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Emerging conflict between conservation programmes: when a threatened vertebrate facilitates the dispersal of exotic species in a rare plant community

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bison; fescue grasslands; invasive species; spatial ecology; zoochory; ecological integrity; exotic plant species.

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Abstract

As an ever-increasing variety of conservation programmes are applied in human-altered environments, there is a growing risk that different conservation actions with conflicting objectives may impede one another. Preventing and resolving the negative impacts of such conflicting conservation programmes could become a key challenge for conservationists. To date, however, the issue of conflicting conservation programmes has been largely overlooked. We explored a potential conflict between the preservation of threatened free-ranging plains bison Bison bison bison and the conservation in a National Park of a rare plant community – native rough fescue Festuca hallii grasslands. We investigated the dispersal of exotic seeds by examining 283 samples of bison faeces and the spatial distribution of exotic plant species in relation to bison behaviour. We showed that bison facilitated the long-distance dispersal of exotic plant species into the park by transporting seeds. Our analysis indicated there was a high probability (>75%) of occurrence of clover Trifolium spp. and timothy Phleum pratense on bison trails across 38% and 27%, respectively, of fescue grassland area. There was also a high probability of occurrence of timothy on bison wallows across 20% of fescue grasslands area. Furthermore, we demonstrated that exotic plant species were most likely to occur within 3 km of potential introduction points, and identified specific grassland patches most at risk of exotic plant species introduction by bison. By revealing the ecological mechanism underlying the emergence of a potential conflict, we were able to delineate spatial variation in the relative threat that bison might pose to the integrity of native fescue plant communities, allowing managers to optimize the allocation of conservation effort. Our study highlights the value of understanding the ecological mechanisms driving conflict between conservation programmes in order to set evidence-based priorities for guiding future conservation decision-making.

Introduction

The negative impacts of humans on wildlife species are increasing at an unprecedented rate (Pereira et al., 2010). As more species are becoming threatened with extinction, and the number and variety of conservation programmes increases, there is growing likelihood that the objectives of different conservation projects may be incompatible. In such cases, sanctioned management measures implemented to favour a specific threatened species might impede ongoing management efforts aimed towards other threatened species, resulting in an inextricable conservation dilemma (Williams et al., 2011). Despite this growing challenge, the potential for conflicting conservation goals is rarely considered in conservation planning and few published examples exist (Jordéan &Béaldi, 2013). Tackling conflicting conservation programmes requires a detailed understanding of the underlying ecological mechanisms that generate conflict so that managers can adjust the type of interventions applied. For example, population declines in an endangered species of pupfish Cyprinodon bovinus in Texas were found to be partially driven by egg predation by another endangered fish species (Gambusia nobilis). Researchers found that changes in the breeding habitat of pupfish had led to increases in egg-predation rates. Consequently, conservation efforts were focused on restoring pupfish breeding habitat, leading to a decrease in egg predation and the recovery of the pupfish breeding population (Winn, 1985)

Conservation actions such as eradicating invasive species or reintroducing native species can have far-reaching, often unexpected, negative effects on other taxa (Setterfield, 2002). This is particularly likely where human activities have strongly altered species interactions (Sinclair & Byrom, 2006). For example, in California the eradication of an invasive plant, hybrid Spartina, is threatening the recovery of an endangered bird, the California clapper rail Rallus longirostris obsoletus, which has become reliant on the invasive plant for nesting (Lampert et al., 2014). Conflict between management actions focused on single species or habitats, which do not consider interactive ecological processes, may be particularly detrimental to conservation objectives (Lipsey & Child, 2007; Armstrong & Seddon, 2008). Exploring the ecological processes that link these different species could clarify the mechanisms through which conflict emerges, and reveal ways to manage them effectively.

