

BISON (*Bos bison bison* L.) AS ECOSYSTEM ENGINEERS IN THE ASPEN PARKLAND

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ABSTRACT

The Aspen Parkland is threatened by many factors including the loss of natural disturbance processes such as fire and herbivory. Bison, as the dominant large herbivore, are suspected to have played an important role in maintaining and structuring the plant community by preventing shrub encroachment into open grassland. In this study we examined the effect of bison on plant communities across the forest – grassland ecotone in Riding Mountain National Park. The impact of bison on rough-fescue grassland communities was examined using range enclosures. We found that over a single year bison reduced sward heights but did not alter the composition of grassland communities, with the possible exception of an important interaction with the invasive *Poa pratensis*. However, the long-term (>80 year) presence of bison was associated with greater species richness, reduced litter accumulation, and a distinct community composition compared to areas without bison. By comparing areas where bison had recently been introduced to areas of long-term presence and absence, we found that the influence of bison on the shrub community at the forest grassland edge is limited. Bison occurred at very low densities in areas with dense, tall shrub understories, and thus cannot be a major factor in limiting shrub growth and survival. Shrub stem mortality due to fire may be a necessary precursor to bison mitigating woody encroachment in the Aspen Parkland.

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1. GENERAL INTRODUCTION

This study examines how bison shape their environment. In the past, tens of millions of plains bison (*Bos bison bison*) weighing up to a tonne each ranged throughout central North America (Forsyth 1985, Shaw 1995). The species is widely acknowledged as having an important impact on the development of the ecosystem in the grasslands at the core of its range (Knapp et al. 1999, Fahnestock and Detling 2002). At the periphery of its range, in the Aspen Parkland, the role of bison is relatively poorly understood. This is despite the fact that transitional ecosystems such as the Aspen Parkland are arguably more susceptible to the influence of large herbivores such as bison. In ecotonal ecoregions such as the Aspen Parkland, where the climate is intermediate between supporting two dramatically different plant communities, disturbance such as that caused by large herbivores can play a decisive role in determining physiognomy. The ecological integrity of the Aspen Parkland is at risk due to a number of threats. These include widespread conversion to cropland (Moss and Campbell 1947, Grilz and Romo 1994, Gerling et al. 1995), invasion by alien plant species (Grant et al. 2009, DeKeyser et al. 2015), and loss of natural disturbance processes (Strong 1977). It has been suggested that bison played a critical role in the historic disturbance regime of the Aspen Parkland (Campbell et al. 1994), but empirical evidence in support of this hypothesis is limited due to the extirpation of the species prior to ecological study during the 19th century (Allen 1876, Hornaday 1889, Malainey and Sherriff 1996, Krech 1999).

In Riding Mountain National Park (RMNP), situated at the northeast edge of the Aspen Parkland in Manitoba, changes due to disruption of the natural disturbance regime are a major concern (Parks Canada 2007). These include loss of biodiversity in grasslands, and forest encroachment into grasslands (Parks Canada 2007). A small enclosed bison herd in the Lake Audy area of RMNP provides an opportunity to empirically test hypothesis about how bison contribute to disturbance and influence plant communities in the Aspen Parkland. This study seeks to better understand that relationship. The objectives were to determine the effect of bison on shrub and tree species along the forest-grassland ecotone, and to assess the effect of bison on

rough fescue grassland community structure. This was done primarily by experimentally manipulating the distribution of bison and observing differences in plant communities in areas where bison were present or absent over short or long time periods.

The purpose of this thesis is to describe how and why bison can influence the structure of the plant community in the Aspen Parkland, with a particular focus on the case of RMNP. To provide context, I begin with a general review of the relevant literature. This includes a description of the Aspen Parkland as an ecoregion, and an explanation of how this ecoregion can be understood as both an ecotone and as a disclimax. As well, I describe how herbivores can introduce disturbance to a system, and contribute to a disclimax. Providing context for how the Aspen Parkland is susceptible to change due to disturbance by a large herbivore, I review the ecological role of bison in particular as an agent of disturbance. I discuss the recent ecological history of bison in the Aspen Parkland, and provide evidence supporting their role as an ecosystem engineer. Next, I describe an empirical study I carried out in RMNP between 2015 and 2016. This includes two separate experiments used to elucidate different components of the relationship between bison and their environment. One is a range-cage experiment examining the relationship between bison and the structure of grassland plant communities. The other tests how bison influence woody plant communities along the ecotone between forest and grassland. The results of these experiments show both the long-term and short-term effect bison have on the grassland community of Riding Mountain, and describe the factors mediating the relationship between bison and the woody plant community at the forest-grassland ecotone. Using these findings, I provide recommendations for land managers in RMNP and throughout the Aspen Parkland. As well, I outline the new questions and information gaps highlighted by the results of this study and describe opportunities for future research.

2. LITERATURE REVIEW

2.1 Introduction

Large herbivores play a critical role in structuring their ecosystems (Hobbs et al. 1996) by introducing disturbance that is species selective (Pastor et al. 1993) and spatially variable (Waldram et al. 2008). This is especially true in transitional ecosystems, where climatic conditions are such that disturbances readily shift communities between alternate stable states (Dublin et al. 1990). Throughout the world, many populations of large wild herbivores are contracting or have been severely reduced (Laliberte and Ripple 2004, Craigie et al. 2010). The loss of these animals is likely to have important, and in many cases unforeseen, implications for the conservation of these ecosystems. By understanding how large herbivores modify their environment, we will be able to better predict what the effects of their removal from a system could be and determine what impact the loss of such a species has already had on anthropogenically modified ecosystems.

The interaction between plains bison (*Bos bison bison*) and the structure of communities of the Aspen Parkland provides an intriguing model of this process. The Aspen Parkland, the broad transitional ecoregion between the grasslands and boreal forests of central North America, has been heavily impacted by Euro-Canadian settlement (Moss and Campbell 1947). This mosaic landscape of grassland and forests is sited on rich soils ideally suited to agriculture. As a result, large portions of the region have been converted to agricultural use. It is estimated that less than 5% of the original extent of rough fescue grasslands remain globally (Grilz and Romo 1994, Gerling et al. 1995). The small remaining area of natural habitat continues to experience a number of threats including ongoing conversion to cropland, industrial use, urban expansion, fragmentation (Gerry and Anderson 2002, Fu et al. 2008), and invasion by alien species. In addition, the few remaining grassland patches continue to be reduced by the encroachment of trees and shrubs (Maini 1960, Campbell et al. 1994). This encroachment has often been attributed to the suppression of wildfire (Strong 1977). However, it is now suggested that the loss of bison from the landscape may have contributed significantly to the encroachment of aspen

forests into rough fescue grasslands (Campbell et al. 1994). Bison were historically the most abundant large herbivore in the Aspen Parkland. They are now functionally extinct in the wild in the ecoregion, save a few small protected areas (Gates et al. 2010). The loss of this large herbivore may have had a profound effect on the structure and composition of the ecoregion.

2.2 Aspen Parkland

The Aspen Parkland is the ecoregion found at the transition from the northern prairies of North America to the southern boreal forest (Ecological Stratification Working Group 1996). It occurs in a broad arc from southern Manitoba and North Dakota, through central Saskatchewan, to central Alberta where it abuts the Rocky Mountain foothills. It varies in width along its length from a few tens of kilometres to a few hundred kilometres. The exact distribution of the ecoregion varies depending on the source (Brandt 2009). However, the northern boundary is generally defined as the southern distribution of the four boreal cold-tolerant conifers; *Picea glauca*, *Picea mariana*, *Pinus banksiana*, and *Larix laricina* (Zoltai 1975). The southern boundary is defined as the northern limit of open mixed-grass prairie (Bird 1961). In addition, an isolated area in the Peace River valley with consistent phytogeographical traits is generally included as a part of the ecoregion (Bird 1930).

The geology of the Aspen Parkland is dominated by post-glacial features; glaciolacustrine, glaciofluvial, and till deposits (Bird 1930). The soils deriving from these parent materials are dominated by black chernozems. Dark gray chernozems are found at the northern edge of the ecoregion where it abuts the Boreal Transition zone, and dark brown chernozems can be found along its southern edge. Dark gray luvisols can be found under extensive aspen stands (Thorpe and Anderson 2010), and gleysols are prevalent in poorly drained areas (Ecological Stratification Working Group 1996).

The Aspen Parkland is dominated by a mosaic of trembling aspen (*Populus tremuloides*) groves and grasslands. The proportion of grassland decreases across the ecoregion from the northern prairies to the boreal forest, so that it transitions from open grassland to closed forest (Bird 1930). Grasslands are limited to small, isolated pockets at the northern edge, and aspen groves are restricted to moist landscape depressions at the southern edge (Coupland and Brayshaw 1953). Wetlands are an important landscape component throughout the ecoregion (Bird 1961).

The forested communities of the Aspen Parkland are dominated by trembling aspen (Bird 1930). In addition to *P. tremuloides*, *Populus balsamifera* can occasionally be abundant in forest stands (Bird 1930), particularly in moist depressions (Rowe 1972). *Quercus macrocarpa* is abundant in the southeastern portion of the region, which is occasionally referred to as Aspen-Oak Parkland (Rowe 1972). This species is found both on well-drained, drier sites and along river bottoms. Also found along rivers in the eastern portion of the region are *Acer negundo*, *Fraxinus pennsylvanica*, and *Populus deltoides*. In the far eastern portion, *Tilia americana* and *Fraxinus nigra* are occasionally found.

The tall shrub layer is important in these communities, with species such as *Amelanchier alnifolia*, *Prunus virginiana*, *Prunus pensylvanica*, *Corylus cornuta*, and *Cornus stolonifera* predominant (Thorpe and Godwin 2008). In some sites, *Corylus cornuta* may form an especially dense understory which severely limits the productivity of the herbaceous layer (Thorpe and Godwin 2008). Shorter shrub species which are prevalent include *Symphoricarpos occidentalis*, *Rubus idaeus*, *Shepherdia canadensis*, and *Rosa* species (Thorpe and Godwin 2008).

Common grasses found in the understory of these forest stands include *Oryzopsis asperifolia*, *Schizachne purpurascens*, and *Helictotrichon hookeri* (Thorpe and Godwin 2008). *Carex* species are abundant, and there is a large number of native forb species (Thorpe and Godwin 2008).

The grasslands of the Aspen Parkland have been described and classified by numerous authors (Bird 1930, Moss and Campbell 1947, Coupland and Brayshaw 1953, Bird 1961, Looman 1963, Looman 1969, Wroe 1971, Anderson 1972, Coupland 1973, Wheeler 1976, Fehr 1982, Looman 1982, Legris and Cornish 1997, Weerstra and Holcroft Weerstra 1998). The primary grassland community of the Aspen Parkland is dominated by plains rough fescue *Festuca hallii* (Moss and Campbell 1947, Coupland and Brayshaw 1953), formerly referred to as *Festuca scabrella* (Pavlick and Looman 1983). This rough fescue grassland community or association is considered to be the predominant native grassland of the black soil region of the Canadian prairies (Moss and Campbell 1947). To the south of the Aspen Parkland proper this rough fescue grassland formed continuous prairies in central Alberta and west-central Saskatchewan before giving way to *Stipa-Agropyron* mixed grasslands further south (Moss and Campbell 1947). Coupland and Brayshaw (1953) considered the *Festuca* community to develop in a successional series from the *Stipa-Agropyron* community of the mixed grasslands and succeed to the *Populus* grove community of the Aspen Parkland.

Festuca hallii is found in association with numerous other species, the most important of which is *Stipa curtisetata* (formerly *Stipa spartea* var. *curtiseta* (Moss 1983)). *Stipa curtisetata* is found as a co-dominant with *Festuca hallii* under drier conditions, such as in the southern portion of the ecoregion (Coupland and Brayshaw 1953) or on upper, south facing slopes (Looman 1963, Wroe 1971). Shifting to a more mesic moisture regime, *Festuca hallii* becomes completely dominant (Coupland and Brayshaw 1953, Looman 1963). *Festuca hallii* is a perennial bunchgrass with narrow leaves (Pavlick and Looman 1984). The resistance of these leaves to decomposition (Dormaar 1975) results in a build-up of a thick litter layer. This litter layer may serve to exclude other species, resulting in a community with relatively low diversity (Moss and Campbell 1947, Letts, B. et al. 2015).

Other herbaceous species that are often co-dominant with *Festuca hallii* in the prairies of the Aspen Parkland include *Elymus trachycaulus*, *Danthonia intermedia*, *Stipa viridula*, *Koeleria macrantha*, *Helictotrichon hookeri*, *Calamovilfa longifolia*, *Bromus ciliatus*, and various *Carex*, *Poa*, *Artemisia*, and *Antennaria* species (Weerstra and Holcroft Weerstra 1998). These associations primarily occur on drier or well drained, sandy sites (Moss and Campbell 1947, Fehr 1982, Gerling et al. 1996) or on sites affected by grazing (Moss and Campbell 1947, Wheeler 1976, Vujnovic 1998). The bunchgrass physiognomy of *Festuca hallii* positions the apical meristem above-ground, where it is susceptible to grazing damage. Therefore, grazing can reduce the abundance of *Festuca hallii*, resulting in an increase in species more closely associated with the mixed grasslands (Coupland 1973, Vujovic 1998). Frequent fires may also cause a transition to a species composition more indicative of mixed grassland (Anderson and Bailey 1980).

Shrub species are also found as co-dominants in rough fescue grasslands. Some species, including *Juniperus horizontalis*, and *Arctostaphylos uva-ursi* are found on drier sites (Legris and Cornish 1997, Willoughby et al. 1997). Most however are more prevalent in moister sites at the northern edge of the ecoregion or in landscape depressions (Anderson 1972, Fehr 1982), including *Symphoricarpos occidentalis*, *Elaeagnus commutata*, *Amelanchier alnifolia*, and *Prunus virginiana* (Weerstra and Holcroft Weerstra 1998). *Symphoricarpos occidentalis* is particularly important (Anderson 1972, Wheeler 1976, Fehr 1982).

