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Invasion or retreat? The fate of exotic invaders on the northern prairies, 40 years after cattle grazing

Peter A. Sinkins · Rafael Otfinowski

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Abstract Despite the detrimental impacts of invasive plants on native biodiversity, ecosystem function, and management cost, few studies have focused on the long-term persistence of invaders. Here, we use a unique, long-term dataset to examine the recovery of northern rough fescue prairie communities, 41 years after the removal of livestock from Riding Mountain National Park, Manitoba, Canada. Our 1973 data suggest that summer grazing of plains' rough fescue (*Festuca hallii* (Vasey) Piper) leads to its displacement from the plant community and increased dominance by exotic invaders. After 41 years of recovery time, historic grazing intensity remained an excellent predictor of community structure and composition. Areas classified as heavily grazed in 1973 remained characterized by exotic grasses and had significantly lower richness and diversity. While some exotic invaders persisted despite 41 years of community recovery, others were ephemeral. For example, both *Poa pratensis* (L.) and *Bromus inermis* (Leyss.) persisted, increasing in abundance across all classes of grazing intensity, suggesting that their control requires active restoration of the invaded areas. In contrast, passive restoration may be possible for a subset of ephemeral exotic species such as *Taraxacum officinale*, which had virtually disappeared from invaded prairies by 2010. Our long-term data provide a rare perspective into the long-term dynamics of plant invasions. Based on our findings, conservation managers will need to consider the dichotomy between persistent and ephemeral invaders and their impact on the recovery of northern prairie communities as they focus their restoration efforts against the mounting impacts of exotic plant invaders.

Keywords Grassland restoration · Northern fescue prairie · Grazing intensity · *Bromus inermis* · *Festuca hallii* · *Poa pratensis*

Introduction

Invasive plants pose a serious threat to the endemic biodiversity and function of ecosystems (D'Antonio and Vitousek 1992; Davis 2003; Yurkonis et al. 2005; Grant et al. 2009) and a growing cost to conservation and resource managers (Colautti et al. 2006). While a

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P. A. Sinkins (✉)
Riding Mountain National Park, Parks Canada,
Wasagaming, MB R0J 2H0, Canada
e-mail: p.sinkins@gmail.com

R. Otfinowski
Western and Northern Service Centre, Parks Canada,
Winnipeg, MB R3B 0R9, Canada

Present Address:
R. Otfinowski
Department of Plant Science and the McGill School of
Environment, McGill University, 21,111 Lakeshore Road,
Ste. Anne de Bellevue, QC H9X 3V9, Canada

large number of exotic species do not become serious invaders, contributing instead to local species richness (Williamson and Fitter 1996; Rosenzweig 2001), the few that do become invasive have serious impacts on biodiversity and ecosystem function (Vilà et al. 2009; Davies 2011). Although many studies assume that the invasiveness of a species will continue to increase as a function of its residence time (Ahern et al. 2010; de Albuquerque et al. 2011, see Rejmanek et al. 2005 for review), few incorporate sufficiently long temporal scales to evaluate long-term changes in ecological communities that determine the persistence of exotic organisms (Usher 1988; Dietz and Edwards 2006). Where long-term data are available, observations of the persistence of exotic invaders offer mixed results. For example, Forcella and Harvey (1983) reported the long-term persistence among species of *Echium* (Boraginaceae), while Perrins et al. (1993) observed local extinctions of species of *Impatiens* (jewelweed). Following extensive observation of the exotic flora of woollen mills around Montpellier (France) and Tweedside (Scotland), Crawley (1987) reported their failed persistence, where among the 348 exotic plants present on the gravel banks of the River Tween in 1919 none were found in 1987. The persistence of a small number of exotic species has been articulated as the "tens rule," defining a small (<10 %) subset of imported species that appear in the wild, establish, and cause ecological damage (Williamson and Fitter 1996). It is this proliferation and persistence of a subset of exotic species that motivates and helps to prioritize management and the active restoration of invaded communities (Holl and Aide 2011).

Since exotic species often respond positively to the disturbance in the early stages of their establishment (Davis et al. 2000; Fansler and Mangold 2011), disturbed ecosystems are important for investigating the proliferation and persistence of invaders. Within protected areas, restoration of disturbed communities offers a unique opportunity to investigate the fate of introduced exotic invaders. Many protected areas contain anthropogenic disturbances that predate park establishment or reflect more intense, historic use of park resources (McKinney 2002). Our research focuses on the long-term recovery of northern fescue prairies following the removal of domestic cattle grazing. Although intense grazing of prairie communities leads to large changes in their flora (Peper et al. 2011), research demonstrating long-term recovery of disturbed communities is often lacking for the northern prairies (Johnston et al. 1971; Willms et al. 1985; Dietz and Edwards 2006, but see Frank et al. 1995). Here, we explore the hypothesis that a large number of exotic invaders correlated with intense grazing are ephemeral. Focusing on northern fescue prairies in Riding Mountain National Park, MB, Canada, we explored whether the long-term recovery of disturbed prairies is confounded by a small number of persistent invaders. By helping to distinguish between ephemeral and persistent invaders, our work will improve the conservation management of remnant protected prairie ecosystems in western Canada.