We explored this issue using a potential conflict between the conservation of free-ranging plains bison Bison bison bison and native rough fescue Festuca hallii grasslands in Prince Albert National Park (PANP), Saskatchewan, Canada, as a case study. The plains bison has been designated a threatened subspecies of the American bison B. bison by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) due to the few free-ranging populations that remain (COSEWIC, 2013). PANP and the surrounding area harbour one of the only free-ranging populations within the plains bison's historic range in Canada. The distribution of bison within PANP overlaps with that of fescue grasslands, one of the rarest and most vulnerable plant communities in the Northern Great Plains of North America (Clark, 1998). The invasion of exotic plants is a threat to fescue grasslands (Tyser & Key, 1988; D'Antonio & Meyerson, 2002; Pyssek et al., 2012), and bison – being a major seed disperser (Constible et al., 2005; Rosas et al., 2008) – could jeopardize the preservation and restoration of fescue grasslands by facilitating the establishment of exotic plant species. Exotic plants are a major issue in ecological restoration because of their ability to proliferate in disturbed environments, their plentiful seed sources in agricultural areas and their intense competition with native plants (D'Antonio & Meyerson, 2002; Pyssek et al., 2012).

The dispersal of exotic plant species by bison is a potential threat to the ecological integrity of fescue grasslands, and thus could drive conflict between these two conservation programmes with contrasting goals. The maintenance of ecological integrity was first formalized as a principle under the National Parks Act in 1988. The ecological integrity of a national park implies 'a condition that is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes' (Canada National Parks Act, 2000). This concept is used as a guiding framework for restoration and monitoring efforts (Koike et al., 2011). Accordingly, non-native species disrupt ecological integrity simply by being present. Preservation of ecological integrity often necessitates management interventions to prevent non-native species from impacting native plant populations through competition or other mechanisms. As such, reducing the abundance and spatial distribution of invasive plant species is a central objective in the PANP fescue management plan to maintain and restore the integrity of fescue grasslands (Parks Canada, 2012).

We focused on the role of bison as a vector of dispersion. While other large herbivores forage in the study site and potentially also disperse seeds of exotic plant species, the high density of the bison population (>94% of all ungulates observed in meadows during any season, Fortin et al., 2003) and their intensive use of agricultural lands (Sigaud et al., 2017) – the source of exotic plant seeds – make them the most likely major disperser of non-native plant seeds. We tested the potential mechanism of conflict between bison and fescue grasslands by testing the following three hypotheses:

(1) bison transport seeds of exotic plant species via endozoochory; (2) exotic species are more likely to occur inside PANP on sites that were locally disturbed and intensively used by bison (wallows and trails) than on random transects; and (3) bison activity influences the probability of exotic species occurrence near wallows and along trails in PANP. Based on the outcomes of our investigations, we developed models of the spatial distributions of exotic plant species in fescue grasslands for predicting spatial variation in the severity of this potential conflict. Our results will help to set evidence-based priorities for future conservation efforts.

Materials and methods

Study area

Our study took place in PANP (53°44^{0}N, 106°39^{0}W), where ~220 plains bison (Merkle, Cherry & Fortin, 2015; Cherry et al., 2019) roam an area composed of forests (75%), agricultural lands (7%), water bodies (6%), meadows (4%) and other land cover types (8%, including shrubs and riparian areas). Other large mammals in the study area include elk Cervus canadensis, white-tailed deer Odocoileus virginianus, mule deer O. hemionus, moose Alces alces, black bears Ursus americanus and gray wolves Canis lupus. Bison are the most numerous large herbivore in our study area (Fortin et al., 2003). Meadows are of particular interest because they include fescue grasslands. The bison range (c. 960 km^{2}) overlaps with seven spatially distinct fescue grassland patches (mean = 52 ha; range: 5–155 ha).

During summer and autumn, bison groups travel almost daily between PANP and agricultural lands. They typically use agricultural lands at night when human activities are at their lowest and return to habitats inside PANP during the day to forage in meadows (Sigaud, 2018). In particular, 11 such locations are heavily used by bison to access agricultural lands from PANP, hereafter referred to as potential 'introduction points' (Fig. 1). We focused on two exotic plants that bison might transport into PANP: timothy Phleum pratense and clover species Trifolium spp. Timothy is one of the most frequently consumed plant species by bison on agricultural lands (Sigaud et al., 2017). The presence of