A large portion of the original rough fescue grasslands of the Aspen Parkland has been broken for cultivation (Moss and Campbell 1947). Rowe and Coupland (1984) estimated that 80

percent had been converted to cropland. North (1976) estimated that as much as 90 to 95 percent had been converted, leaving only 5 to 10 percent remaining. Of that remaining unbroken grassland, a majority has been significantly modified by agricultural practices such as mowing and intensive cattle grazing (Moss and Campbell 1947). These practices have contributed to the introduction of several invasive non-native species. The non-native grass *Poa pratensis* (DeKeyser et al. 2015) is now widespread throughout the remnant grasslands of the Aspen Parkland (Slopek and Lamb. 2017, Stotz et al. 2019), and in many cases has replaced rough fescue as the dominant species (Grace et al. 2002, Grant et al. 2009, Sinkins and Otfinowski 2012). By displacing native plants, species like *P. pratensis* negatively impact biodiversity and ecosystem functioning.

2.2.1 Ecotones and Transitional Ecosystems

The term ecotone may refer to a boundary separating two distinct communities within a landscape, across which there is a high species turnover (Clements 1905, Holland et al. 1991, Gosz et al. 1992, Risser 1995, Fagan et al. 2003). These ecotones are often dynamic and shift with disturbance (Holland et al. 1991), reflecting the patch dynamics that determine the structure of the overall landscape (Pickett and White 1985). Ecotone may also refer to an area where the transition zone between two biomes or ecoregions is a relatively narrow, sharp boundary (Livingston 1903, Curtis 1959, Van Leeuwen 1966, Van der Maarel 1990). In this sense ecotones often constitute an unstable landscape due to the role of disturbance, consisting of discrete patches of two internally homogeneous community types (Van der Maarel 1990). The organization of terrestrial biomes (Clements and Shelford 1936, Carpenter 1939) on earth is thought to be in large part determined by climate (Holdridge 1947, Whittaker 1975). However, large areas exist as broad climatic ecotones where two biomes abut each other (Bird 1930). In these ecotones climatic conditions are typically close to the thresholds where the dominant physiognomy of the plant community switches between one type and another (Carpenter 1935, Carpenter 1939). Examples include the oak savanna of central North America (Pool et al. 1918), transition zones between tropical rainforest and savanna (Monteiro et al. 2014), and the circumpolar forest-tundra transition (Bluthgen 1970). Aspen Parkland is another such environment (Bird 1961).

Climate is a central influence on the distribution of the Aspen Parkland. The primary climatic factor involved is thought to be drought and soil moisture deficit (Looman 1979, Zoltai et al. 1991), factors which are a function of both precipitation and temperature. Hogg (1994) showed that the northern boundary of the Aspen Parkland was closely aligned with the Jensen-Haise climatic moisture index isoline of 0. That is, where total annual precipitation was equal to total annual potential evapotranspiration. This aligns with the southern limit of the five boreal conifer tree species (Hogg 1994). The limiting factor for these species appears to be insufficient moisture during germination and establishment of seedlings (Maillet et al. 2017), though, there is sufficient moisture for mature conifers to survive throughout the Aspen Parkland (Maillet et al. 2017). The southern boundary of the Aspen Parkland occurs where the mosaic of aspen forest and grassland is replaced with continuous mixed grassland (Bird 1961). This boundary coincides with the climatic moisture index isoline of -15 mm, where potential evapotranspiration exceeded precipitation by 15mm (Hogg 1994). Insufficient moisture can lead to the decline and mortality of aspen (Hogg et al. 2008). However, within the CMI range of 0 to -15 conditions are suitable for the growth and survival of aspen. In fact, within this range, aspen stands are able to outcompete and encroach on grassland communities (Moss and Campbell 1947, Maini 1960, Bailey and Wroe 1974). The encroachment of aspen into grasslands has been documented throughout the Aspen Parkland since Euro-Canadian settlement of the prairies.

Despite the competitive advantage of aspen, the Aspen Parkland isn't solid forest but rather a mosaic of grassland and forest. Both community types are supported within the ecoregion because conditions for these trees are marginal enough (Hogg 1994, Hogg et al. 2008, Michaelian et al. 2011) that disturbance can shift the ecosystem to an alternative state. Evidence suggests that the loss of major disturbance factors as a result of Euro-Canadian settlement contributed to the encroachment of aspen now observed (Campbell et al. 1994). There is a relatively low energetic barrier to switch to the other state (Holling et al. 1995). A disturbance within the boreal forest (such as a forest fire) typically results in the community then proceeding through secondary succession. Within the Aspen Parkland, the forest community is susceptible enough, and disturbance is frequent enough to prevent the community from proceeding through succession to closed forest. A community maintained by disturbance in this manner is referred to as a disclimax (Daubenmire 1968).

2.2.2 Disclimax

A disclimax is a state in which frequent disturbance (White and Pickett 1985) prevents a community from succeeding to an equilibrium climax community (Daubenmire 1968). The frequency of disturbance at a given site is dependent on climatic, biophysical, and historical factors (Liu and Wimberley 2015). A disclimax can be said to occur where these factors contribute to a disturbance frequency that disrupts succession and prevents the community from reaching an equilibrium state (Meeker and Merkel 1984). The community is maintained in a state of disequilibrium, in which disturbance exerts an important controlling effect on the type of dominant vegetation (Borchert 1950, Staver et al. 2011, de L. Dantas et al. 2016). Often, this vegetation community will support more frequent disturbance, creating a positive feedback loop that reinforces the disequilibrium (Rossiter et al. 2003, Bowman et al. 2014).

Wildfire is an important example of a type of disturbance that can disrupt succession (Bird 1961, Staver et al. 2011). This has been demonstrated in woodland and savanna ecosystems around the world (Trollope 1984, Brown and Smith 2000). Woody plants accumulate biomass in their above-ground tissues each year, and the meristematic tissue from which the above-ground portion of the plant is also positioned above-ground. Herbaceous plants in contrast typically replace their above-ground tissues each year, and the meristems from which these tissues developed are often protected belowground. When fires destroy above-ground tissue, herbaceous plants are able to respond quickly by producing new shoots from meristems insulated by the soil or from seed as they do following each dormant season, whereas trees and shrubs may take many years to re-accumulate the lost shoot biomass, and only if they are able to survive the loss of the shoot meristems. By damaging trees and shrubs, fires can maintain grasslands or open understoreys dominated by herbaceous plants (Nelson and England 1971). This herbaceous fuel type is often then subject to more frequent fire return intervals (Rossiter et al. 2003, Bowman et al. 2014). However, as fires become more frequent, they may become less intense due to reduced fuel loading (Godwin 2011, Lydersen et al. 2014), allowing the woody component of the community to persist.

The Aspen Parkland can be considered as an example of a fire-maintained disclimax (Bird 1961). Although the ecoregion receives sufficient moisture to support the growth of trees, the climate results in periods of significant drying (Michaelian et al. 2011). The fire return interval was historically relatively high (Stockdale 2014). Historical evidence suggests that large,

unchecked wildfires maintained open areas of grassland by killing the stems of aspen and other woody plants (Bird 1961). Fire suppression following Euro-Canadian settlement of the ecoregion has been pointed to as a cause of the encroachment of aspen stands into fescue grasslands now being observed (Moss and Campbell 1947; Maini 1960; Bailey and Wroe 1974).

The dominant woody species of the Aspen Parkland are well adapted to fire. Species such as aspen and snowberry (*Symphoricarpos occidentalis*) respond to the death of above-ground stems by suckering; triggering vigorous regrowth (Pelton 1953, Lastra 2011). In some cases, this response can result in a fire initiating aspen encroachment across a previously static forest-grassland ecotone (Lastra 2011). Guedo and Lamb (2013) found that even very frequent fire may in some cases have no effect, or even contribute to aspen encroachment. Campbell et al. (1994) suggest that the arrival of Euro-Canadian settlers triggered widespread aspen encroachment not by removing fire from the landscape, but by removing large herbivores such as bison.

2.2.3 Herbivory as Disturbance

Herbivory may be as important a disturbance factor as fire (Hobbs 1996). Large or abundant herbivores can sufficiently modify the dominant vegetation type so as to maintain ecosystems in alternate states (Dublin et al. 1990), creating a zootic disclimax (Daubenmire 1968). This is a persistent state which, if the faunal influence were removed, would succeed to a climatic climax (Beetle 1974). The ways in which herbivores can generate disturbances are diverse. Mechanisms include moderating competitive interactions among plant species (Bakker et al. 2006), altering plant physiognomy (Diaz et al. 2007), influencing fire regimes (Fuhlendorf et al. 2009), and altering rates of nutrient cycling (Frank et al. 1994).

Large herbivores can alter plant diversity and community composition by preventing competitive exclusion by dominant plant species (Bakker et al. 2006), or by causing a shift in abundance to species selected against by the herbivore (Bryant and Kuropat 1980). By consuming the relatively small amounts of biomass in seedlings, herbivores can prevent recruitment to mature shrubs and trees (Sankaran et al. 2013), altering the process of succession following a disturbance such as a fire (Davis 1967, Dublin et al. 1990). As large herbivores do not use landscapes uniformly (McNaughton 1992), they can create mosaics of grazed and ungrazed vegetation; this variation in fuel loading can then alter the way fire moves through a landscape (Waldram et al. 2008, Fuhlendorf et al. 2009). Herbivores can also place selective

pressure on plant architecture, resulting in shifts in the physiognomy of communities (Danell et al. 1994, Diaz et al. 2007). Physiognomy changes in turn affect the distribution of resources such as light (Scholes and Archer 1997) and refugia (Callaway 1992, Atstatt and Odowd 1976), with knock on effects to the composition of plant communities (Callaway 1992, Scholes and Archer 1997). Ultimately selective foraging on preferred species or within preferred habitats regulate the occurrence of alternative stable states within ecosystems (Pastor et al. 1993), or sharpen ecotones (Wilson and Agnew 1992)

By modifying the cycling of nitrogen and other nutrients, herbivores can exert a large influence on the productivity and structure of ecosystems (Horner et al. 1988, Hobbs 1996). High grazing intensities by wild ungulates increase the rate of nitrogen cycling (Ruess and McNaughton 1987, McNaughton 1992, Frank et al. 1994). A large portion of the above-ground plant biomass is consumed and the nutrients therein are deposited as feces and urine rather than as litter; these products are more rapidly decomposed by soil microbes than litter and result in greater rates of nitrogen mineralization due to lower carbon:nitrogen ratios (Ruess and McNaughton 1987). This may result in a positive feedback, wherein animals preferentially graze in areas that have previously been fertilized with urine or feces, resulting in further deposition of the same (Day and Delting 1990). These patches, known as grazing lawns, are maintained in an immature, rapidly growing state through grazing (McNaughton 1984) have higher concentrations of nutrients such as nitrogen in their tissues, have higher bulk densities, and increased primary production. Foraging may also result in negative feedbacks, as in cases where it triggers the production of secondary defensive compounds (Bryant et al. 1991, Haukoija 1991), or increases silification (McNaughton and Tarrants 1983) or where consumption is not offset by rapid growth (Hobbs and Swift 1988). This can result in increased landscape homogeneity (Hobbs and Swift 1988). These effects are often in large part due to the spatially explicit behaviour of the large herbivores, specifically their selectivity while foraging (Senft et al. 1987, Seagle et al. 1992). However, the outcome of this ecosystem modification is in many cases largely dependent on other factors including; edaphic condition, the history of coevolution between the herbivore and plant species involved, and the climate (Hobbs 1996).

2.3 Ecological Role of Bison

The American bison is the largest extant native terrestrial animal species in North America (Forsyth 1985). Over the course of the nineteenth century, bison were exterminated over most of their range and nearly went extinct (Allen 1876, Hornaday 1889, Krech 1999). Wild bison are now primarily restricted to protected areas in small herds, with a larger population of domestic animals on commercial farms (Gates et al. 2010).

2.3.1 History of Bison

Prior to European colonization of continent, plains bison likely numbered in the tens of millions; it was the most abundant ungulate in North America (Shaw 1995). Its range covered much of the interior of the continent, centered on the Great Plains. It is believed that the plains bison range extended through the Aspen Parkland into the southern fringe of the boreal forest (Allen 1876). The ecological role of bison in the Aspen Parkland ecoregion is poorly understood in comparison to their historic core range on the open steppes of North America. In contrast to short and mixed-grass prairies, there have been relatively few studies of the direct effects of bison on the composition and structure of plant communities in the plains rough fescue or aspen communities of the Aspen Parkland. What research that has occurred has primarily focused on bison foraging ecology (Hudson and Frank 1987, Fortin et al. 2002) and the paleoecological reconstruction of migratory patterns and regional ecological effects (Morgan 1980, Campbell et al. 1994, Malainey and Sherriff 1996). The rapid extermination of bison in the 19th century occurred prior to any systematic scientific survey of the Aspen Parkland. As a result, the historical abundance and seasonality of bison in the ecoregion is uncertain (Campbell et al. 1994, Malainey and Sherriff 1996). A predominant theory is that a large portion of the Northern Plains population annually shifted north from the mixed-grass plains into the Aspen Parkland during the winter to shelter from winter storms and to take advantage of the high-quality winter forage provided by the rough fescue prairie (Morgan 1980, Dormaar and Willms 1990, Campbell et al. 1994) as well as extensive sedge (*Carex* sp.) meadows. Another theory points to evidence of large bison populations remaining on the mixed-grass plains during the winter (Malainey and Sherriff 1996) to suggest that bison were present in the Aspen Parkland only in small numbers. Bison may also have exhibited a dual dispersion strategy (Fryxell et al. 1988) with a large migratory population and a smaller resident population remaining in the Aspen Parkland at low

levels year-round (Epp 1988). Finally, there is uncertainty as to whether bison movements were primarily seasonal or rather directed by factors such as forage quality, fires, predation, winter storms, and snow depth (Morgan 1980, Malainey and Sherriff 1996). Despite this uncertainty, rough fescue grasslands, and specifically the dominant species *Festuca hallii*, are theorized to have evolved under intermittent, light grazing pressure by bison primarily during the winter when the above-ground apical meristems of the plant would have been protected by a layer of snow (Moss and Campbell 1947, Domaar and Willms 1990). This ecosystem may therefore respond differently to bison grazing than grasslands which developed under more intense grazing disturbance; conclusions drawn from those ecosystems may not apply equally to the Aspen Parkland.