Methods

Study area

Research was conducted in Riding Mountain National Park (RMNP), MB, Canada. The park occupies an area of 2,978 km^2 in western Canada (Latitude: 50.6580 Longitude: −99.9721) (Fig. 1) and consists of large areas of rolling upland (Elevation: 550–640 m), underlain by glacial tills (Lang 1974). The region is characterized by mean annual precipitation of 450–500 mm and a growing season of 168–173 days; mean temperatures range between −18 °C in January and 18 °C in July (Leeson et al. 2005). The park lies in the Mixedwood section of the Boreal Forest region (Rowe 1972) and protects some of the last remaining *Festuca hallii* (Vasey) Piper (plains rough fescue) communities in western Canada (Trottier 1986).

Fescue prairie communities in RMNP are distributed along its southern and western portions (Blood 1966a). Most are isolated and small (mean = 8.12 ha; max = 212.01 ha) (Fig. 1) and associated with broad river valleys. Historic grazing by cattle, horses, and sheep, as well as the harvesting of native hay, predates the establishment of the park in 1930 (Department of the Interior 1921). Although these practices were continued during early years of the park's operation (Trottier 1986), they were banned in 1969, following rangeland management studies demonstrating the negative impact of grazing on fescue grasslands (Blood 1966b; Trottier 1986). Although, historically, the area of RMNP was important for plains bison (*Bison bison*) and mule deer (*Odocoileus hemionus*), only re-introduced bisons remain and are confined

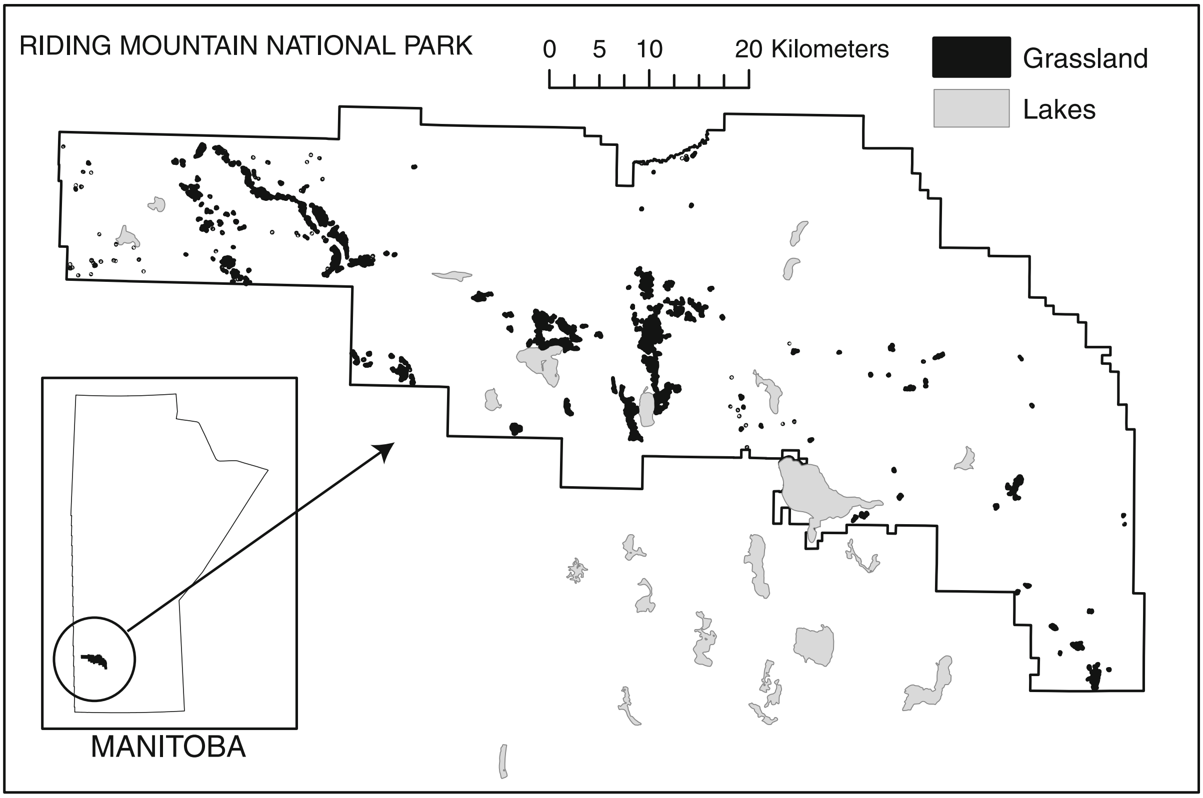

Fig. 1 Riding Mountain National Park, located in southwestern Manitoba, Canada. Plains rough fescue (*Festuca hallii*) grasslands in the park are relatively isolated, located along riverine systems or on upland areas

within a fenced range established in 1931 (Ringstorm 1981). Today, RMNP continues to support native ungulates, including elk (*Cervus elaphus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*), of which only elk are associated with the park's grasslands in high numbers (Blood 1966b). Given its long grazing history, followed by complete removal of domestic grazers, the park offers an important model in the study of grassland restoration.

