISBN No. 0-7785-3939-3

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invisibility and the role of environmental stress in the spread of non-native plants. Persp Plant Ecol Evol Syst 3:52–66

Archer S, Schimel DS, Holland EA (1995) Mechanisms of shrubland expansion: land-use, climate or CO_2. Clim Change 29:91–99

Asner GP, Elmore AJ, Olander LP, Martin RE, Harris AT (2004) Grazing systems, ecosystem responses, and global change. Ann Rev Env Res 29:261–299

Bai YG, Abouguendia Z, Redmann RE (2001) Relationship between plant species diversity and grassland conditions. J Range Manage 54:177–183

Bai Y, Wu J, Pan Q, Huang J, Wang Q, Li F, Buyantuyev A, Han X (2007) Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe. J Appl Ecol 44:1023–1034

Bardgett RD, Wardle DA (2003) Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84:2258–2268

Borer ET, Seabloom EW, Mitchell CE, Cronin JP (2014) Multiple nutrients and herbivores interact to govern diversity, productivity, composition, and infection in a successional grassland. Oikos 123:214–224

Bork EW, Willms W, Tannas S, Alexander M (2012) Seasonal patterns of forage availability in the fescue grasslands under contrasting grazing histories. Rangel Ecol Manage 65:47–55

Bork EW, Carlyle CN, Cahill JF, Haddow RE, Hudson RJ (2013) Disentangling herbivore impacts on *Populus tremuloides*: a comparison of native ungulates and cattle in Canada's Aspen Parkland. Oecologia 173:895–904

Bork EW, Hewins DB, Tannas S, Willms WD (2017) *Festuca campestris* density and defoliation regulate abundance of the rhizomatous grass *Poa pratensis* in a fallow field. Rest Ecol. https://doi.org/10.1111/rec.12532

Briggs JM, Knapp AK, Brock BL (2002) Expansion of woody plants in Tallgrass Prairie: a fifteen-year study of fire and fire-grazing interaction. Am Mid Nat 147:287–294

Budd AC, Looman J, Best KF (1987) Budd's flora of the Canadian prairie provinces. Agriculture Canada Research Branch, Ottawa, p 863

Burkinshaw AM, Bork EW (2009) Shrub encroachment impacts the potential for multiple use conflicts on public land. Environ Manage 44:493–504

Downing DJ, Pettapiece WW (2006) Natural regions and subregions of Alberta. Pub T/852. Government of Alberta, Edmonton

Dudwinnie PW (1977) Recent tree invasion of subalpine meadows in the Wind River Mountains, Wyoming. Artic Alp Res 9:393–399

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345–366

Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitform WG (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol Lett 14:709–722

Elton C (1958) The ecology of invasion by animals and plants. Methuen and Co Ltd, London

Fitzgerald RW, Bailey AW (1984) Control of aspen regrowth by grazing with cattle. J Range Manage 37:156–158

Girard TL, Bork EW, Nielsen SE, Alexander MJ (2013) Seasonal variation in habitat selection by free-ranging feral horses within Alberta's Forest Reserve. Rangel Ecol Manage 66:428–437

Government of Alberta (2017) Cattle river range reference area report. ISBN: 978-1-4601-2893-0, p 9

Grime JP (1973) Control of species density in herbaceous vegetation. J Env Manage 1:151–167

Gross JA, Knight JE (2000) Elk presence inside various-sized cattle exclosures. J Range Manage 53:287–290

Hart RH (1978) Stocking rate theory and its application to grazing on rangelands. In: Proceedings of the 1st International Rangeland Congress, Peerless Printing, Denver, Colorado, USA, pp. 547–550. ISSN 0163-173X

Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implication for conservation. Cons Biol 6:324–337

Kaufmann J, Bork EW, Blenis PV, Alexander MJ (2013) Cattle habitat selection and associated habitat characteristics under free-range grazing within heterogeneous Montane rangelands of Alberta. Appl Animal Behav Sci 146:1–10