2.3.2 Bison as Disturbance

Bison have and do still play a fundamental role as ecosystem engineers in the tall, mixed, and shortgrass prairies of central North America that formed the core of their range (Knapp et al. 1999). Through actions such as grazing, trampling, horning, and wallowing, as well as the deposition of urine, feces, and carcasses, herds of bison are known to have a substantial impact on the structure of their environment (McHugh 1958, Campbell et al. 1994, Knapp et al. 1999). Bison wallows have an important influence on surface hydrology (Butler 2006) and create ephemeral habitat for amphibians (Bragg 1940, Corn and Peterson 1996) and aquatic plants (Polley and Wallace 1986, Collins and Uno 1987). Bison disperse seeds (Gokbulack 2002, Rosas et al. 2008). They also recycle nutrients and contribute to the buildup of prairie soils (McHugh 1958, Day and Detling 1990). Through grazing they modify floral community composition (Coppock and Detling 1986) and create a mosaic of grass heights (Virchow and Hygnstrom 2002, modifying habitat structure which ultimately influences bird diversity (Knapp et al. 1999) and abundance (Fuhlendorf et al. 2009, Powell 2006). By modifying fuel loads they also interact with fire, altering patch dynamics (Fuhlendorf et al. 2009).

Campbell et al. (1994) suggest that it was ultimately the extirpation of bison from the Aspen Parkland, rather than the suppression of fire that triggered the current woody encroachment trend. They cite the study by McAndrews (1988) which shows that a sharp increase in the deposition of *P. tremuloides* pollen in Pasqua Lake in central Saskatchewan in the 1880's and Pine Lake in central Alberta in the 1890's. These times match very closely to when

the settlers associated with fire suppression arrived in those locations (Bird 1961, Richards and Fung 1969). However, because aspen ramets do not become mature and begin to produce pollen until ten to twenty years of age (Perala 1990), the increase in aspen encroachment would have had to have begun one to two decades earlier to result in increased pollen deposition at those times (Campbell et al. 1994). Those earlier time periods correspond closely to the dates of extirpation of bison from the vicinity of the two lakes, respectively (Campbell et al. 1994). The authors posit that without bison to graze, trample, and otherwise quash the growth of shoots resprouting following fires (McHugh 1958, Meagher 1973, Edwards 1978, Coppedge and Shaw 1997), woody plants such as *P. tremuloides* were able to encroach on the grassland. While some degree of damage to woody species has been quantified in other ecosystems (Edwards 1978, Coppedge and Shaw 1997), and long-term changes in abundance of bison and aspen have been correlated at a regional scale with the Aspen Parkland (Campbell et al. 1994), the effect of bison on the demographics of woody species has not been determined at the scale at which woody encroachment of grasslands occurs; the grassland-forest ecotone.

3. MODIFICATION OF PLANT COMMUNITIES BY BISON IN RIDING MOUNTAIN NATIONAL PARK

3.1 Abstract

Plains bison (*Bos bison bison*), as a dominant large herbivore, are suspected to have played an important role in maintaining and structuring the plant communities throughout the Aspen Parkland. However, they are now largely extirpated from this ecoregion. In this study I examined the effect of a captive bison population on plant communities in Riding Mountain National Park. I examined the relationship between bison and woody plant encroachment along the forest-grassland ecotone, as well as the effect that short- and long-term occupation by bison has on *Festuca hallii* grassland communities. I found that the influence of bison on the shrub community at the forest grassland edge is limited. Bison occurred at very low densities in areas with dense, tall shrub understories, and thus cannot be a major factor in limiting shrub growth and survival. Shrub stem mortality due to fire may be a necessary precursor to bison mitigating woody encroachment in the Aspen Parkland. I also found that over a single year bison reduced sward heights but did not alter the composition of grassland communities, with the possible exception of an important interaction with the invasive *Poa pratensis*. However, the long-term (>80 year) presence of bison was associated with greater species richness, reduced litter accumulation, and a distinct community composition compared to areas without bison.

3.2 Introduction

The role of plains bison (*Bos bison bison*) in structuring Aspen Parkland plant communities is poorly understood. The Aspen Parkland is a transitional ecosystem with a mosaic of grassland and forest (Bird 1961). It can be described as a disclimax; the structure of the ecosystem is strongly determined by disturbance (Beetle 1974). In similar ecosystems large herbivores are an important component of that disturbance (Dublin et al. 1990, Sankey et al. 2006). Bison, historically the dominant large herbivore in the Aspen Parkland, were almost completely extirpated during the 19th century (Meagher 1986), prior to any systematic scientific study of the Aspen Parkland. Bison are now confined to a tiny fraction of their former range, and there is little conclusive evidence for how they may currently influence the structure of the Aspen Parkland.

The Aspen Parkland ecosystem faces significant threats. A large portion (80-95%) has been converted to cropland (Moss and Campbell 1947, North 1976, Rowe and Coupland 1984). The remnant grassland component is at risk due to the invasion of alien species, such as *Poa pratensis* (Slopek and Lamb 2017, Stotz et al. 2019). This invasive non-native grass (DeKeyser et al 2015) is widespread and often dominant in these grasslands (Grace et al. 2002, Grant et al. 2009, Sinkins and Otfinowski 2012). Encroachment by trees and shrubs is also an important threat (Guedo and Lamb 2013). The disruption of natural disturbance processes is thought to be responsible for the rapid encroachment of woody species into the few remaining grassland patches (Campbell et al. 1994). The suppression of wildfire following Euro-Canadian settlement is likely an important contributing factor (Romo 2003). However, there is evidence that fire alone is insufficient to suppress aspen (Guedo and Lamb 2013), and that the onset of forest expansion more closely matches the timing of the extermination of bison than the beginning of fire suppression (Campbell et al. 1994). Bison may have directly limited encroachment of woody species into grasslands (Moss 1932, England and DeVoss 1969, Campbell et al. 1994). Since bison diets are largely graminoid (Coppedge et al. 1998, Bergmann et al. 2015), these bison effects on woody species have been generally attributed to physical damage from horning and trampling leading to stem mortality (McHugh 1958, Meagher 1973, Edwards 1978, Coppedge and Shaw 1997, Bork et al. 2013). Some impacts by bison on woody species have been quantified in other ecosystems (Edwards 1978, Coppedge and Shaw 1997), and long-term changes in the abundance of bison and aspen are correlated at a regional scale in the Aspen Parkland (Campbell et al. 1994). No studies, however, have directly examined the effects of bison on the demographics of woody species at the scale at which woody encroachment of grasslands occurs: the grassland-forest ecotone.

Bison effects on grassland community structure are well studied in the mixed and tall-grass prairies (Knapp et al. 1999, Fahnestock and Detling 2002), however there have been relatively few studies of the direct effects of bison on the composition and structure of plant communities in the rough fescue communities of the Aspen Parkland. Existing research has primarily focused on bison foraging ecology (Hudson and Frank 1987, Fortin et al. 2002) and paleoecological reconstruction of migratory patterns and regional ecological effects (Morgan 1980, Campbell et al. 1994, Malainey and Sherriff 1996). Rough fescue grasslands, and particularly the dominant species plains rough fescue (*Festuca hallii*), are theorized to have

evolved under intermittent, light bison grazing pressure, primarily during the winter when the above-ground apical meristems of fescue would have been protected by a layer of snow (Moss and Campbell 1947, Domaar and Willms 1990). Aspen Parkland grasslands may therefore respond very differently to bison grazing than grasslands which developed under more intense summer grazing disturbance.

The objective of this project was to examine bison impacts on an Aspen Parkland plant community in Riding Mountain National Park, Manitoba, Canada (RMNP). The park is situated along the northern edge of the Aspen Parkland ecoregion and contains some of the few remaining intact patches of plains rough fescue grassland in Canada. The park is also home to a small enclosed herd of bison that ranges over a mosaic of rough fescue grasslands, aspen forest, mixed coniferous-deciduous forest, and wetlands. Parks Canada has identified both the encroachment of aspen forests into the remnant rough fescue grasslands, and the absence of bison from the wider ecosystem of RMNP as issues of concern (Parks Canada 2007). This location provides an opportunity to assess the role of bison in the Aspen Parkland, both on the structure and composition of the grassland community and the dynamics of woody plants along the grassland forest ecotone. My specific objectives were to 1) determine the effects of bison on the structure, mortality, and recruitment of shrub and tree species at the grassland forest ecotone, and 2) assess the effects of bison on rough fescue grassland community structure including species composition, sward structure, and the distribution of live biomass and litter.

3.3 Methods

3.3.1 Study Area

RMNP is in southwestern Manitoba on an upland which forms a part of the Manitoba Escarpment. This upland forms a southeasterly extension of the mid-boreal uplands ecoregion surrounded by Aspen Parkland (Ecological Stratification Working Group 1995). Approximately 3000 km² in area, the park is dominated by deciduous and mixed-wood forests, along with areas of Aspen Parkland and small remnant rough-fescue grasslands (Parks Canada 2007). The Lake Audy bison enclosure is a fenced 500 ha range holding a captive display plains bison herd of approximately 40 head (Fig. 1). The herd is managed to maintain ecological integrity of habitats within the enclosure, contribute to the conservation of the species, and serve as an educational tool (Parks Canada 2008).

The enclosure area includes a mix of rough fescue grassland (212 ha), mixed wood/aspens forest (250.4 ha) and wetlands (11.3 ha) (Parks Canada 2008). The habitat mosaic found at the site is representative of the broader Aspen Parkland ecoregion. The enclosure is divided into two sections; a north pasture and south pasture. The south pasture contains the largest contiguous patch of native grassland in RMNP, and has the highest recorded vascular plant richness of any grassland in the Park (Sinkins 2010). The north pasture is dominated by a mosaic of forest and grassland. In the summer of 2015, an area adjacent to the north pasture was fenced and included within the enclosure area (Fig 1). The newly included area had not been occupied by bison for at least 165 years (Allen 1876), providing an opportunity to assess the short-term effects of bison reintroduction on plant community structure at the aspen forest-rough fescue grassland ecotone.

3.3.2 Bison Spatial Data

Bison use intensity within the enclosure was measured by fitting six adult bison cows (age 3-17 years) with Lotek 7000MU UHF direct-downloadable GPS/VHF collars. The use of animal subjects was reviewed and approved by the Parks Canada Animal Care Task Force (animal care protocol number 23003). The collars were deployed on November 17, 2015 (n=3) and November 24, 2015 (n=3) during the annual round-up of the display herd conducted by Parks Canada. Mature cows were collared to avoid adjustments to collar size due to the growth of juvenile animals, and to the high rate of collar loss among male bison (Shury 2015, pers. com.). Individual mature cows are also significantly more likely than males to be found within a herd and their movements are more closely correlated with the mean behaviour of the population (Meagher 1986). Collars recorded a location every half-hour from mid-November 2015 to December 14, 2016 when the collars were removed. A total of 110125 locations (UTM coordinates) were recorded, with between 18435 and 18858 locations for each individual collar.

3.3.3 Effect of Bison on Shrub Community Structure

Prior to the expansion of the enclosure in 2015, the north end of the study area was divided into three treatment areas. These were 1) a historically occupied area extending approximately 150 m into the pasture from the existing northern fence line, 2) the planned area of expansion between the existing and planned fence lines, and 3) a historically unoccupied area extending approximately 150 m north of the planned fence line that remained unoccupied.

Each treatment area was divided using Quantum GIS software (QGIS Development Team 2015) into grassland and forest polygons separated by the aspen-grassland ecotone. The centre of the ecotone was defined as the edge of the contiguous forest canopy, as identified in orthophoto imagery collected for Parks Canada in the summer of 2007. The imagery used was a true-colour, georectified, digital mosaic with a resolution of 1 m. Wetlands were excluded from these polygons, and a 5 m buffer around fences and trails was added to avoid confounding edge effects. Fifteen random points were selected in each of the grassland and forest polygons in each of the three treatment areas, for a total of 90 points. In the early spring of 2015, each random point was located using a GPS and marked with a 20 cm steel pin and steel washer. A 1x1 m plot was established with the pin at the northwest corner.

These plots were sampled initially in the spring of 2015 prior to bison release and leaf-out. They were sampled subsequently in the fall of 2015 after leaf-fall and again in the spring and fall of 2016. In each plot, all live woody plants were counted and identified to species. For the purposes of measurement, each separate stem emerging from the soil was considered an individual. For plants less than 200 cm in height, the height of the tallest leader was recorded. Where plants exceeded 200 cm in height, it was not possible to accurately measure height by hand. Height could not be measured with a clinometer due to difficulty in visually discerning individual canopies. For these plants the diameter at breast height (dbh = 1.3 m) of the dominant stem was measured.

During the leaf-free period, the amount of light intercepted by the woody canopy is proportional to the density of woody tissue in the canopy. To obtain an objective measurement of the effect of bison release on the density of the canopy, the percentage of incident photosynthetically active radiation (PAR) intercepted was measured. To determine this a baseline of incident PAR was taken from the average of three PAR ($\mu\text{mol photons/s}$) measurements (using a handheld PAR sensor) above or outside of the woody canopy. Immediately afterward three measurements of PAR taken across the breadth of the plot just above the litter layer and averaged. The difference between these two values indicates the percentage of light intercepted by the canopy.

$$\text{Percent intercepted by canopy} = (\text{Incident PAR} - \text{PAR above litter}) / \text{Incident PAR} \dots\dots\dots(3.1)$$

The effect of bison release on the incidence of browsing and other physical damage to woody species was assessed for each woody plant under 200 cm in height in the 1x1m plot by checking the highest leader for evidence of browsing (sheared apical bud). This thus provides a measure of browsing intensity by non-bison ungulates, after Painter et al. (2015).