Study design

In 1973, 4 years after the removal of cattle from RMNP, 33 permanent transects were established in the park and sampled to describe and monitor the recovery of its grasslands (Trottier 1986). At the time, permanent transects were installed in all the park's major grassland areas, selected to be homogeneous in vegetation composition and located in historically grazed, upland areas in which livestock grazing and grassland condition had been previously quantified (Blood 1966b). Selected transects were stratified based on five classes of grazing intensity (degree of defoliation by livestock) as reported in the 1962–1963 survey: slight (0–5 %), light (6–25 %), moderate (26–50 %), heavy (51–75 %), and severe (>75 %).

Following the original protocols, we resampled each transect in 2010, 37 years after their initial establishment and 41 years after the removal of domestic grazers from the park. For each sample, we stretched a 100-ft (30.5 m) measuring tape between two permanent stakes to establish the linear transect. We then carefully lowered a metal pin at 1-ft (30.5 cm) intervals along the transect and recorded each plant species that touched the pin at each of the 100 intervals. Since species were recorded only once at each interval, each had a maximum transect count of 100 hits, one possible hit per interval. Since multiple pin-hits were not recorded, our approach underestimates the relative abundance of the most abundant plants. Transects were sampled between mid-July and mid-August of 1973 and 2010 (Trottier 1986). Plant nomenclature follows VASCAN (Brouillet et al. 2010).

Owing to their similarities in livestock use before 1973, and in order to increase the sample size per grazing class, we reclassified the original transects from five into three broader groups. Based on the degree of defoliation (%) by livestock between 1962–63, the three groups included: (A) lightly grazed (0–25 %, $n = 11$); (B) moderately grazed (26–50 %, $n = 13$); and (C) heavily grazed transects (>51 %, $n = 9$). Since selected grasslands were confined to areas previously measured for livestock grazing utilization (Trottier 1986), control areas were not possible to include in this study and our focus remains on the observation of differences among classes of grazing intensity.

Data analysis

Owing to the broadly linear nature of plant community data, we used principal component analysis to describe the abundances of species among three classes of grazing intensity in both sample years. Species data were log-transformed to mitigate any confounding effects of rare outliers (Kenkel 2006). We further examined the recovery of disturbed prairies by three measures of floristic composition: absolute richness (S), effective richness ($N2$), and frequency of invasives (%). By means of raw data from each transect, we compared these among sampling years and between groups, by a two-way, repeated-measures analysis of variance (Zar 1999). Effective richness (Hill 1973) describes plant communities based on the proportional abundance of species (Kvalseth 1991) and is helpful in examining species responses to environmental manipulations (Legendre and Legendre 1998).

We examined temporal changes in the abundance of species by an unstandardized Mantel test (Legendre and Legendre 1998). Dissimilarity matrices were calculated by means of Bray–Curtis indices to give equal weight to both abundant and rare species. For each grazing class, we compared distance matrices for both sample years and graphically illustrated the results by an ordination bi-plot, modified to highlight the temporal community shifts, based on non-metric multidimensional scaling (NMDS) (Legendre and Legendre 1998). Species abundance data were log-transformed before analysis to reduce the effects of rare outliers (Kenkel 2006). Sensu Thompson and Davis (2011), we consider both exotic and native species as potentially invasive, depending on their response to human disturbance, their threat to ecological integrity, and their ability to proliferate beyond their normal distribution.

Results

Short-term impacts of grazing on northern fescue grasslands

Four years after the removal of livestock from RMNP, grazing intensity was a good predictor of plant community composition. The three grazing groups were clearly separated along the first principal axis, accounting for 25.7 % of the variance in plant species abundance (Fig. 2). Grazing intensity was significantly correlated with community richness ($F_{2,30} = 27.37$, $p < 0.0001$), diversity ($F_{2,30} = 10.98$, $p < 0.0001$), and invasive abundance ($F_{2,30} = 32.41$, $p < 0.0001$; Table 1). Lightly grazed transects were characterized by higher species richness ($S = 31 \pm 1.1$; $N2 = 9.0 \pm 0.8$, Fig. 3) and greater abundance of native graminoids (e.g., *Festuca hallii* 52.0 %, *Carex* spp. 22.1 %, *Koeleria macrantha* (prairie junegrass, 14.3 %), *Heterostipa spartea* (porcupine needle grass, 14.2 %), and herbs (e.g., *Solidago rigida* (stiff goldenrod, 5.8 %), *Symphyotrichum laeve* var. *laeve* (smooth aster, 5.5 %), *Geum triflorum* (three-flowered avens, 5.4 %); Table 2). In contrast, heavily grazed transects were characterized by lower richness ($S = 14 \pm 2.8$; $N2 = 4.4 \pm 1.0$) and a greater proportion of invasive species (Fig. 3), including *P. pratensis* (Kentucky bluegrass, 77.7 %), *Taraxacum officinale* (dandelion, 6.2 %), and *Solidago canadensis* (Canada goldenrod, 5.9 %; Table 2). Other disturbance-tolerant species were also exclusive to heavily grazed transects. For example, *Cirsium arvense* (Canada thistle), *Urtica dioca* (stinging nettle), and *Rumex triangulivalvis* (triangular-valve dock) were not found in any other grazing classes. With their high species richness ($S = 28 \pm 1.0$, $N2 = 9.4 \pm 0.9$, Fig. 3) and a combination of exotic (e.g. *P. pratensis*, 51.8 %; *T. officinale*, 7.4 %) and native species (e.g. *F. hallii*, 15.0 %; *K. macrantha*, 10.5 %; *H. spartea*, 9.7 %), moderately grazed communities were similar to lightly and heavily grazed areas (Table 2).