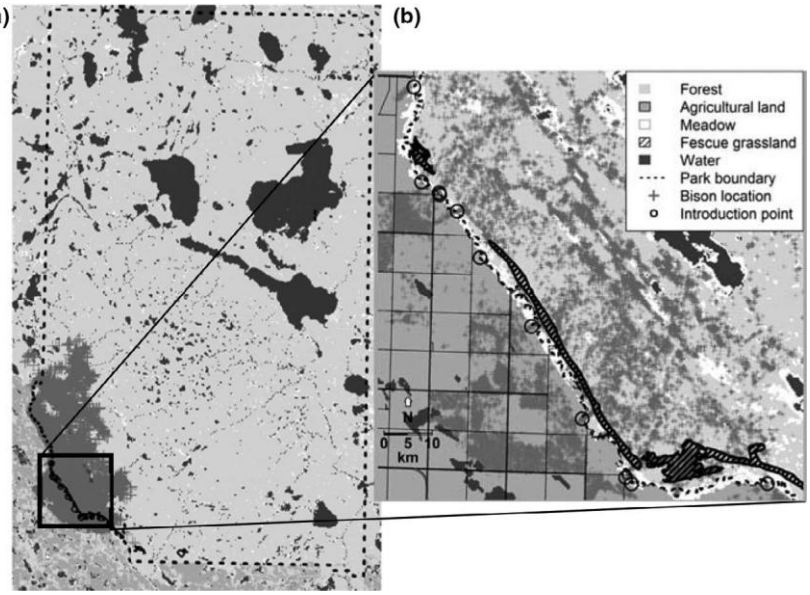


Figure 1 Overview of the study area (a) Prince Albert National Park (PANP), Saskatchewan, Canada (dashed black line) and locations of female plains bison(n = 21) during autumns 2011–2013 depicting the bison range and the area sampled, (b) close-up on the locations used by bison to travel between PANP and agricultural lands, that is, introduction point. Land cover types displayed are: forest, water, meadow and agricultural land. Identified patrimonial fescue grasslands are delimited as well as potential exotic plant species introduction points (i.e. preferred locations used by bison to access agricultural lands) on the park boundary.

attachment structures on timothy seeds makes this species a good candidate for transportation on the fur and hooves of bison (Royer & Dickinson, 1999). Clover species are widespread on agricultural lands, and some of these species (e.g. Trifolium repens L.) are invasive in North America (van Kleunen, Dawson & Dostal, 2011). Although germination success tends to decrease with the passage through the ruminant digestive tract, seeds of various clover species can still germinate (Constible et al., 2005; Milotiéc & Hoffmann, 2016), while digestion can even stimulate germination of T. pratense L. (D'hondt & Hoffman, 2011). Vegetation surveys performed during previous years (1998–1999 and 2005– 2008) on various sets of meadows (8–109 meadows) within the bison range did not record the presence of these species, indicating that these species were either not present previously, or not numerous enough to be reported (Fortin, Fryxell & Pilote, 2002; Fortin et al., 2003; Courant & Fortin, 2010; Babin et al., 2011).

Dispersal of exotic seeds by bison

To investigate our first hypothesis, that bison disperse seeds of exotic plant species via endozoochory, we collected seed from 283 samples of bison faeces at 66 locations in the park and on agricultural lands, during August–November 2012, a time period when bison intensively use agricultural lands (Sigaud et al., 2017). Locations were chosen opportunistically when bison groups were observed in the field or based on recent (<24 h) clusters of GPS locations from 18 collared female bison. Only females were collared because they tend to be group leaders (McHugh, 1958; Ramos et al., 2015) and thus represent the movements of much of the population. Moreover, females constitute the majority of the adult population (70% in 2011, Merkle & Fortin, 2014). To avoid contamination of our samples by seeds already present on the ground, which might come from neighbouring plants, we only collected the inner part of the dung not in contact with the ground. We sampled one to five bison faeces at each location. We washed all faecal samples (150–200 g) and passed them through a series of sieves (2, 1 and 0.5 mm screen size) to recover seeds. For each sample, intact seeds above 0.5 mm long were identified to species level whenever possible, based on their physical characteristics (see Davis, 1993; Royer & Dickinson, 1999; Sedinger et al., 2010; SeedImages, 2012 for seed identification).