3.3.4 Effect of Bison on Rough Fescue Grassland Community Structure

Effects of the removal or introduction of bison from rough fescue grassland on species composition and structure of that plant community were tested using a randomized, paired range enclosure experiment. Range cages were used to compare the short-term effects of bison introduction or removal on the plant community. The south pasture of the Lake Audy bison enclosure has a long history of bison occupation (1931-present (Tarleton 1989)); here range cages were used to experimentally exclude bison and compare the affected community to adjacent, occupied plots. In the north pasture, where bison were being introduced, cages acted as a control against the experimental addition of bison to the system. The short-term effects of bison removal or introduction was assessed by measuring percent cover of all plant species, live above-ground biomass, litter biomass, sward height. These variables were first measured immediately prior to installing the cages in July and August of 2015 to establish a baseline condition from which to measure change. The enclosure cages were then deployed on the treatment plots and left in-situ until the summer of 2016, at which time the plots were then reassessed. Sampling of treatment plots occurred in July and August to coincide with the period of peak live biomass and peak flowering in the system (Stout et al. 1981, Redmann et al. 1993).

Cages were built with a rebar frame and page-wire sides in a truncated pyramidal shape with an open top and bottom. They were 1.26 X 1.26 m at the base, 0.5 X 0.5 m at the top, and approximately 1m in height. Four large rebar pins held each cage in place, and the angled sides prevented bison from applying excessive force when rubbing on the cages; no cages were displaced during the course of the experiment. As the intensity of bison grazing and other influences on the landscape can be highly heterogeneous, spatial data from GPS collared bison were used to correlate observed effects to the frequency of bison occupancy adjacent to any given cage.

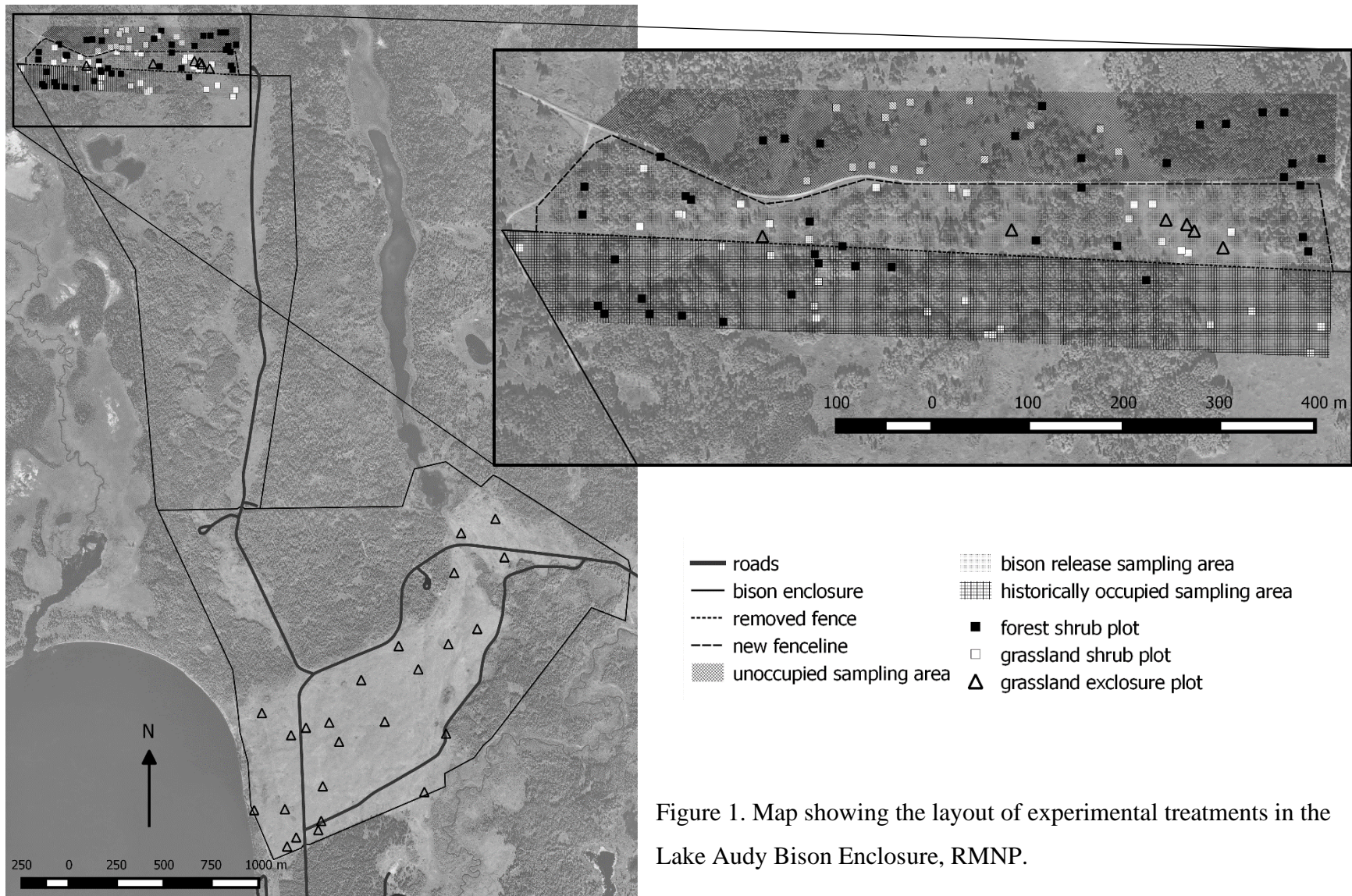


Figure 1. Map showing the layout of experimental treatments in the Lake Audy Bison Enclosure, RMNP.

Cage locations were randomly selected. Using QGIS software (QGIS Development Team, 2015), polygons mapping the south pasture and north pasture extension were overlaid on a georeferenced orthophoto (Parks Canada, 2007) of the study site. Road and trail beds, and forested and wetland areas were excluded from the polygons. This resulted in 13 polygons with a total area of 136.6 ha being included in the south pasture, and five polygons in the north pasture being included with a total area of 2.8 ha. Twenty-three random points (UTM coordinates) were assigned within the south pasture polygons, and six random points were assigned within the north pasture extension polygons (Fig. 1).

These random points were located in July and August of 2015 using GPS. Each point was marked with a permanent pin to facilitate relocation. After arriving as close to the point as possible given GPS accuracy error, the pin was dropped over the shoulder and inserted into the ground where it landed. This pin location marked the southwest corner of a rectangular cover plot extending 20 cm north and 50 cm west. Ten centimetres north of this plot, 4 potential biomass sampling plots were designated; each 20 X 20 cm (0.04 m²) and separated east to west by 10 centimetres. Following sampling, the range cage would be centred over these plots so that the southwest corner of the base of the cage was approximately 54 cm southwest of the pin (Fig. 2).

The first paired plot was randomly assigned to a position two metres from one of the four corners of the cage using a random number chart. The distance of two metres was required to avoid edge effects on the control plot from the cage, e.g. bison rubbing against (Coppedge and Shaw 1997). A pin was placed in the ground a further 53.74 cm in that direction, and the layout of the cover plot and biomass plots was repeated. A second paired plot was then established in the same manner in the opposite direction (Fig. 2). This second paired plot was necessary due to the extensive small scale (~ 1 m²) heterogeneity of both plant species composition and sward height in grazed areas.

Treatment and control plots were sampled in July and August of 2015 prior to the installation of range cages, and prior to the release of bison to the expansion of the north pasture. Plots were resampled in July and August of the following year (2016).

Richness and percent cover of vascular plant species were assessed in 2015 and again in 2016 in order to measure the effects of bison removal or introduction of bison on the composition and diversity of species within the rough fescue grassland community. All plant

species within a 20 X 50 cm (0.1 m²) plot (Fig. 2) were identified and their aerial extent, as a percentage of the total plot area was estimated by two separate observers. The average of these two observations was recorded. In cases where the cover was less than 1 % it was recorded as 0.5 %.

Above-ground standing-live biomass and litter biomass were sampled to assess the production and forage yield of the community, rate of forage utilization by bison, effect of bison on production and standing crop, and the effect of bison on litter accumulation. In 2015, adjacent to each cover plot, one of four possible 20 X 20 cm (0.04 m²) biomass clipping plots (Fig. 2) was randomly selected using a number chart. All live plant biomass rooted within the plot was clipped at soil level and separated into graminoid, and forb and shrub biomass. All litter (including standing dead material) was also collected. Both litter and live biomass samples were oven dried at 80 °C and weighed.

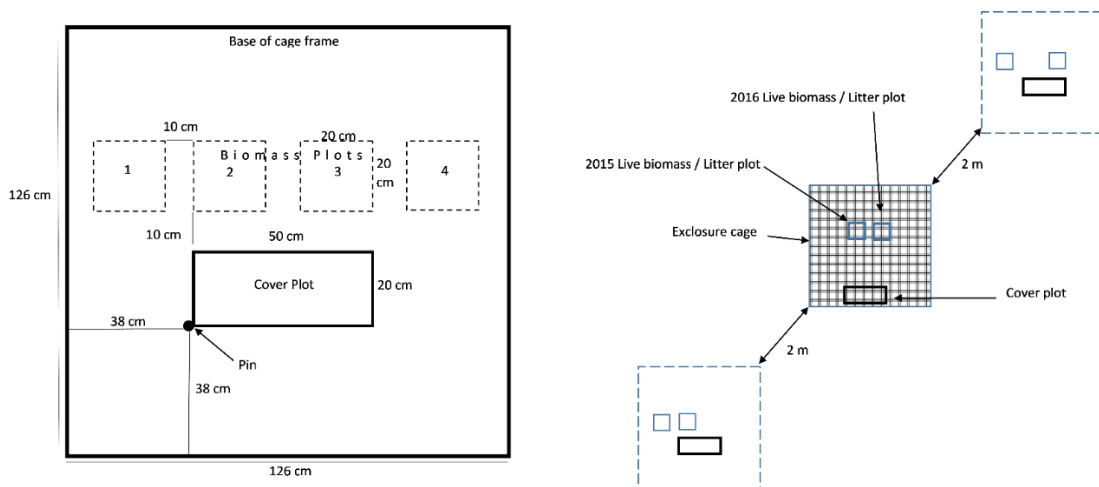


Figure 2. Configuration of range enclosure experiment plots. Two control (uncaged) plots with identical layouts were situated 2m distance from the central caged plot.

Prior to sampling each biomass plot, sward height was measured. This was done by placing a metre stick through a slot in the centre of a 10 cm diameter waxed corrugated cardboard disk. The metre stick was then placed vertically in centre of the biomass plot and the

disk was dropped along the stick from 1m above the ground until it rested on the vegetation. The height of the lower side of the disk was recorded. In 2016, biomass sampling was repeated, excluding the previously clipped plot.

3.3.5 Statistical Analysis

Bison intensity of use of in areas adjacent to individual shrub plots and grassland enclosures was determined by analyzing bison collar data using QGIS software (QGIS Development Team, 2015). For each grassland enclosure site, all bison fixes within a 10 m radius of the random sampling point were counted. This number was then used as an index of overall intensity of use at that site, including both grazing and non-consumption related effects. The 10 m radius incorporated the maximum radius of the plot layout (5.56 m) (Fig. 2), in addition to the maximum length (3.8 m) of an adult bison (Meagher 1986). For each shrub plot, all bison fixes within a 5 m radius of the plot datum were counted.

To determine the factors affecting the structure of the shrub community, including bison density, structural equation modelling (SEM) was used. Structural equation modeling allows complex networks of causal relationships among variables to be examined (Grace 2006, Lamb et al. 2011). Variables selected for inclusion in the model (Table 1) captured the relationships between bison presence, bison habitat selection, and the structure of the woody vascular plant community. The initial SEM model included twenty-four directional paths and a single non-directional path as described in the following paragraph (Fig. 3). The SEM model was fit using the sem function in package lavaan (Rosseel 2012) in R (R Core Team, 2017).

Table 1. Definitions of variables included in the structural equation model

Variable	Definition
Bison Density	Total number of GPS fixes recorded by all six collared cows within 5m of the plot from November 2015 to December 2016
Current Bison	Presence (1) or absence (0) of bison in the treatment area in the sampling year
Historic Bison	Presence (1) or absence (0) of bison prior to fenceline extension
Ecotone Distance	Distance of plot (m) from the forest canopy edge into grassland areas (positive) or forested areas (negative)
Plant Height	Average maximum height of all woody stems within the sampling plot in the spring of 2015
Density	Number of woody stems within the sampling plot in the spring of 2015
Canopy	Average proportion of PAR intercepted leafless woody vegetation in the sampling plot in spring of 2015
Browsing	The proportion of apical buds browsed in the sapling plot in the fall of 2016
Change in Density	Change in the number of woody stems within the sampling plot from the spring of 2015 to the fall of 2016

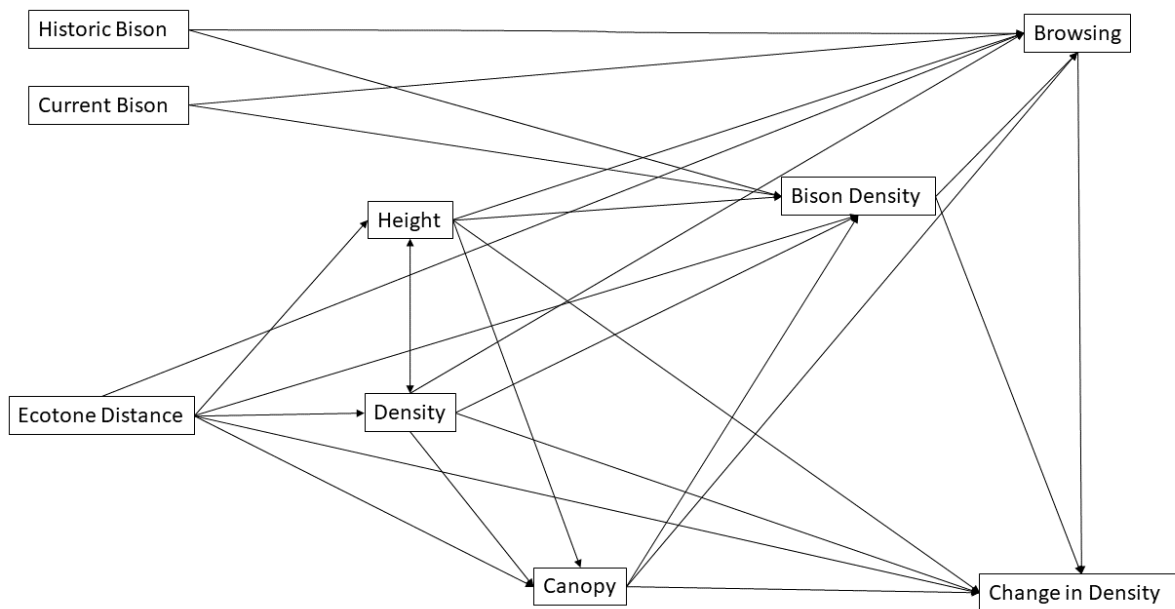


Figure 3. The initial structural equation model of the relationship between bison and the shrub community in the Lake Audy bison enclosure. Variables in boxes (Table 1) are linked by pathways that reflect logically defined causal relationships.