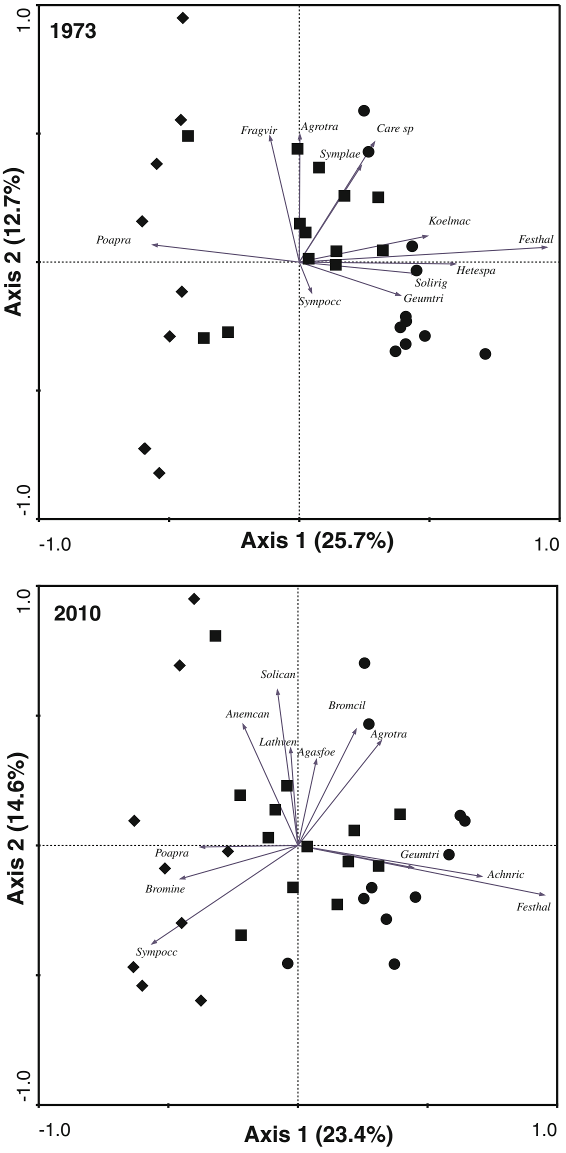

Fig. 2 Principal component analyses for both 1973 (*top*) and 2010 (*bottom*) vegetation data. Species providing little weight to the ordination were removed for clarity. Envelopes surround each group to help readers differentiate between them. Each point is the location of a given transect, shaped to associate them with a specific group: *filled circle* lightly grazed, *filled square* moderately grazed, *filled diamond* heavily grazed. Abbreviations represent the first three letters of species binomials with full species names available in Table 2

Long-term recovery of northern fescue grasslands

Forty-one years after the removal of livestock, grazing intensity remained a good predictor of plant community composition. The first principal axis continued to clearly separate historic grazing groups, accounting for 23.4 % of the variance in plant species abundance (Fig. 2). Historic grazing groups remained distinct despite temporal changes in their species composition. Significant changes in the heavy and moderately grazed communities (Mantel $r = -0.041$, $p = 0.864$, Mantel $r = 0.189$, $p = 0.252$; Table 3) were characterized by an increasing dominance of invasive species (Table 2; Fig. 3), including the exotic grasses *P. pratensis* and *Bromus inermis*, which accounted for 82.3 % and 14.2 % of plant abundance among heavily grazed transects, respectively (Table 2). Heavily grazed prairies remained correlated with lower species richness ($S = 18 \pm 2.7$; $N2 = 5.3 \pm 0.9$; Fig. 3); however, significant declines in diversity were also characteristic of moderately grazed areas ($F_{2,30} = 4.81$, $p = 0.0153$, Table 1). Heavily grazed transects also illustrated a number of ephemeral exotic and weedy forbs that were highly abundant in 1973 that were no longer characteristic of this group in 2010. Among these, species such as *Trifolium repens*, *Crepis tectorum* (narrow-leaved hawksbeard), *Urtica dioica*, *R. triangulivalvis*, *Capsella bursa-pastoris* (common shepard's purse), and *T. officinale* were replaced by native species such as *Anemone canadensis* (Canada anemone, 7.3 %), *S. canadensis* (7.4 %), and the shrub *Symphoricarpos occidentalis* (western snowberry, 29.6 %; Table 2).