Our second hypothesis was that exotic plant species are more likely to occur in areas that are locally disturbed and intensively used by bison. To investigate this we first explored whether exotic species were present in PANP in general, by recording the presence of exotic plant species along 147 random transects (100–200 m) in the forest in the core range of the bison population, near to the park boundary [mean (SE) = 678 m (87)]. We then measured if exotic species were present in sites that were locally disturbed and intensively used by bison, by recording their presence around wallows and along trails. During August–October 2012 and 2013, we recorded the presence of exotic plant species around all bison wallows [n = 360; mean (SE) = 12 (2) per meadow] located in a set of 40 meadows within the bison range. Wallows are depressions in the ground created when bison trample the earth and roll in the exposed soil. Wallows are approximately oval in shape and vary in depth and in diameter (Polley & Collins, 1984). In PANP, observed wallows had average diameters of 1.5–3 m, similar to those observed in other areas (Barkley & Smith, 1934). We identified whether exotic plant species were present in and around (<50 cm from the edge) each wallow. When clover or timothy was found near a wallow, we verified whether this species was also present elsewhere in the meadow by recording its occurrence in 20–40 (number selected proportionally to meadow area) randomly distributed quadrats (0.25 m^2). We also investigated the presence of exotic plants along 432 bison trails (mean length = 329 m; length range: 25– 1941 m). Bison trails are large, conspicuous and are mostly exposed bare soil where abundant bison faeces and tracks are present. They generally occur in the forest and connect meadows. These trails require the repeated passage of several individuals, such as ungulate groups, to be maintained. Moreover, the number of trails

observed in the bison range was directly linked to the bison density (Sigaud, 2018). On every observed bison trail and random transect, we recorded the GPS locations of exotic plant species directly on the bison trail (or transect) or <50 cm from the edge, as represented by one or more individual plants <1 m from each other.

Drivers of exotic plant spatial distribution

Our final hypothesis was that bison activity influences the probability of exotic species occurrence near wallows and along trails in PANP. To test this, we fitted logistic regression models contrasting the environmental characteristics of discrete locations where exotic plant species were present near wallows or on bison trails with the characteristics of randomly selected locations in meadows or bison trails where exotic species were absent (Manly et al., 2002). Using these models, we could identify whether the probability of each exotic plant species being present was associated with variables related to bison activity, while accounting for other environmental characteristics.

Attributes from the plant, the landscape and animal vector need to be integrated to study the patterns of seed dispersal (D'hondt et al., 2012). In particular, distance to the nearest parent plants and the activity pattern of the vector are major determinants of spatial pattern of seed dispersal (Jordano et al., 2007; Nathan et al., 2008). Here, we considered two variables related to bison activity as predictors of the probability of exotic plant species occurrence in our models: distance to potential introduction points (reflecting distance to parent plant) and intensity of bison utilization. Introduction points represent discrete locations linking agricultural lands to PANP along the river constituting the boundary of PANP. These locations are heavily used by bison to cross the river and access agricultural lands. We measured the Euclidian distance between each exotic species location and the nearest potential introduction point. Local intensity of use by bison was evaluated from the kernel estimation of the mean utilization distribution of individual bison (Worton, 1989). We used the data from the 18 adult female bison equipped with Argos/GPS collars (TGW 4780H; Telonics Inc., Mesa, AZ, USA), taking locations every 3 h between July and October, from 2010 to 2012. This time of the year encompasses more than 80% of the bison locations that occurred on agricultural lands. For each collared bison, we computed the utilization distribution standardized over the bison range based on kernel density using the ad hoc method for the smoothing parameter (see Worton, 1989; Lichti & Swihart, 2011 for details). The utilization distribution is a bivariate probability density function giving the probability density than an animal is found at a given point in space. We then assigned a value of bison utilization to each exotic plant species location (i.e. on trails and wallow) according to the mean score of the utilization distribution in a 20 m buffer.

We also included land cover variables in our models because the substrate available at the microhabitat where seeds are deposited can strongly influence germination, seedling growth and survival, and can therefore affect plant distribution patterns (Nathan & Muller-Landau, 2000). We used a classified SPOT5 image (August 2008; 10-m resolution, Dancose, Fortin & Guo, 2011) to delineate the following seven land cover types: water, conifer stands, deciduous stands with hazelnut Corylus cornuta (Marsh), deciduous stands without hazelnut, mixed stands, roads and meadows. We included the distinction between deciduous stands with and without hazelnut in our analysis because deciduous stands with hazelnut present a dense understorey that could negatively influence the establishment of exotic plant species. We included all land cover types as predictors in our models

(i.e. meadow, conifer forest, mixed forest, deciduous forest and deciduous forest with hazelnut), using deciduous forest, the most common land cover type around trails surveyed, as the reference category.