The initial SEM model included a path from Historic Bison to Browsing to account for the effects of the pre-experimental fence configuration on the behaviour and movement of the major browsers (cervids). A path from Historic Bison to Bison density accounted for effects of the previous fence configuration on bison distribution during the experiment, such as avoidance of the new portion of their range due to philopatry. The path from Current Bison to Bison Density was included because bison did not have access to the control plots. Therefore, the bison density in these plots would automatically be zero, regardless of other variables. The potential effect that the current configuration of the fence and bison occupancy could have on the browsing behaviour of wild cervids accounted for with path from Current Bison to Browsing.

A path from Ecotone Distance to Browsing was included to account for variation in the browsing behavior of cervids with the distance from the cover of the forest canopy. A path from ecotone distance to height was incorporated into the model on the assumption that the height of shrubs and saplings would change in response to differences in competition and the availability of resources within and outside the forest canopy. As well, species associated with forest

communities grow to different heights than those associated with grassland communities, as they are adapted to different conditions. A path from Ecotone Distance and Bison Density was included in the model to reflect the habitat preferences of bison. The path from Ecotone Distance and woody stem density was included as a directional path in the model. As with Height, this path reflected both the separate environmental conditions inside and outside the forest canopy as well as the different species composition. The path from Ecotone Distance and Change in Density was included to account for any difference growth or decline of shrub and sapling populations along the ecotone, for example due to forest encroachment into the grassland. The path from Ecotone Distance to Canopy accounts for the fact that where the forest canopy is present (negative ecotone distance), the abundance of aerial woody tissue (Canopy) will, by definition, be higher.

To account for the potential for shrubs and saplings to reach a browse escape height, and preferred foraging heights for browsing cervids, a path from Height and Browsing was included. A path from Height to Bison density was included under the assumption that shrub height would have an effect on bison behaviour. A path from Height to Change in Density was included to account for the effect of plant height on mortality and recruitment. A path from Height to Canopy was included as plant height contributes to overall plant size and thereby the amount of light blocked. A non-directional path between Height and Density was included to account for the correlation between the height and density of shrub stems.

A path from Density to Browsing was included as the density of stems might influence the selection of those stems for browsing. A path from Density to Bison Density was included under the assumption stem density influences bison behaviour by impeding their movement or otherwise influencing the suitability of habitat. A path from Density to Change in Density was included, as stem density is expected to influence the ongoing recruitment and mortality of stems in a plot. A path from Density to Canopy was included, as the overall number of stems in a plot will directly affect the total abundance of woody tissue in that plot and how much light it blocks.

A path from Canopy to Bison Density was included, as the overall abundance of woody tissue could influence the distribution of bison by impeding their movement or influencing the overall suitability of habitat. A path from Canopy to Browsing was included as the overall abundance of woody tissue in a plot would influence the probability that the terminal buds were browsed by cervids. A path from Canopy to Change in Density was included under the

assumption that the availability of light would influence mortality and recruitment of individual stems.

A path from Bison Density to Browsing was included to account for how bison would influence the distribution of browsing cervids, for example by creating pathways facilitating their movement through dense cover. To account for how bison directly influence the mortality or recruitment of woody plants, for example by trampling and uprooting individual stems, a path from Bison Density to Change in Density was included. Finally, a path from Browsing to Change in Density was included, as browsing may either directly cause stem death or trigger a compensatory response and suckering.

Long-term impacts of bison absence on the composition of rough fescue communities in RMNP were assessed using multivariate approaches. The abundances of all species in all plots in the south (occupied) pasture were compared with those in the northern (unoccupied) extension in 2015 prior to the installation of range cages. To assess if the two communities were statistically different, a PERMANOVA analysis (Anderson, 2001) was conducted using the *adonis* function from the R *vegan* package (Stevens 2017; Oksanen et al. 2017; R Core team), using Bray-Curtis distance and a half root transformation of the data. The assumption of equal dispersion was confirmed with an ANOVA on the homogeneity of multivariate dispersions ($F = 0.004$, $p = 0.952$).

The long-term effects of bison absence on grassland structural variables (i.e. species richness, sward height, and biomass) were examined using the 2015 (i.e. pre-range cage and bison release) data. For each structural variable, mixed effects models were fit with bison presence or absence as a fixed effect, and cage site as a random effect. Cage site was included as a random effect to account for the spatial autocorrelation of the three adjacent plots at each site. These analyses were conducted in R (R Core Team, 2017), using function *lme* from the *lme4* package (Pinheiro and Bates, 2017).

The short-term impact of bison addition or removal on the composition of rough fescue communities in RMNP were analysed using two multivariate tests. The first analysis compared all treatment plots in the south (occupied) pasture in 2015, prior to the installation of range cages, to those same plots one year later. The second compared plots without cages in the northern extension in 2015 prior to the release of bison to those same plots one year later. In each test, a PERMANOVA (Anderson, 2001) was used to test for a shift in community structure between the

2015 and 2016 data using Bray-Curtis distance and a half root transformation of the data. Non-metric multidimensional scaling was used to visualize changes in community structure between the years. The assumption of equal dispersion was tested with an ANOVA on the homogeneity of multivariate dispersions (south pasture $F = 0.142$, $p = 0.708$; north pasture $F = 0.261$, $p = 0.621$). All analyses were conducted using the *vegan* package (Oksanen et al. 2017) in R (R Core Team, 2017).

The effect of short-term bison absence or presence on the structure on the rough fescue community was assessed by examining changes in structural variables in treatment plots relative to control plots. To determine this value for a given plot in the south pasture, the average of the two occupied control plots was subtracted from the treatment plot value, giving a treatment-control difference for 2015. Since range cages had not been placed at this time, this difference accounts for the small-scale spatial heterogeneity of the variable prior to the establishment of the range cage. A treatment-control difference was similarly calculated for 2016 where the difference measures both spatial heterogeneity and the effect of grazing exclusion. Calculating treatment-control differences separately for each year accounts for any year effects (i.e. any changes that occurred in both the control and treatment plots due to weather etc.) The 2015 treatment-control difference was then subtracted from the 2016 treatment-control difference, giving a single change value for each site that reflects the effect of the treatment after confounding factors (year effects and spatial heterogeneity) had been accounted for. A one sample t-test was then used to test if these change values were significantly different from 0. A change value of zero would indicate that there was no change in the variable from 2015 to 2016 due to the treatment alone. It is important to note that in the north extension, there were two treatment plots for every one caged control plot. There to calculate the treatment-control difference, the single control value was subtracted from the average of the two treatment values. Otherwise, the calculation was the same.

The relationship between intensity of use of a site by bison and the abundance of the dominant non-native grass *Poa pratensis* was examined using linear regressions of *P. pratensis* abundance in all non-caged plots against bison density in both the south pasture and northern extension. Similarly, linear regressions were used to examine change in *P. pratensis* from 2015 to 2016 in caged plots (relative to control plots) as a function of bison density in both the south pasture and the northern extension.

3.4 Results

3.4.1 Relationship Between Bison and the Shrub Community

The structural equation model of the shrub and sapling community in the Lake Audy bison enclosure had adequate fit ($\chi^2=15.064$, $p=0.058$, $CFI=0.940$, $df=8$; Fig. 4). Unstandardized coefficients and tests of path significance are reported in Appendix A. Greater shrub layer heights in 2015 caused increases in the density of woody stems over the study period. Tall shrub layer heights also resulted in lower bison densities. The average height and density of woody plants in plots is positively correlated. Height declined as the distance of a plot outside the forest canopy edge increased. Therefore, both density and ecotone distance had indirect effects on bison density and change in stem density. Canopy density increased with greater stem height and density, and declined as the distance of a plot outside the forest canopy edge increased.

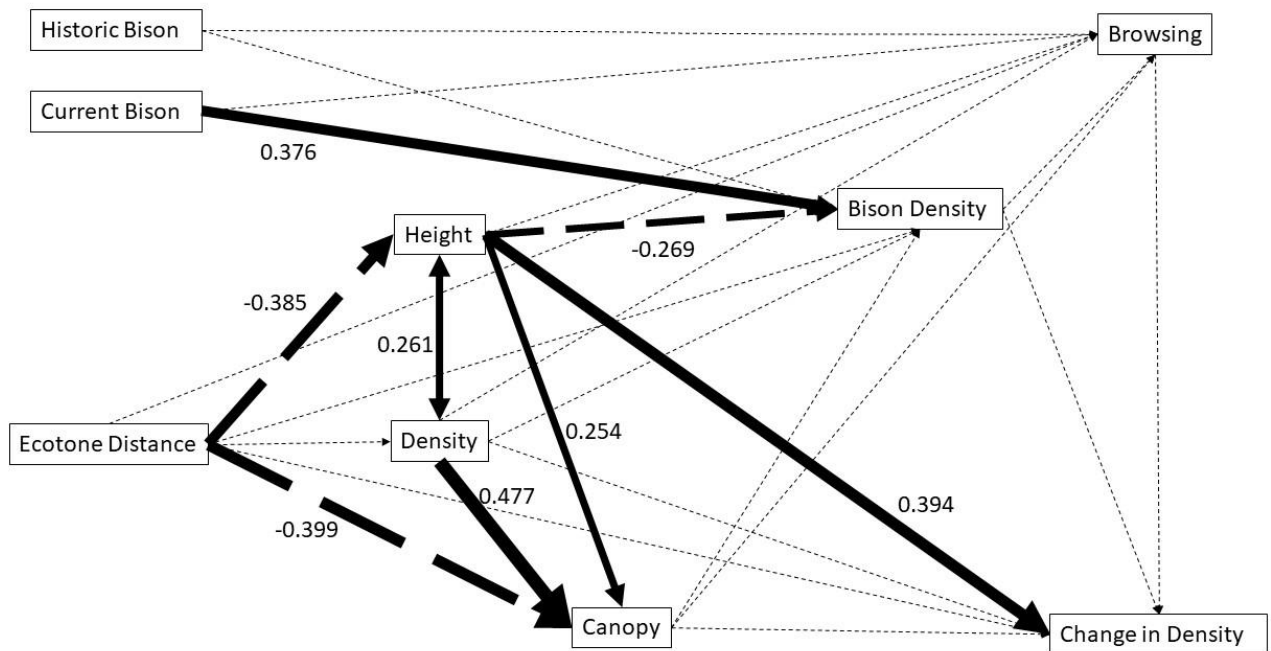


Figure 4. Fitted structural equation model of the shrub and sapling community in the Lake Audy bison enclosure and its relationship with bison. For variable definitions refer to Table 1. Dotted arrows indicate non-significant relationships. Dashed arrows indicate significant negative relationships, and solid arrows indicate significant positive relationships. The magnitude of standardized path coefficients are shown by arrow width.

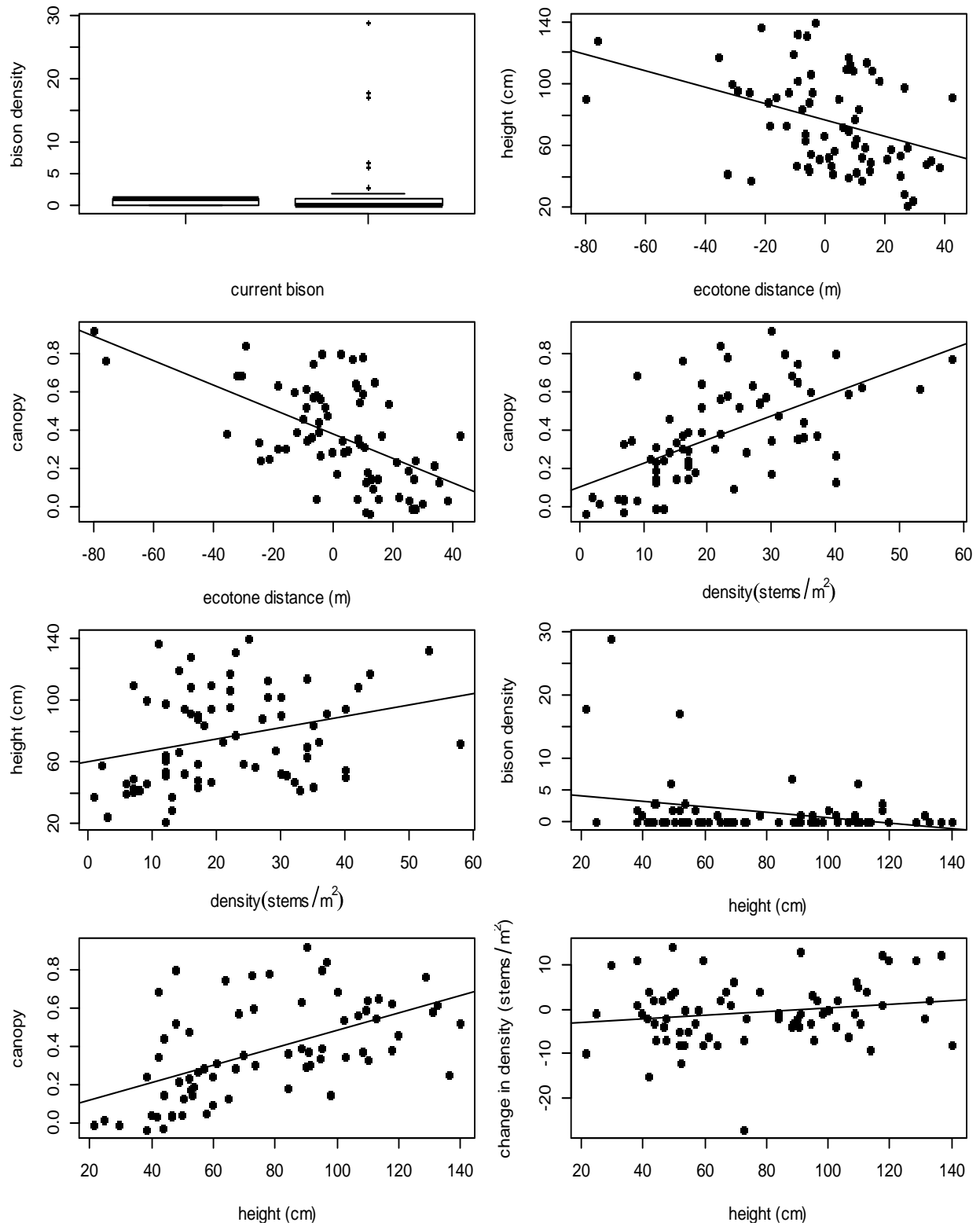


Figure 5. Pairwise relationships showing all significant direct paths in the SEM. For variable definitions, refer to Table 1.