In contrast, lightly grazed sites remained compositionally similar among years (Mantel $r = 0.365$, $p = 0.02$; Table 3) and continued to be dominated by native species, including the grasses *F. hallii* (56.7 %), *Achnatherum richardsonii* (Richardson's needlegrass, 19.6 %) and *H. spartea* (9.3 %), as well as the forbs *S. laeve* var. *laeve* (7.6 %) and *G. triflorum* (7.2 %). Despite the long period of recovery, the exotic *P. pratensis* persisted in lightly grazed areas, increasing from a frequency of 12.0 % in 1973 to 42.3 % in 2010 and from 52 to 79 % in moderately grazed areas (Table 2). Its increasing abundance was accompanied by an overall increase in the frequency of invasive species (Fig. 3; Table 4). The invasion of moderate and heavily grazed transects is further illustrated by the large shift in their centroids along the first two axes of the NMDS analysis ordination (Fig. 4).

Table 1 Two-way ANOVA testing the effect of grazing intensity, in three classes, and 41 years of time on the species richness, diversity, and invasive plant abundance in the northern plains rough fescue grasslands of Riding Mountain National Park, MB, Canada

Effect	Richness (*S*)			Diversity (*N*2)			Invasive abundance		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Grazing intensity	41.39	2	<0.0001[a]	14.51	2	<0.0001[a]	39.84	2	<0.0001[a]
Time	0.88	1	0.3517	1.76	1	0.1898	13.31	1	0.0006[a]
Time + grazing intensity	0.54	2	0.5885	3.27	2	0.0449[a]	1.15	2	0.3237

The *F*-values and their significance values are shown

[a] Result is statistically significant

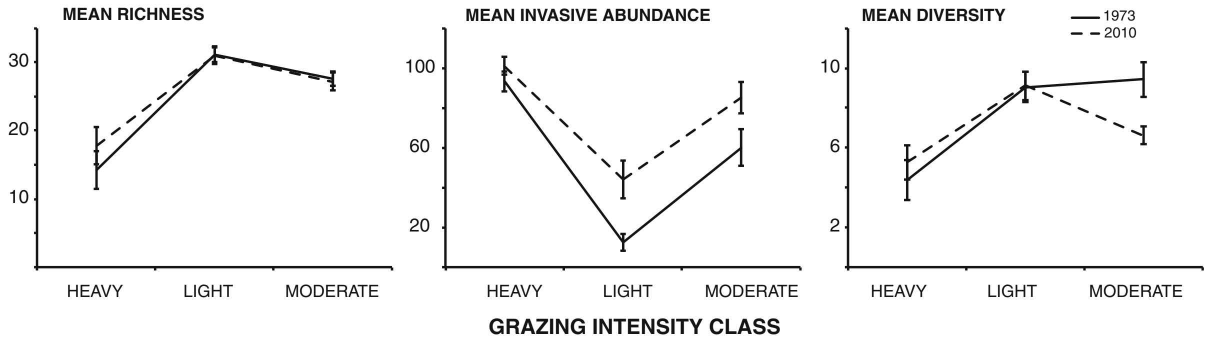

Fig. 3 Impacts of grazing intensity (three classes: light ($n = 11$), moderate ($n = 13$) and heavy ($n = 9$)), and time (41 years) on the mean species richness (*S*), mean abundance of invasives (cover/transect), and mean diversity (*N*2) of plains rough fescue grasslands in Riding Mountain National Park, MB, Canada. Transects have been recovering from grazing disturbance for 41-years. Error bars represent the standard error of the mean (SE)

Discussion

Impacts of grazing on the northern prairies

Grazing intensity was highly correlated with the structure and composition of northern fescue prairie communities. Heavy grazing was associated with a dramatic decline in the diversity of native grasslands and their dominance by the invaders *Poa pratensis*, *S. canadensis* and *T. officinale*. Photos from the 1960s and early 1970s, an era of expansive grazing pressure in RMNP, show grasslands with vast stands of *P. pratensis* or large tracts of bare soil speckled sparsely with weedy species such as *R. triangulivalvis*, *T. officinale* or *U. dioica*. This initial abundance of invasive species may be attributed to their morphology and life history. For example, the ability of *P. pratensis* to produce lateral tillers and translocate nutrients between ramets, as well as its low growing points contribute to its success in heavily grazed habitats (Hull 1987). In contrast, the erect growth form of the native *F. hallii*, as well as its limited ability to produce lateral tillers, makes it more susceptible to grazing (Johnston and MacDonald 1967). Despite the higher diversity of native species, moderately and even lightly grazed prairies were also invaded by *P. pratensis*. This colonization was essentially park wide by the early 1970s with only two of the 33 transects remaining un-invaded (Trottier 1986). The dramatic conversion of diverse, native prairie communities into mono-dominant stands of *P. pratensis* following heavy grazing by domestic cattle has been observed in other areas of mixed-grass (Bahm et al. 2011) and fescue prairie (Li et al. 2009; Trottier 1986).