As we found only few occurrences of clover near wallows, we did not build a model for the occurrence of clover around wallows. For the occurrence of timothy around wallows, we built a model with only distance to the nearest introduction point and bison utilization because all wallows surveyed were located in meadows. Models did not have any multicollinearity issues, as variance inflation factors were consistently <2 (Graham, 2003). We used our fitted models to predict the probability of presence of clover and timothy for each 10 m pixel across our landscape. These probabilities are conditional on the presence of a bison trail (timothy and clover) or a wallow (timothy only). Using this information, we computed the percentage of pixels with a high probability (>75%) of exotic plant species occurrence inside each fescue grasslands patch. All analyses were performed using R (R Core Team, 2017).

Results

We recovered 9466 seeds from faecal samples and identified 73% (n = 6960) of them to species level. We recorded 52 plant species from 15 families, including 22 species that are exotic in North America (Supporting Information Table S1). From all the recovered seeds identified to species level, 80% belonged to exotic plant species. On average, 46% (SE = 3; range 0–100%) of the seeds recovered from each faecal sample were exotic. Seeds of two exotic clover species were most abundant, representing 53% of all seeds recovered

Table 1 Parameter estimates of logistic regressions characterizing the effects of the land cover type (reference category being deciduous forest), distance to nearest introduction point and utilization of 18 collared bison on the probability of clover (*Trifolium* spp.) and timothy (*Phleum pratense*) occurrence along bison trails and around wallows in Prince Albert National Park, Saskatchewan, Canada, during autumns 2012 and 2013. Each model covariates is presented with estimated coefficients (β) and 95% CI

Variable	Clover on trails β [95% CI]	Timothy on trails β [95% CI]	Timothy on wallows β [95% CI]
Intercept	1.26 [0.58, 1.95][b]	−1.94 [−5.55, 0.89]	−1.35 [−4.60, 1.50]
Coniferous	−1.37 [−3.07, 0.11]	–	–
Mixed forest	−0.46 [−0.97, 0.06]	1.78 [−0.80, 4.98]	–
Deciduous with hazelnut	−0.38 [−0.81, 0.05]	1.28 [−0.62, 4.27]	–
Meadow	−0.15 [−0.85, 0.58]	4.50 [2.26, 7.75][b]	–
Distance[a]	−0.61 [−0.76, −0.46][b]	−1.46 [−2.48, −0.69][b]	−1.18 [−2.11, −0.45][b]
Utilization[c]	0.71 [0.31, 1.11][b]	0.42 [−1.12, 2.12]	3.02 [1.42, 5.15][b]

[a]Distance correspond to the Euclidian distance to nearest introduction point.

[b]Confidence intervals that exclude 0.

[c]Utilization correspond to mean utilization computed from 18 collared bison.

(n = 4978; Supporting Information Figure S1). Previous studies of bison foraging did not report the consumption of timothy or clover by bison inside the park (Fortin et al., 2002; Courant & Fortin, 2012), suggesting that these species, if present at all, were not numerous enough to be recorded. As such, it is unlikely that seeds recovered from faeces originate from patches of these species established in the park.

The exotic plant species most frequently encountered alongside bison trails were white clover T. repens and red clover T. pratense. We recorded the presence of clover only once on random transects (i.e. <1%) and found no timothy on random transects. Clover and timothy were present in 37% and 4%, respectively, of the 432 bison trails surveyed. We also observed flowering individuals of clover and timothy along these trails. This information was not recorded for wallows. Timothy occurred in 5% of surveyed wallows (n = 360), with 27.5% of surveyed meadows (n = 40) containing at least one wallow with timothy. Neither timothy nor clover occurred in any random quadrats surveyed in these meadows.

Utilization by bison had a positive effect on the probability of clover occurrence on trails and on the probability of timothy occurrence around wallows. Both clover and timothy occurrence on trails, and timothy occurrence around wallows, decreased with distance to the nearest introduction point (Table 1; Fig. 2). We found that 89% of the clover locations were recorded within 3 km of the nearest potential introduction point. Timothy was more likely to occur on trails in meadows than trails in deciduous forest, a trend that was not observed for clover.