3.4.2 Long-Term Change in the Grassland Community

Long-term bison impacts on rough fescue prairie were examined by comparing the 23 sites in the south pasture that had been occupied by bison over the previous 84 years to the 6 sites in the north pasture that have not been occupied by bison since the mid nineteenth century (Table 2). Sward canopy height was 19% lower in the occupied south pasture than the unoccupied north pasture. Similarly, the litter layer in the south pasture was less dense, and total standing and forb biomass was lower. Species richness was 50.4% higher in the occupied plots than in the unoccupied plots. Other aspects of community structure including graminoid biomass, the relative percentage of graminoid forb and shrub cover, and the cover of non-native species however did not differ between the occupied and unoccupied plots (Table 2).

Table 2. Comparison of plant community characteristics between occupied and unoccupied enclosure sites prior to installing range cages. Test statistics are from mixed effects models with site as a random effect, and occupied vs. unoccupied as a fixed effect

Variable	Occupied (mean ± SE)	Unoccupied (mean ± SE)	F- and p-values
Sward Height (cm)	22.1 ± 1.9	27.4 ± 4.0	46.19, p<0.001
Species Richness	18.5 ± 0.8	12.3 ± 1.7	13.61, p=0.001
Litter Biomass (g/m ²)	586.1 ± 25.0	873.8 ± 54.9	27.41, p<0.001
Forb Biomass (g/m ²)	334.9 ± 27.9	475.8 ± 61.3	5.28, p=0.030
Graminoid Biomass (g/m ²)	309.9 ± 8.2	331.3 ± 18	1.42, p=0.244
Live Standing Biomass (g/m ²)	644.7 ± 27.4	807.1 ± 60.1	7.29, p=0.012
% Graminoid Cover	36.2 ± 1.9	30.4 ± 4.1	1.98, p=0.171
% Forb Cover	59.1 ± 2.1	60.0 ± 4.6	0.04, p=0.846
% Shrub Cover	4.7 ± 1.2	9.6 ± 2.5	3.65, p=0.067
% Invasive Alien Species	14.8 ± 2.7	21.1 ± 5.9	1.17, p=0.290

Community composition was significantly different between occupied and unoccupied sites (PERMANOVA F = 8.451, p=0.001, df= 86). An NMDS ordination with a final stress of 0.266 separated the occupied and unoccupied communities along ordination axis 1 (Fig 6). This axis represents a gradient from, on the unoccupied (negative) end, a community dominated by

shrubs such as *Rubus idaeus* and *Prunus virginiana*, and tall forbs and grasses such as *Aster ciliolatus*, *Cirsium arvense*, *Solidago canadensis*, *Thalictrum dasycarpum*, and *Calamagrostis canadensis*, to a occupied community dominated by low growing forbs such as *Erigeron glabellus*, *Geum macrophyllum*, *Potentilla pensylvanica*, *Solidago missouriensis* and *Zygadenus elegans* (Appendix B).

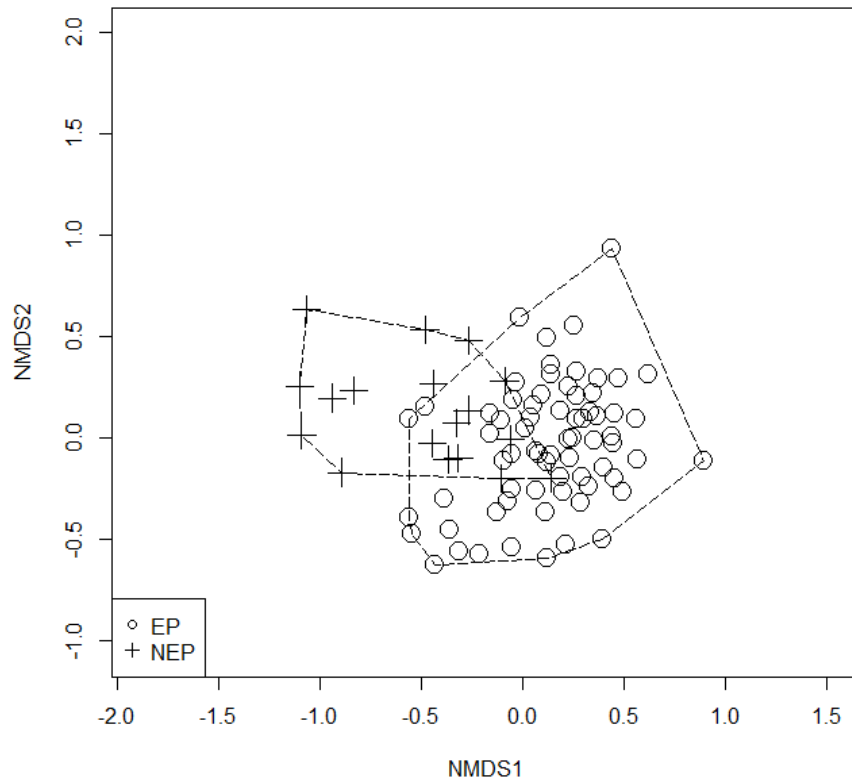


Figure 6. Non-metric multidimensional scaling ordination comparing unoccupied (NEP) and occupied (EP) grassland communities

3.4.3 Short-Term Change in the Grassland Community

The short-term addition or removal of bison alters the physical characteristics of grassland communities, but not the species composition of those communities. Sward canopy height, relative to control plots, increased by an average of 50.8% when bison were removed; there was a non-significant ($p=0.069$) 61.1% decline when bison were added (Table 3). No significant changes were observed in species richness, or the areal cover of graminoids, forbs,

shrubs, or invasive species (Table 3). There is some evidence that graminoid biomass increased with the introduction of bison, relative to control plots protected from bison; however, no other significant biomass changes were observed (Table 3).

Table 3. Results of one sample t-tests examining the change in plant community characteristics from 2015 to 2016 in treatment plots relative to control plots in both the north and south pastures. Zero values indicate that treatment plots on average did not change relative to control plots. Positive mean values indicate that the treatment plot values increased more from 2015 to 2016 than did those in the control.

Variable	South (mean \pm sd)	t and p-Value	North (mean \pm sd)	t and p-Value
Relative change in sward height (cm)	10.4 \pm 18.9	2.63, 0.015	-34.1 \pm 36.1	-2.31, 0.069
Relative change in species richness	-0.22 \pm 4.4	-0.24, 0.815	-0.5 \pm 2.5	-0.49, 0.644
Relative change in Biomass density (g/m ²)	24.7 \pm 147.3	1.45, 0.16	-76.3 \pm 195.4	-0.28, 0.79
Forb biomass (g/m ²)	87.1 \pm 185.2	1.10, 0.28	53.8 \pm 83.2	-1.35, 0.24
Graminoid biomass (g/m ²)	24.3 \pm 95.5	1.22, 0.236	144.2 \pm 154.9	2.28, 0.072
% Graminoid Cover	1.5 \pm 17.4	0.40, 0.690	7.1 \pm 21.1	0.83, 0.445
% Forb Cover	-3.0 \pm 15.5	-0.92, 0.370	-2.4 \pm 22.6	-0.26, 0.803
% Shrub Cover	1.5 \pm 11.0	0.65, 0.521	-4.7 \pm 15.9	-0.73, 0.501
% Invasive Alien Species	1.6 \pm 13.7	0.56, 0.579	10.6 \pm 32.8	0.79, 0.465

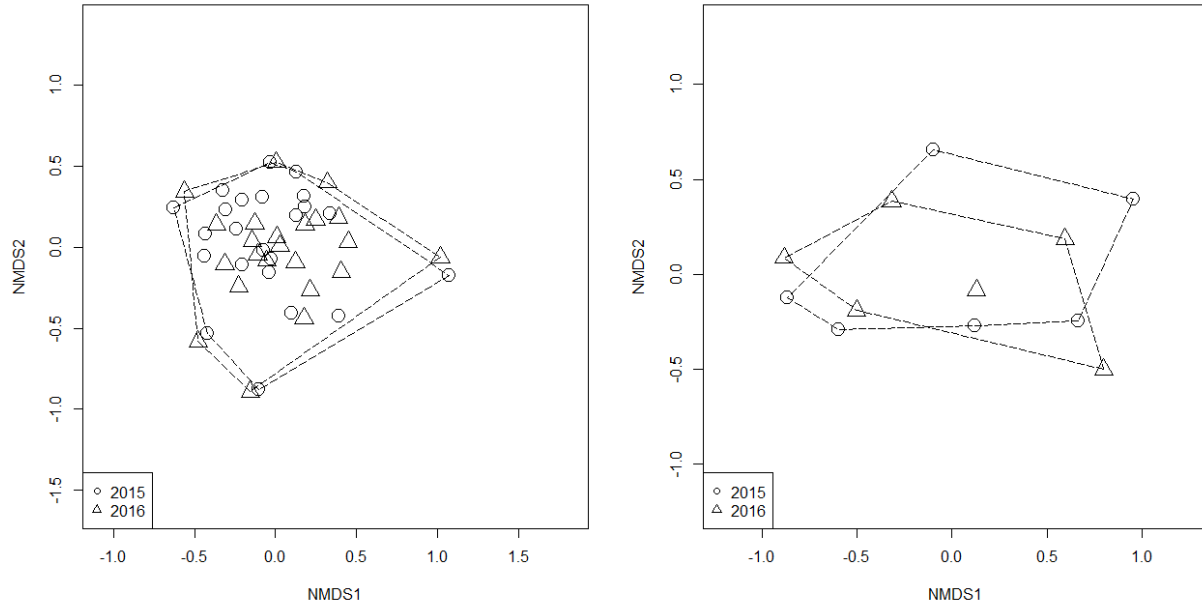


Figure 7. Non-metric multidimensional scaling ordination of south (left) and north (right) pasture plant communities before (2015) and after (2016) one year of experimental treatment.

The NMMDS ordination comparing the plant community composition of the north pasture sites to which bison had been added before and after one year of bison occupation had a final stress of 0.1238 (Fig. 7). A PERMANOVA showed no difference in north pasture plant community composition before and after one year of bison introduction ($F = 0.214$, $p = 0.95$, $df = 11$). The primary variation among sites is along the first axis which separates species typical of intact grasslands from those representative of moist or forest margin areas. Species with high first axis scores include the dominant native grass *Festuca hallii*, as well as forbs typical of intact grasslands such as *Agastache foeniculum* and *Astragalus agrestis*. The low end of the first axis is dominated by tall forbs such as *Thalictrum dasycarpum* and *Aster ciliolatus* and the moisture loving grass *Calamagrostis canadensis* (Appendix C).

The NMMDS ordination comparing the plant community composition of the historically occupied south pasture sites before and after one year of bison exclusion had a final stress of 0.2574 (Fig. 7). Similar to the north pasture no major changes were identifiable after a year in the south pasture (PERMANOVA F value = 1.31, $p = 0.151$, $df = 45$). The ordination shows almost complete overlap of the data from 2015 (before the exclosures were applied) and 2016 (after the

exclosures were applied) (Fig. 7). In this ordination, an increase in the first axis indicates an increase in grazing intensity, with the positive end of this axis dominated by small forbs typical of grazing lawns, such as *Orthocarpus luteus*, *Potentilla pensylvanica*, and *Erigeron glabellus*. The second axis appears to track invasion by non-native species. The negative end of this axis is dominated by the non-native grass *Bromus inermis*, which is primarily found in the south pasture spreading outward from along roadsides and fence-lines. Other species with low second axis scores include the non-native *Trifolium repens*, as well as the native forbs *Agrimonia striata* and *Asclepias ovalifolia*, both of which are commonly found along gravel roadsides (Appendix C).

The most abundant species in the grasslands at the site was the invasive non-native grass *Poa pratensis* (Kentucky bluegrass). In areas with historic bison grazing *Poa pratensis* had the highest relative abundance in areas of low bison use (Fig. 8). In the north pasture, where bison were added the proportion of *Poa pratensis* in the community increased. Though, this relationship was not significant, as these data were highly variable among plots. Changes in the relative abundance of *Poa pratensis* appear to be negatively correlated with the density of bison at the site (Fig. 8). *Poa pratensis* increased in abundance when bison were removed from a plot, though not significantly so; this change was highly variable. The change in *Poa pratensis* abundance within exclosures was not correlated with the density of bison adjacent to the exclosure (Fig. 8).