The persistence of invasive plants after 41 years

Despite their initially high abundance in heavily grazed prairies, not all invasive species persisted and many declined in abundance following 40 years of recovery. For example, *T. repens*, *C. tectorum*, *U. dioica*, *R. triangulivalvis, C. bursa-pastoris*, and *T.*

Table 2 The top 15 most abundant species per transect, averaged for each grazing group, for both sample years

Rank	Group 1—light (1973)			Group 2—moderate (1973)			Group 3—heavy (1973)		
	Species	Hits	SD	Species	Hits	SD	Species	Hits	SD
1	*Festuca hallii*	52.0	15.4	***Poa pratensis***	51.8	26.8	***Poa pratensis***	77.7	29.5
2	*Carex sp.*	22.1	15.5	*Carex sp.*	21.2	10.8	*Agropyron trachycaulum*	23.1	25.1
3	*Koeleria macrantha*	14.3	7.7	*Agropyron trachycaulum*	15.2	13.3	*Carex sp.*	12.1	17.3
4	*Heterostipa spartea*	14.2	12.7	*Festuca hallii*	15.0	11.5	*Vicia americana*	9.2	12.7
5	***Poa pratensis***	12.0	14.3	*Koeleria macrantha*	10.5	9.7	*Achillea millefolium*	7.8	10.5
6	*Agropyron trachycaulum*	7.4	3.9	*Vicia americana*	9.8	8.3	*Fragaria virginiana*	7.8	9.5
7	*Galium boreale*	7.4	7.7	*Heterostipa spartea*	9.7	10.7	***Rumex triangulivalvis***	7.2	21.7
8	*Solidago rigida*	5.8	2.9	***Taraxacum officinale***	7.4	7.1	***Taraxacum officinale***	6.2	5.9
9	*Symphyotrichum laevis*	5.5	6.5	*Galium boreale*	6.6	4.2	*Galium boreale*	5.9	5.9
10	*Fragaria virginiana*	5.4	8.2	*Achillea millefolium*	6.5	4.4	***Solidago canadensis***	5.9	12.4
11	*Geum triflorum*	5.4	3.7	*Fragaria virginiana*	6.3	8.3	*Thalictrum venulosum*	4.0	8.1
12	*Achnatherum richardsonii*	4.0	3.6	*Symphyotrichum laevis*	5.5	8.4	*Stellaria longpipes*	3.3	9.3
13	*Achillea millefolium*	4.0	3.3	*Erigeron glabellus*	4.6	5.0	*Bromus ciliatus*	3.0	5.7
14	*Vicia americana*	3.9	4.2	*Thalictrum dasycarpum*	4.4	5.9	***Symphoricarpos occidentalis***	2.3	6.6
15	*Helictotrichon hookeri*	3.8	6.6	*Solidago rigida*	4.2	5.3	*Achnatherum richardsonii*	2.0	5.0

Rank	Group 1—light (2010)			Group 2—moderate (2010)			Group 3—heavy (2010)		
	Species	Hits	SD	Species	Hits	SD	Species	Hits	SD
1	*Festuca hallii*	56.7	21.6	***Poa pratensis***	78.8	18.5	***Poa pratensis***	82.3	12.8
2	***Poa pratensis***	42.3	30.6	*Festuca hallii*	25.6	24.2	***Symphoricarpos occidentalis***	29.6	26.2
3	*Achnatherum richardsonii*	19.6	14.1	*Agropyron trachycaulum*	17.0	12.2	*Carex sp.*	16.2	20.2
4	*Carex sp.*	19.5	14.1	*Carex sp.*	12.2	7.9	***Bromus inermis***	14.2	15.3
5	*Galium boreale*	15.3	8.1	*Symphyotrichum laevis*	11.6	11.9	*Galium boreale*	11.1	6.1
6	*Agropyron trachycaulum*	9.3	5.8	*Galium boreale*	11.5	7.3	*Calamagrostis canadensis*	7.6	21.2
7	*Heterostipa spartea*	9.3	9.5	*Artemisia ludoviciana*	6.4	3.8	***Solidago canadensis***	7.4	16.0
8	*Bromus ciliatus*	7.8	9.3	***Bromus inermis***	5.6	20.2	*Anemone canadensis*	7.3	12.5
9	*Symphyotrichum laevis*	7.6	6.6	*Thalictrum venulosum*	5.1	4.0	*Thalictrum dasycarpum*	7.1	13.8
10	*Geum triflorum*	7.2	8.0	*Vicia americana*	4.7	4.5	*Agropyron trachycaulum*	4.3	5.4
11	*Rosa acicularis*	5.6	6.3	*Anemone canadensis*	4.0	6.3	*Bromus ciliatus*	4.2	8.1
12	*Thalictrum venulosum*	5.5	5.6	***Solidago canadensis***	3.6	10.7	*Vicia americana*	4.0	4.5
13	*Fragaria virginiana*	4.6	5.0	*Lithospermum canescens*	3.5	4.2	*Artemisia ludoviciana*	2.7	4.0
14	*Lithospermum canescens*	4.2	4.7	*Monarda fistulosa*	3.3	4.3	*Lathyrus ochroleucus*	2.7	6.2
15	*Vicia americana*	4.1	2.5	*Solidago rigida*	3.3	6.7	***Cirsium arvense***	2.4	3.7

Invasive species, as defined in the text, are highlighted in bold. Grazing groups are demarcated by the degree of grazing intensity prior to the banning of domestic cattle in the study area in 1969

officinale declined in abundance following long-term absence of domestic grazers. Many of these species have been reported to be ephemeral in other systems. For example, *T. officinale* (Stewart-Wade et al. 2002), *T. repens* (Turkington and Bourdon 1983) and *C. tectorum* (Blumenthal et al. 2005) have been reported to respond negatively to increasing native grass cover.