Kent M, Coker P (1992) Vegetation description and analysis: a practical approach. CRC Press, Boca Raton, p 363

Knops JM, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol Lett 2:286–293

Lamb EG, Cahill JF (2008) When competition does not matter: grassland diversity and community composition. Am Nat 171:77–787

Lodge DM (1993a) Species invasion and selections: community effects and responses to climate and habitat change. In: Karieva PM, Kingsolver JG, Huey RB (eds) Biotic interactions and global change. Sinauer Associates, Sunderland, pp 367–387

Lodge DM (1993b) Biological invasions: lessons for ecology. Trends Ecol Evol 8:133–137

MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42–55

Mack RN, Thompson JN (1982) Evolution in steppe with few large, hooved mammals. Am Nat 119:757–773

Mayor SJ, Cahill JF Jr, He F, Solymos P, Boutin S (2012) Regional boreal biodiversity peaks at intermediate human disturbance. Nat Comm 3:1142

Mbogga MS, Hansen C, Wang W, Hamann A (2010) A comprehensive set of interpolated climate data for Alberta. Pub. No. T/235. Government of Alberta, Edmonton, p 7

McCune B, Grace JB (2002) Analysis of ecological communities. MJM Software, Gleneden Beach, p 300

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

Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. Am Nat 132:88–106

Morgan RG (1980) Bison movement patterns on the Canadian plains: an ecological analysis. Plains Anthropol 25:143–160

Moss EH, Packer JG (1983) Flora of Alberta: a manual of flowering plants, conifers, ferns, and fern allies found growing without cultivation in the province of Alberta. University of Toronto Press, Toronto, p 685

Nernberg D, Dale MR (1997) Competition of five native prairie grasses with Bromus inermis under three moisture regimes. Can J Bot 75:2140–2145

Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. Cons Biol 4:355–364

Robertson A, Adams BW, Ehlert G (1991) Livestock distribution on rangelands. Range Notes 12 No. T/207

Seabloom EW, Borer ET, Buckley Y, Cleland EE, Davies K, Fim J, Harpole WS, Hautier Y, Lind E, Macdougall A et al (2013) Predicting invasion in grassland ecosystems: is exotic dominance the real embarrassment of richness? Glob Change Biol 19:3677–3687

Seabloom EW, Borer ET, Buckley YM, Cleland EE, Davies KF, Firn J, Harpole WS, Hautier Y, Lind EM, MacDougall AS, Orrock JL (2015) Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. Nat Comm. https://doi.org/10.1038/ncomms8710

Sims PL, Singh JS (1978) The structure and function of ten western North American grasslands: III. Net primary production. J Ecol 66:573–597

Stohlgren TJ, Schell LD, Vanden Heuvel B (1999) How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecol Appl 9:45–64

Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720

Valdivia CE, Simonetti JA (2007) Decreased frugivory and seed germination rates do not reduce seedling recruitment rates of *Aristotelia chilensis* in a fragmented forest. Biodivers Conserv 16:1593–1602

van Kleunen M, Dawson W, Franz E, Pergl J, Winter M, Weber E, Kreft H, Weigelt P et al (2015) Global exchange and accumulation of non-native plants. Nature 525:100–103

Von Holle B, Delcourt HR, Simberloff D (2003) The importance of biological inertia in plant community resistance to invasion. J Veg Sci 14:425–432

Weerstra BG, Willoughby MG (1998) Rangeland reference areas. Alberta Environment. Lands and Forest Service Dept, Edmonton, p 178

West NE (1993) Biodiversity of rangelands. J Range Manage 46:2–13

Willms WD (1988) Forage production and utilization in various topographic zones of the Fescue Grasslands. Can J Animal Sci 68:211–223

Willms WD, Smoliak S, Dormaar JF (1985) Effects of stocking rate on a rough fescue grassland vegetation. J Range Manage 38:220–225