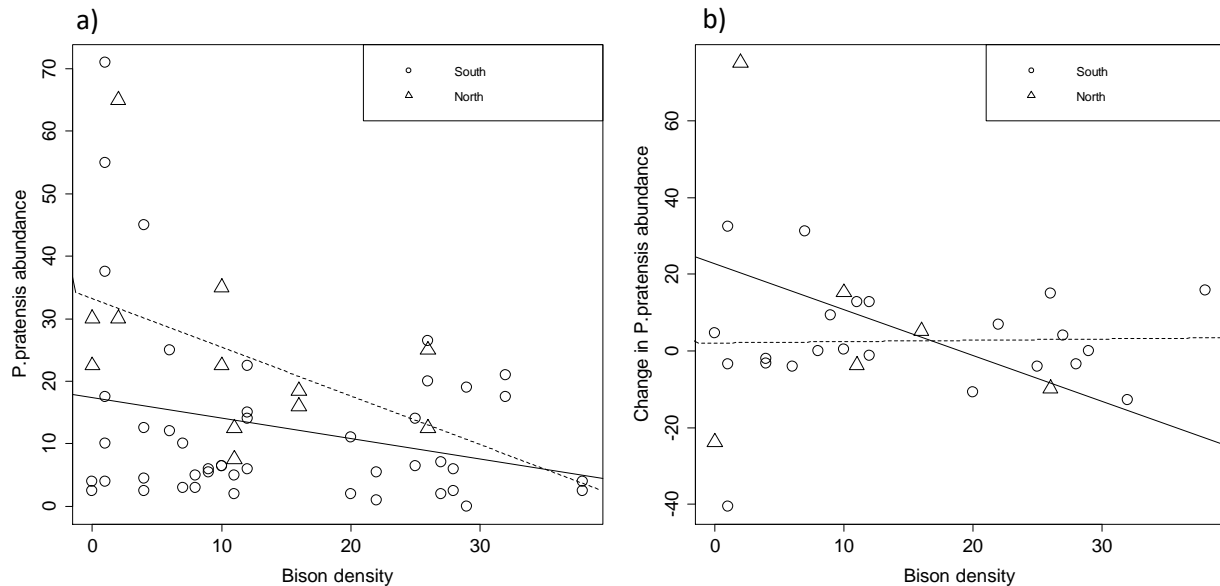


Figure 8. a) Relationship between bison density and the abundance of *Poa pratensis* in uncaged plots. b) Relationship between the change in abundance of *Poa pratensis* and bison density in plots where bison were excluded (south) and plots where bison were introduced (north).

3.5 Discussion

3.5.1 Relationship between Bison and the Shrub Community

The first objective of this study was to determine the effect of bison on the structure, mortality, and recruitment of shrub and tree species at the grassland forest ecotone. If bison influence the structure of the woody vegetation of the Aspen Parkland by increasing mortality or decreasing recruitment among shrubs and saplings (McHugh 1958, Meagher 1973, Edwards 1978, Coppedge and Shaw 1997, Bork et al. 2013), it would be expected that the density of stems in the shrub layer would decrease as bison density increases. However, variation in bison density had negligible effects on the density of shrubs. This runs counter to the hypothesis that bison can mitigate or reverse woody encroachment into grasslands by killing woody stems (Campbell et al. 1994). The lack of bison effects on shrubs can be explained by close examination of the bison movement data, specifically the strong negative relationship between shrub height and bison density. Bison avoided areas with a tall shrub layer. These areas also had the highest density of shrubs. Why bison do not occupy these areas with tall, dense shrub layers is not immediately clear, but several contributing factors are plausible. Graminoid forage is limited due to shading of the herb layer by the tall, dense shrub canopy (Thorpe and Goodwin

2008). The woody stems may present a physical barrier. Stem height and stem density both contribute to the overall volume of woody material in the shrub layer through which bison would have to pass to access tall shrub areas. Abrasion by a dense matrix of shrubs at or above head level could serve as a sufficient deterrent when suitable habitat is available elsewhere. Alternatively, the tall shrubs may serve as a visual barrier that bison avoid to ensure better predator detection.

In the absence of evidence for bison-caused stem damage or mortality in tall shrub communities encroaching into grassland along the forest-grassland ecotone, the question of how woody encroachment was historically limited remains. A second disturbance, likely fire (Romo 2003, Guedo and Lamb 2013), may be required to initiate stem mortality. After fire removes the barrier posed by the physical structure of the shrub canopy, bison may enter the site from adjacent grassland to take advantage of graminoids in the herb layer that have been released from competition for light by the fire. At this point bison activity may be sufficient to limit the recovery of woody vegetation along the ecotone that would otherwise be expected post-disturbance (Lastra 2011, Guedo and Lamb 2013).

3.5.2 Long-Term Impact of Bison on Grassland Communities

The second objective of this study was to assess the effects of bison on rough fescue grassland community structure including species composition, sward structure, and the distribution of live biomass and litter. Bison presence reduced standing crop with a shorter canopy and less litter accumulation. These changes are linked to a range of ecosystem function changes. By cropping vegetation and reducing sward height in certain areas, bison create a mosaic of sward heights that creates habitat for a greater diversity of plant and other species. Here plant species richness was significantly higher in occupied sites with an average of 12 species of forbs per plot under grazing sites and 7.2 species of forbs in unoccupied plots. As has been observed in other communities, bison are likely suppressing dominant graminoid species and thus opening niche spaces for lower growing species (Tilman 1982, Olff and Ritchie 1988, Ritchie and Olff 1999). These positive effects of grazing can extend to other groups of species, notably, grassland birds (Knapp et al. 1999). Finally, by reducing litter accumulation, bison can increase rates of nutrient cycling (McHugh 1958, Day and Detling 1990).

Bison primarily feed on graminoids (Peden et al., 1974, Larter and Gates, 1991, Coppedge et al. 1998, Bergmann et al. 2015). It would be expected then that forbs would be at a competitive advantage over graminoids under grazing pressure (Damhoureyeh and Hartnett 1997, Fahnestock and Knapp 1993). However total graminoid biomass was similar both with and without bison, while forb biomass was significantly lower where bison were present. Aerial cover of forbs did not decline at the same time. This suggests that the decline in forb biomass with grazing is due to a decline in the height or density of forbs rather than areal extent. This may be due to the high abundance of tall forb species with heavy, stiff stems such as *Solidago canadensis* or *Thalictrum dasycarpum* in unoccupied sites. These species may be less tolerant of mechanical damage or incidental grazing by bison. In the presence of bison, these tall competitive forbs are replaced by a wider variety of forb species that may be poorer competitors for light but are more tolerant of trampling.

Grassland communities with and without bison had distinct compositions. However, there were no significant differences in the aerial cover of either graminoids or forbs. This suggests that bison alter community composition not simply by reducing abundance graminoids, allowing a competitive release of unoccupied species, particularly forbs, but by causing a shift within each of those groups to a suite of more grazing-tolerant species. These “grazing tolerant” communities are more diverse. The difference in species richness suggests that by modifying the environment bison create niche space for, or prevent the exclusion of, certain species. This may be due to a reduction in the abundance of a few dominant species, thereby preventing the competitive exclusion (for example by reducing shading) of a number of other species. In areas accessible to bison, their presence is heterogeneous, resulting in a mosaic of high and low use patches. As a result of this heterogeneous use, grazing adapted communities and grazing intolerant communities coexist at small spatial scales (Fahnestock and Knapp 1993, Catchpole 1996, Adler et al. 2001).

In the context of conservation, factors that maintain or increase richness are often seen as valuable. This is especially true in the case of small and fragmented habitat patches such as most remnant rough fescue grassland. While the value of retaining bison in small habitat patches which severely limit population size and natural behaviours is sometimes questioned (Gates et al. 2010, Lammers et al. 2013), we have shown here that these places benefit from bison presence. Bison have been absent from the majority of grassland patches in RMNP for at least 165 years,

and cattle grazing has been prohibited for more than 45 years. The evidence shown here suggests that this has led to reduced plant species richness (Table 2). This supported by surveys which show that the bison enclosure has the highest richness among grasslands in RMNP (Sinkins 2011). Without grazing, the mosaic of habitat types has not been maintained, and there is likely less suitable habitat available for the suite of grazing adapted species. This loss of habitat may even have resulted in the local extirpation of grazing adapted species. For example, *Symphotrichum falcatum* is absent from surveys of all RMNP grasslands except the bison enclosure (Sinkins 2011).

3.5.3 Short-Term Impact of Bison on Grassland Communities

Removing bison resulted in a significant increase in sward height, while the introduction of bison resulted in the opposite (Table 3). The exclusion or introduction of bison did not however significantly alter the abundance of forbs, graminoids, shrubs, litter, or non-native species (Table 3). Eliminating grazing pressure allows the sward to reach a greater canopy height at peak biomass, while introducing grazing trims grass tillers, reducing sward height. By allowing for a taller sward and higher accompanying litter levels, elimination of grazing should reduce the amount of light available to plants germinating and growing below the canopy. This increased light competition might be expected to influence community composition (Lamb 2008). However, neither the removal nor the addition of bison was reflected by a change in composition (Fig. 7). Community composition and richness remained stable in both cases, likely because these communities are predominately made up of perennials with extensive root systems and energy stores they can draw on while being shaded during spring emergence. In addition, changes in the availability of light may also be moderated through grasses compensating for reduced leaf area due to clipping by increasing the density of tillers/leaves. When bison were removed, graminoid biomass remained relatively high (with some evidence of actually increasing), despite the decline in sward height (Table 2). This short but dense sward and accompanying litter likely prevents the establishment of new species germinating from seed, and eliminates some perennials intolerant of high litter levels (Hilger and Lamb 2017). A single year may be insufficient for differential survival of seedlings or gradual decline of mature plants to be detected. These communities are dominated by long-lived perennials; if the stress of altered

environmental conditions is insufficient to kill mature plants outright, several years will be required for the effects of differential reproduction to accumulate.

The presence of invasive non-native species can impair the ecological integrity of ecosystems by displacing native species and altering ecosystem processes. In RMNP the invasive non-native grass *Poa pratensis* (DeKeyser et al. 2015) has now replaced the native *Festuca hallii* as the dominant species in RMNP grasslands (Sinkins and Otfinowski 2012). High densities of bison can reduce the abundance of *Poa pratensis*, however bison may avoid well established *Poa pratensis* stands (Fig. 8) due to reduced productivity associated with litter accumulation in these areas (Hilger and Lamb 2017). Increasing abundance of *P. pratensis* at unoccupied sites (Fig. 8, Sinkins and Otfinowski 2012) may result in a positive feedback loop where bison spend less time in areas with high *P. pratensis* abundance, allowing the grass to increase further. This could in turn reduce the attractiveness of invaded habitat for bison, causing the concentration of activity in un-invaded areas. This would then result in overgrazing of the most ecologically intact patches of grassland. This has important implications for how bison should be managed in RMNP. Bison stocking rates should be taken under consideration when managing *P. pratensis*; the bison population should not be reduced to the point that the grass is released from grazing pressure, nor should it be increased to the point that relatively un-invaded communities become overgrazed. Other management techniques, such as fire, should be considered to make areas currently dominated by *P. pratensis* more suitable for bison.

3.5.4 Synthesis

Where the shrub community is sufficiently tall to limit bison access, bison cannot influence the growth and mortality patterns of the shrubs. Tall shrub communities restrict bison habitat to more open areas, and concentrate their impact there. In these areas, bison alter the physical structure of the plant community over a relatively short period. Over the long-term, they can increase biodiversity, and alter community composition. Unlike in areas with an existing tall shrub layer, bison impacts in more open sites may be sufficient to limit shrub abundance; in sites with a long history of bison occupancy shrub cover was on average lower (Table 2). Within the Aspen Parkland, this positive feedback ultimately may reinforce a discrete, stable ecotone between forested areas with a dense, tall shrub layer, and species rich grassland community.

4. GENERAL DISCUSSION AND SYNTHESIS

4.1 Discussion

The purpose of this project was to investigate the role of bison in structuring plant communities in the Aspen Parkland. I found that the impact of bison on woody plant dynamics at the forest-grassland ecotone is limited by the effect of tall shrubs on bison behaviour. The interaction between bison and fire may be important in structuring the mosaic of the Aspen Parkland. Within rough fescue grasslands, bison may modify only the physical structure of grasslands over a single year. However, over the course of many years they can dramatically alter the composition and biodiversity of these plant communities by disrupting community equilibrium in grasslands. Overall the role of bison in the Aspen Parkland is complex, and deserving of ongoing research and careful consideration by land managers.

There is a large body of research demonstrating that patterns of movement by bison and their foraging decisions are influenced by factors such as; forage quality (Senft et al. 1987) and quantity (Frank and McNaughton 1992), distance from water (Van Vuren 2001, Fisher and Gates 2005, Bruggeman et al. 2009a, Dancose et al. 2011), slope (Zeigenfuss and Singer 2003, Fisher and Gates 2005, Bruggeman et al. 2009b), snow depth (Telfer and Kelsall 1984), and predation risk (Simon 2019). The evidence presented here suggests that the height of the shrub community also influences those decisions. Although other factors, such as limited forage

availability, could be involved in limiting bison use of areas with tall shrub communities, the data presented here demonstrate that the average stem height of these communities is a critical factor. This may be due to the energetic cost of moving the bulk of the head and body through the physical barrier of shrub stems where they exceed the height of the chest and nose. Above this height, the cross-sectional area that the animal would have to push past shrub stems increases dramatically. Similar effects have been observed with snow depth in a number of ungulate species (Parker, 1983). Another possibility is that bison avoid these areas due to poor visibility. Tall, dense shrubs likely reduce the animals' ability to detect predators. Ultimately, it's likely that multiple factors contribute to bison avoiding areas with tall shrubs.

Bison cannot directly influence the growth and mortality patterns of shrubs if they aren't present. If tall shrubs restrict bison movement, then tall shrubs should limit bison from influencing plant community dynamics in much of the forested component of the Aspen Parkland, where tall shrub understoreys are widespread (Thorpe and Godwin 2008). Bison impacts (including mortality of shrubs and aspen suckers) should be limited to areas without a tall shrub stratum. The widespread distribution of such strata likely limits the habitat available for bison. In the case of the Lake Audy herd and other enclosed conservation herds, this may further concentrate grazing effects on occupied grasslands, where impacts on low shrubs and young aspen suckers beyond the tall shrub line may in fact be higher due to the concentration of bison. In this study I found some evidence that bison limit shrub growth in these areas. Specifically, in grassland sites with a long history of bison occupancy, shrub cover was on average lower (Table 2). Further, average shrub cover declined, though not significantly so, in grassland sites when bison were introduced (Table 3).