Among invasive species, *P. pratensis* was by far the most abundant and persistent following the removal of grazing, and constituted 90 % of all invasive plants

Table 3 Mantel test results comparing Bray–Curtis distance matrices (1973 vs. 2010) for each grazing intensity group

Mantel statistic	Grazing group		
	Light	Moderate	Heavy
n	11	13	9
rM	0.365	0.189	−0.041
p	0.02	0.252	0.864

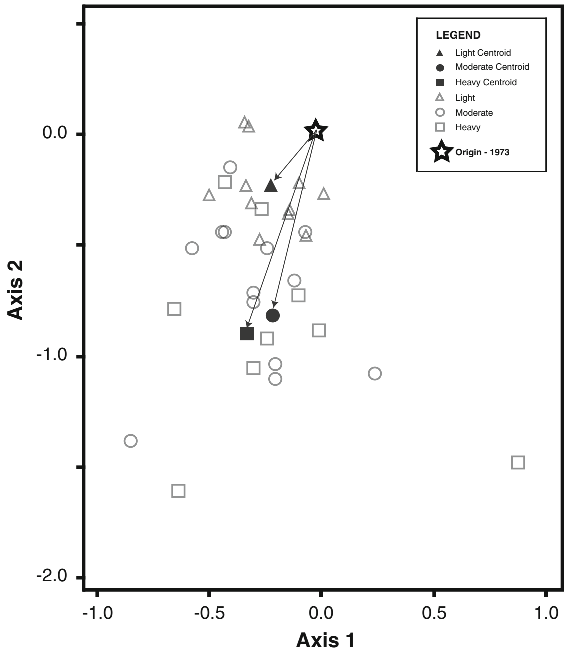

Fig. 4 Non-metric multidimensional biplot of plant community permanent transect data, based on Bray–Curtis distance. To facilitate interpretation, 1973 data is collapsed to a single origin. Thus, temporal change in the 2010 data can be viewed as distance from that origin. Centroids for each grazing group (*light*, *moderate*, *heavy*) are plotted with vectors, describing the degree of change

surveyed in 2010. For the large majority of prairies, the abundance of *P. pratensis* was either stable or increasing, and decreased only when displaced by other invaders, including *B. inermis* or *S. occidentalis*. Our results, illustrating the ability of *P. pratensis* to persist and proliferate into areas where domestic grazing had ceased, should be alarming to conservation managers. The persistence of invasive species in transects that were heavily grazed in the past suggests that these areas could act as foci for the establishment of non-native species in adjacent native prairies. Existing models of biological invasions demonstrate that disturbed areas often promote the establishment of non-native species, and may facilitate their invasion into healthy ecosystems by acting as core sources of propagules (MacIsaac et al. 2001; DiVittorio et al. 2007). This model appears to accurately describe grasslands in RMNP and has been linked to the proliferation of *B. inermis* in the park (Otfinowski and Kenkel 2009) although the spatial arrangement of our data did not allow us to test this hypothesis in this study.

Despite the long absence of disturbance and the protection afforded by the National Park, the recovery of heavily grazed transects was compromised by the persistence or proliferation of a few, very specific invasive species. Although by 2010, some heavily grazed prairies were re-colonized by *F. hallii*, the long period of establishment and sporadic flowering of this species may be complicating grassland recovery (Blood 1966a; Johnston and MacDonald 1967). Resource competition between native species and the established non-native flora may also reduce recovery. For example, the lack of recovery of heavily grazed transects may be the result of the pre-emption of space by non-native species during periods of high disturbance (Buckling et al. 2000). As a result, the initial pattern of invasion, following heavy grazing, may compromise the recovery of disturbed prairies (Murrell et al. 2001).

Although it was not possible within our study to quantify the impacts of native grazers on the recovery of *F. hallii*, prairies in RMNP are subjected to grazing by elk (Blood 1966a). Grazing by elk is light and most important during the winter (Trottier 1986) when it appears to be focused along the forest margins (McIntosh and Murray 2004; Trottier et al. 1980). Nonetheless, it remains possible that elk could inhibit the recovery of native species through selective grazing. For example, although smooth brome is palatable to elk (Hobbs et al. 1981), animals could avoid larger patches due to their low forage quality, contributing to patchy recovery and heavier grazing of adjacent native plants (Frank and McNaughton 1992; Moisey et al. 2005).