We found that, on average, 38% (±19% SE, Fig. 3a,d) of the 10 m pixels constituting a fescue grasslands patch presented a high probability (>75%) of clover occurrence if a bison trail was present, and 27% (±14% SE, Fig. 3b,e) for timothy occurrence. Also, there was a high probability of timothy occurrence on pixels within 0.5 m of bison wallows across 20% (±11% SE; range 0–76%, Fig. 3c,f) of total fescue grassland area. Of the seven fescue grasslands present in the bison range, three had a high probability of occurrence

of at least one exotic species (i.e. either timothy, clover or both) across at least 10% of their total area.

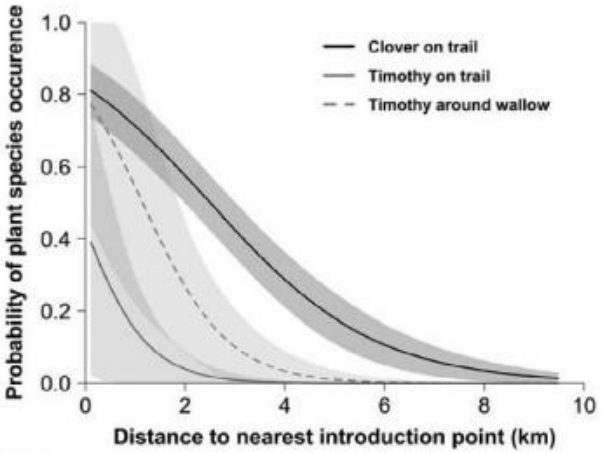


Figure 2 Probability of occurrence and 95% CIs (shaded polygons) of two exotic plant species along bison trails in deciduous forest and around wallows (based on model results shown in Table 1), in Prince Albert National Park, Saskatchewan, Canada, in relation to distance to the nearest introduction point from surrounding agricultural areas. Predictions were computed based on the reference category 'deciduous forest', and using mean values of the bison utilization distribution recorded at 346 random points along bison trails.

Discussion

Our study illustrates how conservation projects focusing on the recovery of different individual components of natural ecosystems might come into conflict. In our case study, we found that bison transporting exotic plant species from agricultural lands into adjacent protected areas can impede the restoration of fescue grasslands. Therefore, the objective of maintaining a freeranging bison population can impact the ecological integrity of fescue grasslands via the propagation of non-native plant species. By quantifying the drivers of spatial variation in this ecological process, it is possible to identify the hotspots of potential conflict where the progression of exotic plant species should be carefully monitored, and where conservation and restoration efforts might be prioritized in the future. Studies of the ecological mechanisms underpinning conflict between conservation programmes are vital for understanding how such conflict can emerge and how they can be managed at early stages in their development.

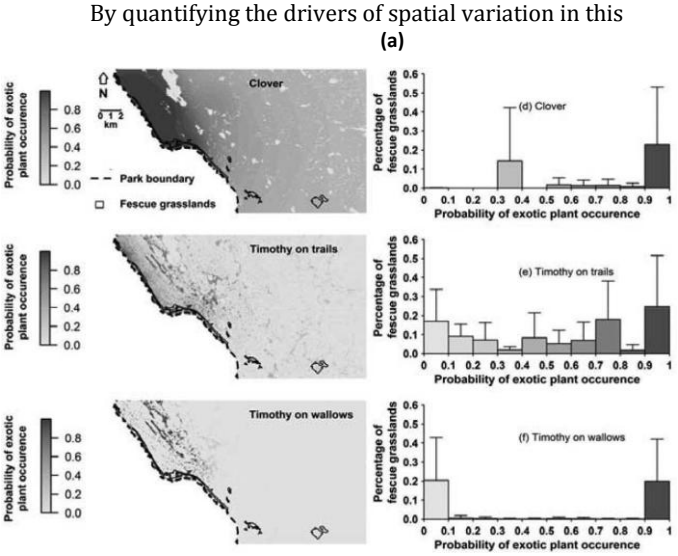


Figure 3 Predicted spatial variation in probability of occurrence of exotic plant species in and around fescue grasslands (a–c) and the distributions of predicted probabilities of exotic plant species occurrence within fescue grassland patches (d,f) in Prince Albert National Park, Saskatchewan, Canada.Predictions are based on models (Table1) for clover(Trifolium spp.) on bison trails (a,d), timothy(Phleum pratense)on bison trails (b–e) and timothy around bison wallows (c,f).

Transport and establishment are the two first stages of the invasion process. While disturbance generated by bison activities at microsites (trails and wallows) is likely to create favourable conditions for the establishment of exotic plant species, further research, such as germination trials on disturbed and undisturbed sites, is required to conclude this definitively (e.g. Winn, 1985; Setterfield, 2002) and to evaluate the extent of the impact that these introduced species have on fescue grassland populations. Bison use a complex network of trails (Dancose et al., 2011), and while adjacent meadows might remain connected over numbers of years, the specific locations of the trails used to travel between these meadows can change from 1 year to the next (Sigaud, 2018). Such changes are likely to lead to the widening of the spread of exotic species over time especially if exotic plant species are more likely to get established in these disturbed sites. Once established, exotic invasive species can compete directly with native species, and also indirectly by changing various aspects of native ecosystems including nutrient cycling, hydrology, litter accumulation, fun-gal mutualism and disturbance regimes (Vitousek et al., 1996; Brooks et al., 2004; Callaway et al. 2008). For example, the introduction of nitrogen (N)-fixing legumes, such as clover species, can affect nutrient cycling and alter competition between native and non-native plant species (Carino & Daehler, 2002).

This was the case for yellow sweet clover Melilotus officinalis, which facilitated the invasion of native grasslands of the northern Great Plains by an exotic grass species through nitrogen enrichment (Dornbusch, Limb & Gasch, 2018). While the presence of the surveyed non-native plant species (P. pratense, T. repens and T. pratense) has been documented in grasslands (Tyser, 1992; Tyser & Worley, 1992; Kennedy et al., 2002) and other North American plant communities (Weaver, Lichthard & Gustafson, 1990; Dukes & Mooney, 2004; van Kleunen et al., 2011), more research is needed to document their impact on native rough fescue grasslands.

The probability of exotic species occurrence varied spatially depending on the plant species concerned (Albert et al., 2015). Spatial patterns of dispersion are not only shaped by specific characteristics of the vector species but also by each plant species. Bison have long-digestive retention times (~78 h; Schaefer, Young & Chimwano, 1978) and both retention time and survival rate following defecation are influenced by the characteristics of the seed species. For instance, feeding trials showed that 90% of T. repens seeds ingested by cattle were excreted after 71 h and 9.1% were able to germinate. These numbers varied greatly among plant species, with some species being excreted faster with a higher percentage of germination (e.g. 49.8% of Centrosema pubescens seeds excreted were able to germinate, Gardener, McIvor & Jansen, 1993) and most likely among vector species (Cosyns et al., 2005; Milotiéc & Hoffmann, 2016). The few germination trials that have been conducted for seeds following passage through the digestive tract of bison demonstrate that generally a proportion is able to germinate (e.g. G€okbulak, 2002 reported that 36.9–48.7% of undamaged seeds of Elymus cinereus recovered from bison dung germinated while, Eyheralde, 2015 found that fewer than

10% of seeds extracted from bison dung were viable but hardcoated seeds such as Trifolium spp. were the most likely to germinate). We could not quantify the part played by epizoochory in the observed spatial pattern of dispersion, but it is likely that a plant species with attachment structures on seeds like P. pratense L. (Royer & Dickinson, 1999) might also be transported externally by bison (see Couvreur et al., 2004 for experiments on P. pratense external transport by several large herbivore species) or through hoof-epizoochory (Schulze, Buchwald & Heinken, 2014; Baltzinger et al., 2019).

Assessments of trade-offs between social, economic and environmental values and attributes underpin decision-making in biodiversity conservation (Burgman & Yemshanov, 2013). While risk assessments play a vital role in preventing negative side effects of conservation actions (Kilpatrick, Gillin & Daszak, 2009), they rarely take into account potential conflict between different conservation programmes (Adamowicz, 2016). Here, we illustrate that, by integrating the identified ecological mechanisms of conflict into spatially explicit models, we can delineate areas at high risk of negative impacts from conflicting conservation programmes. This information allows the identification of priority areas where conflict is likely to be most intense (e.g. fescue grasslands patches close to introduction points with or without exotic species, depending on management objectives). Our spatial model could also provide valuable information to the protocol of quantitative risk assessment proposed by Kolar & Lodge (2002), as our model pertains to the first component (transport and establishment) of the process of alien species invasion outlined by these authors. The management of invasive plant species is a complex challenge that can be lengthy and expensive. Choosing the appropriate strategy, such as eradication or containment, depends on a number of factors including the extent of the invasion (Hester et al., 2013). Our results could help to organize surveillance efforts of both studied exotic species. For instance, depending on the ecological value of each fescue grasslands patch and the available resources for restoration, the conservation of more distant fescue grasslands from introduction points might be prioritized. In contrast, fescue grasslands close to the introduction points could benefit most from both restoration efforts and from conservation actions aimed at limiting bison access to agricultural lands.