The recovery of northern fescue grasslands

Grazing intensity remained an excellent predictor of community composition, and changes in plant community composition were driven by the proliferation

Table 4 Exotic species located in, and adjacent to, sample transects

Lightly grazed species	Freq	Moderately grazed species	Freq	Heavily grazed species	Freq
1973					
Poa pratensis	12.0	*Poa pratensis*	51.8	*Poa pratensis*	77.7
Cirsium arvense	P	*Taraxacum officinale*	7.4	*Taraxacum officinale*	6.2
Descurainia sophia	P	*Trifolium repens*	0.5	*Cirsium arvense*	0.8
Taraxacum officinale	P	*Phleum pratense*	0.1	*Trifolium repens*	0.2
		Crepis tectorum	0.1	*Bromus inermis*	P
				Capsella bursa-pastoris	P
				Chenopodium album	P
				Phleum pratense	P
				Thlapi arvense	P
2010					
Poa pratensis	42.3	*Poa pratensis*	78.8	*Poa pratensis*	82.3
Sonchus arvensis	0.8	*Bromus inermis*	5.6	*Bromus inermis*	14.2
Bromus inermis	0.4	*Cirsium arvense*	0.3	*Cirsium arvense*	2.4
Chenopodium album	P	*Phleum pratense*	0.2	*Sonchus arvensis*	1.7
Taraxacum officinale	P	*Taraxacum officinale*	0.1	*Taraxacum officinale*	0.4
		Chenopodium album	P	*Descurainia sophia*	P

Two sample years are described: 1973—4 years after grazing; 2010—41 years after grazing. For both sample years, sample size remains the same: light ($n = 11$), moderate ($n = 13$), heavy ($n = 9$)

P Species was present adjacent (but not in) at least one transect in a given group

of invasive species and not the recovery of native diversity. In moderately grazed prairies, compositional changes were primarily due to a large increase in the exotic grasses *P. pratensis* and *B. inermis*, the dramatic increases of which led to a significant drop in diversity and an increase in the proportion of invasive plants. Significant increases in the abundance of invasive plants were also characteristic of light and heavily grazed groups.

Equally concerning is the dramatic decline in species diversity in areas characterized by high abundance of invasive plants. For example, in transects where *P. pratensis* cover exceeded 90 %, species richness was 44 % lower than in areas where its cover was less than 50 %. Similar results have been reported in the northern fescue prairies with *B. inermis*, which decreases local diversity by 55–72 %, resulting in the exclusion of native grass species, including *F. hallii* and several needle grasses (Otfinowski et al. 2007; Sinkins 2010). Decreases in native diversity following the proliferation of invasive species have been reported in many ecosystems (Davies 2011, see Vilà et al. 2011 for review).

The rapid emergence of *B. inermis* as an invader of northern fescue prairies was also alarming. Unlike *P. pratensis*, this species was absent from transects in 1973 (Trottier 1986) and reported in less than 1 % of surveyed areas in 1960s (Blood 1966a). By 2010, *B. inermis* occupied over 14 % of heavily grazed areas, often forming dense, monospecific stands. Unpublished data from RMNP confirms that over a single decade (1999–2009) the extent of *B. inermis* cover increased by 513 % in a large grassland mosaic overlapping with the present study area (Sinkins 2010). The initial expansion of *B. inermis* occurred mainly adjacent to existing trails and has expanded into native prairie via seed, rhizomes, animals, and trail mowing (see Salesman and Thomsen 2011 for review).

Implications for restoration managers

Knowledge of the behaviour of invasive plants is critical to grassland managers and requires the consideration of multiple species in order to establish management priorities based on the biology of each potential invader. The great care required in weighing management priorities is best served by local, long-term data. After 40 years of recovery from grazing disturbance, our observations of northern fescue prairies in RMNP illustrate both the persistence and proliferation of invasive plants, as well as the disappearance of a number of ephemeral exotic species. These two classes of invaders, persistent, and ephemeral, illustrate the potential to target only a subset of invasive plants through passive restoration. For others, including aggressive invaders such as *P. pratensis* and *B. inermis*, our findings demonstrate that a passive approach to restoration is ineffective, and that active intervention is required to restore native communities. Among these, fire and the management of nutrients have been shown to be effective in controlling each species in some (Uchytil 1993; Blankspoor and Larson 1994; Gerling et al. 1995; Otfinowski and Kenkel 2008), although not in all circumstances (Grilz and Romo 1994; Sinkins 2010).

Conclusions

The conservation and restoration of remnant fescue prairies often requires an understanding of their recovery from historic grazing disturbances. Our research demonstrates that the recovery of fescue grasslands from heavy grazing may be inhibited by the persistence of exotic and native invaders and that their restoration may require rehabilitative management. Of particular concern were the significant increases in the abundance of the invasive, exotic grasses *P. pratensis* and *B. inermis* in areas of native prairie only lightly grazed in the past. However, not all exotic species persist and many are ephemeral following intense disturbance. Results of this study, which demonstrate an alarming trend in the expansion of exotic grasses in a protected northern prairie, present urgent priorities for future research and a challenge to ecologists faced with managing vulnerable, rare, and increasingly disjunct patches of a native prairie ecosystem.

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