Deterring wildlife species from sensitive areas is a common approach for dealing with damage caused by wildlife in degraded and anthropogenic environments (Conover, 2002). For instance, various methods have been applied to minimize crop-raiding behaviour by wildlife including the use of auditory scaring devices (Suraci et al., 2016), active scaring by humans (Simonsen et al., 2016) and repellent chemicals (Osborn, 2002). Unfortunately, such methods have seen little success against bison. For instance, the use of scaring devices and hazing to keep bison within Yellowstone National Park proved ineffective (Meagher, 1989). Preventing bison access to specific locations can probably only be achieved through bison-proof fencing; temporary exclosures (e.g. exclosures against moose browsing, Pastor et al., 1993) could be constructed to prevent bison from accessing high-priority fescue communities during the sensitive steps of their restoration, such as the time period immediately after prescribed habitat renewal fires. However, excluding bison from grasslands during sensitive periods should be regarded as a temporary mea-sure because grazing is an important component of the longterm restoration of these ecosystems (Koerner & Collins, 2014). Restricting bison access to agricultural lands could also help decrease the transport of non-native plant species within the park but would be challenging to implement. This would require the deployment and maintenance of an extensive network of fences as there are no significant physical barriers between PANP and the surroundings agricultural lands other than a shallow river easily crossed by bison. Moreover, this might have consequences for other non-target wildlife species
(e.g. negative impact on landscape connectivity). Various factors have been identified that influence the use of agricultural lands by bison (e.g. type of plant species cultivated; green biomass available; patch size see Sigaud et al., 2017); these factors could be manipulated to limit this behaviour (Simon & Fortin, 2020). Such actions would require the involvement of the local community, as agricultural lands are owned and managed by private landowners.

Our case study illustrates the inherent difficulties of reconciling conflicting conservation programmes but reveals how an understanding of the underlying ecological mechanisms driving conflict can open up new ways to manage them. In Canada, species listed as endangered, threatened or extirpated under the Species at Risk Act (SARA) require recovery strategies outlining the steps needed to halt or reverse their decline. SARA and most threatened species policies focus on critical habitat as the mechanism for recovery and tend to place less emphasis on other important influences such as invasive species or multispecies interactions (Adamowicz, 2016). Our study shows that the anticipated effects (positive or negative) of proposed recovery plans on non-target species, natural communities or ecological processes should also be identified, as also suggested by the National Recovery Working Group (2005). However, conflicting conservation programmes appear to be currently underappreciated in large-scale conservation efforts (Gerber et al., 2011). While there is a growing body of literature on how to manage conflict between the objectives of conservation and human livelihoods (Redpath, Bhatia & Young, 2014; Mason et al., 2018; Vucetich et al., 2018), conflict between conservation objectives are rarely reported. Such mechanisms may be unique to the type of conflict concerned – such as the transportation of invasive species by large herbivores identified here – and are thus likely to provide valuable information for managing specific types of conflict. Identifying these challenges prior to implementing conservation strategies allows managers to strategically prioritize conservation efforts and make informed compromises where required (Burgman, 2005). The lack of recognition of these conflict could impede ongoing conservation efforts (Lipsey & Child, 2007), posing a specific threat to the success of the growing number of large-scale rewilding projects planning large mammal reintroductions in human-altered landscapes (Seddon et al., 2014).

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. (a) Number of intact seeds recovered in 283 plains bison faeces collected in Prince Albert National Park, Saskatchewan, Canada, during autumn 2012 for the 15 dominant species, on a logarithmic scale. (b) Percentages of faecal samples with at least one seed per species.
Table S1. Identification of seeds recovered from 283 bison faecal samples collected during autumn 2012 in Prince Albert National Park, Saskatchewan, Canada.