Disparate processes operating on either side of the forest-grassland ecotone may sharpen that ecotone. In aspen, suckering is suppressed by the apical dominance of the mature stem (Schier 1981). Given minimal stem mortality inside the forest, due to a lack of disturbance, the growth of new ramets beyond the mature canopy would be inhibited (Barnes 1966). Outside the aspen stand, a relatively concentrated bison population has a magnified impact on the existing woody plant community, and presumably on any aspen ramets that do manage to sprout. This could reinforce a sharp, stable ecotone (Lastra 2011).

Bison are by no means the only potential agent of disturbance in aspen stands. Many other factors can kill mature aspen stems. Stand breakdown due to advanced age and fungal

infection can trigger suckering and encroachment (DeByle and Winokur 1985, Lastra 2011). Fire is also an important disturbance and cause of mortality. The climate of the Aspen Parkland historically contributed to frequent fires (Stockdale 2011). Deciduous forests have low potential fire intensities (Taylor et al. 1997). However, trembling aspen is relatively vulnerable to fire damage due to its thin bark. A temperature of 64 °C is sufficient to kill cambial tissue; lower temperatures can be fatal if sustained (Brown and Davis 1973). Non-fatal fire damage leaves stems more susceptible to infection by fungal pathogens, contributing to elevated mortality in the years following a fire (Hinds and Krebill 1975). Aspen respond vigorously to both stand replacing and low intensity fires (Perala 1974, Schier 1976, Schier and Campbell 1978, DeByle and Winokur 1985, Guedo and Lamb 2013). Shrub species, such as western snowberry (*Symphoricarpos occidentalis*) respond in a similar manner (Pelton 1953). This response can result in aspen and shrubs producing suckers far out into the grassland community (Lastra 2011), widening the ecotone.

The trajectory of the ecosystem following disturbance by fire would depend in part on the density of bison. Where bison are absent or occur at very low densities, fire can trigger further encroachment by aspen (Lastra 2011, Guedo and Lamb 2013), and other woody species (Pelton 1953). Where bison are present, they would be able to occupy sites where tall shrubs had been destroyed by fire, and suppress regenerating woody plants. These burned areas would presumably become more attractive to bison because of the removal of the physical shrub barrier, and increased forage availability. The herbaceous strata would undergo competitive release following the top kill of the tree and tall shrub strata. Abundant bison could prevent or reverse aspen encroachment following fire. However, this would be highly dependent on the speed with which bison occupy burned forested areas. Regenerating stems of the dominant tall shrub species add height very quickly. New stems of beaked hazelnut (*Corylus cornuta*) can reach a height of 0.6 m within two growing seasons of fire, and 2 m within the first two decades following fire (Stearns 1974). If bison don't occupy the area before the shrub strata recovers, they would be excluded and the trajectory of the ecosystem would then depend on the response to fire.

The structure of the Aspen Parkland is influenced by both climate and disturbance (Looman 1979, Zoltai et al 1991, Campbell et al. 1994, Hogg 1994, Hogg et al. 2008, Maillet et al. 2017). Fire and bison combine to disrupt the ecosystem. This prevents it from reaching a state

dominated by continuous aspen forest that would otherwise be supported by the amount of moisture the region receives (Hogg 1994, Hogg et al. 2008, Michaelian et al. 2011). Given that moisture availability decreases moving from the northern edge of the ecoregion to the southern edge, the amount of disturbance required to limit the abundance of woody species likely declines. Woody species such as aspen have relatively high moisture requirements in comparison to herbaceous grassland species. They are more susceptible to drought stress further south (Hogg 1994), and will have lower carbohydrate reserves as a result (Hogg et al. 2008). They will be less able to respond to disturbance via vigorous compensatory growth (suckering) (Hogg et al. 2008). This may account for differences observed between the northern edge of the Aspen Parkland (Prince Albert and Riding Mountain National Parks) (Lastra 2011, Guedo and Lamb 2013), and areas further south. In a site closer to the southern edge of the ecoregion, reversal of woody plant encroachment through fire alone has been demonstrated (Anderson and Bailey 1980). However, changes such as these are limited to very high fire frequencies unlikely to be observed outside of an experimental prescribed fire program.

As well as influencing the forest-grassland ecotone, bison are an important disturbance agent within the grasslands themselves. The removal of biomass by bison through grazing acts as a disturbance. By removing live plant material and preventing the accumulation of litter, bison affect the physical structure of the environment. These changes have important impacts on the habitat of other wildlife species, such as grassland songbirds (Knapp et al. 1999) and ground squirrels (Fahnestock and Detling 2002). Due to the complex suite of decisions driving bison habitat use (e.g. forage selection, predator avoidance, sociality, minimizing energy expenditure, etc.) (Merkle et al. 2014) small-scale bison disturbance occurs in a spatially heterogeneous pattern (Fahnestock and Knapp 1993, Catchpole 1996). This mosaic of habitat structures thus created supports a greater diversity of wildlife (Knapp et al. 1999). There are important consequences for plant community structure driven by bison concentrating in some areas and avoiding in others. For example, where bison are concentrated, grazing and nutrient inputs through defecation and urination can trigger rapid compensatory plant growth. This may result in a positive feedback loop of habitat use, producing a unique community type referred to as a grazing lawn (McNaughton 1984). Other disturbances caused by bison, such as wallowing and horning, are even more spatially concentrated. They have dramatic, but highly localized impacts on the landscape. Horning causes mortality of shrubs and trees and is thought to contribute

directly to the recession of the forest-grassland ecotone. Wallowing removes ground cover, creates habitat for a wide range of ruderal species (Polley and Wallace 1986), and can create ephemeral wetlands (Knapp et al. 1999, Butler 2006). These spatially discrete and heterogeneous impacts likely constitute a considerable share of the total cumulative impact of bison on the environment.

Over a single growing season bison can dramatically reduce sward height, litter, and live biomass (Table 3). However, in the short-term these bison impacts have a minimal impact on species composition. The short-term impact of bison is limited by the ecological inertia of long-lived perennial plant communities (Lauenroth and Adler 2008) and their adaptation to grazing (Diaz et al. 2007). The herbaceous species in these communities are well adapted to grazing. Certain grass species may even avoid any decline in biomass through compensatory growth (McNaughton 1983). However, the short-term impacts on community structure (i.e. biomass and litter) will generate longer-term impacts that can accumulate over time for several reasons. First, the impact of bison is not uniform across all species. Bison make grazing decisions based on foraging efficiency (Merkle et al. 2014); often this will result in a disproportionate impact on dominant species (Collins et al. 1998). Removal of biomass imposes an energetic cost on plants. Over time this energy deficit may reduce the energy available for vegetative and/or sexual reproduction, or may make individual plants more susceptible to pathogens and pests (Briske and Richards 1995). Decreases in rates of reproduction and increases in mortality will then result in a shift in species composition towards species less affected by bison. Second, as bison crop and trample the sward, they modify the abiotic conditions of the community. For example, reducing the sward height reduces shading. As bison continue to occupy the community year-after-year, these alterations to the abiotic conditions persist and magnify. This creates niche space for other species that would otherwise be excluded due to competition. Several plant species, for example, are present in heavily grazed areas of the Lake Audy bison enclosure that are otherwise rare or absent elsewhere in RMNP. These include *Oxytropis campestris*, *Symphyotrichum falcatum*, and *Antennaria neglecta* (Sinkins 2011). Over the period of several decades, the incremental influence of bison adds up to a starkly different grassland community; one that is significantly more biodiverse.

Bison were at one time widespread and abundant throughout the Aspen Parkland (Shaw 1995). The fescue grassland communities of the Aspen Parkland developed under the influence

of this large herbivore. Given that bison were functionally extirpated from the ecoregion during the 1800's, enough time has passed for substantial changes to accumulate in the remaining grasslands that were not converted to cropland. The evidence I present here shows that widespread declines in biodiversity, and shifts in ecosystem function may have occurred in these sites as a result. In the absence of bison, remnant grasslands that have been left ungrazed by livestock such as cattle are often treated as community reference sites in vegetation classification systems (Thorpe 2014a, Thorpe 2014b). These sites are often held as examples of the composition of ecologically intact fescue prairies. In fact, these sites may be heavily altered, and their use as a reference community may dramatically underestimate the biodiversity expected in healthy intact grasslands, and overestimate the importance of dominant grasses such as *Festuca hallii* in ecologically intact fescue grasslands. Bison grazed sites could provide a more relevant reference community, however there are very few sites in the Aspen Parkland with a long-term and ongoing bison presence (Gates et al. 2010). As has been pointed out by many writers, cattle, despite their close taxonomic relationship with bison, may serve as a poor proxy for bison. The behavioural ecology of domestic cattle, and foraging ecology in particular, is substantially different from bison (Gates et al. 2010). This is exacerbated by intensive management of cattle on farms and ranches. The use of untilled fescue grassland sites grazed by cattle as examples of ecologically intact communities is further complicated by the presence of invasive plant species. Invasive plants, in particular the grass *Poa pratensis*, that have proliferated widely in untilled fescue grasslands under traditional cattle grazing regimes (DeKeyser et al. 2015). These species pose their own substantial threat to the ecological integrity of these grassland communities.

The presence of invasive species also complicates the effect bison have on grassland communities. The niche space created by bison, which contributes to greater biodiversity, also provides opportunities for invasive alien plants to invade. Many of the traits of ruderal native species that allow them to colonize open spaces such as wallows are also present in invasive non-native species (Polley and Wallace 1986). Canopy gaps in the sward provide an opportunity for non-native species to germinate and become established (Collins et al. 1998). Bison also likely serve as a vector, dispersing invasive species' seeds in their gut and fur (Rosas et al. 2008). However, where bison are present, grazing prevents these species from becoming super abundant and crowding out native species. At Lake Audy, the invasive grass *Poa pratensis* was widespread and abundant in areas historically grazed by bison; including heavily used areas such

as grazing laws. However, the biodiversity of these sites was high. By maintaining a low sward height, bison likely prevented the thick litter accumulation and shoot competition that would prevent other plants from establishing (Letts et al. 2015). If bison are removed from the system, then the already established invasive species are released from grazing pressure and have the opportunity to become dominant. My evidence suggests that bison avoid areas with a high cover of *Poa pratensis* (Fig. 8). This may be due to the relatively high abundance of thatch and low density of green shoots in *Poa pratensis* dominated stands. Where bison are stocked in sufficiently low densities that they can avoid foraging in *Poa pratensis* dominated stands, the release of the invasive grass from grazing pressure could trigger a feedback loop resulting in expanding populations of the invasive species. This in turn could reduce the area of suitable habitat available to the bison.

In areas of fescue grassland without established invasive plant species and where bison are absent, dominance by native species and lack of disturbance may initially restrict invasion. If invasive species are eventually able to become established in these areas, invasion might occur rapidly. Non-native species would crowd out native species without bison functioning as a disturbance and reducing their populations.

4.2 Future Research

My findings have brought up several questions that would benefit from further inquiry. One of the most surprising findings of this study was the extent to which tall shrubs mediate the influence of bison. Several mechanisms could explain this relationship, including the energetic cost and risk of injury associated with moving through shrub stems, lack of forage under the dense shrub canopy, and poor predator detection in that canopy. The relative importance of these mechanisms could be determined by combining a model of shrub physiognomy with a model of bison behaviour, and tested with a focal animal study. Understanding the mechanics of this relationship will help us predict how bison and the plant community will interact with a third factor such as fire.

In this study, bison density, and the response of plant communities to bison was highly variable site to site. This variability made it challenging to find patterns in the data. Further refining our understanding of the influence that bison have on plant communities in the Aspen Parkland will require explicitly considering the spatial heterogeneity of their impact. There is

reason to believe that much of the ecological impact of bison is concentrated in small, heavily utilized areas such as wallows, grazing lawns, and thermal refugia. Comparing the plant communities in shrub and forest areas of high and low bison density would allow us to test if bison cause localized shrub and sapling mortality in concentrated areas. Similarly, by comparing high and low use grassland areas we would also be able to see how the grassland community shifts in response to different levels of disturbance by bison. In particular, *Poa pratensis* is both highly tolerant of grazing and able to thrive under a lack of disturbance and the accumulation of litter (Letts et al. 2015). Understanding how this invasive species responds to subtle variation in bison density will be crucial to managing bison with an eye to minimizing the impacts of this invasive species.

It is generally thought that historically the structure of the Aspen Parkland was dependent on the dual disturbances of fire and bison. However, the combined effect of bison on the trajectory of the plant community in the Aspen Parkland remains untested empirically. It is uncertain whether bison would readily occupy aspen forests with dense shrub layers following fire, and whether they would reduce shrub and sapling recruitment. A factorial experiment combining varying bison densities, and varying prescribed fire frequencies interact will allow us to understand what combination of those factors are required to cause woody vegetation to recede and restore grassland.

The groundwork laid by this study provides an excellent opportunity to understand how the short-term modification of the structural environment (sward height, litter accumulation, etc.) by bison contributes to a long-term shift in community composition. All sites used in the study were permanently marked, and the range-cages used were kept in place. By periodically revisiting these sites, we will be able to observe how the cumulative impact of bison removal or introduction alters plant communities.

4.3 Management Recommendations

The loss of bison has been cited as an important cause of encroachment of trees and shrubs into grasslands in the Aspen Parkland (Campbell et al. 1994). Given that the primary alternate strategy, prescribed fire, is not sufficient alone to arrest woody plant encroachment (Guedo and Lamb 2013), I recommend that land managers across the ecoregion consider reintroducing bison to restore the biodiversity and ecological function associated with these

grasslands. The evidence in my thesis shows that reintroducing bison alone is unlikely to reverse forest encroachment, especially in areas with tall shrub communities, therefore the reintroduction of bison should be combined with the use of prescribed fire. As outlined in the previous section, experimental testing of the combined bison-fire strategy is recommended.

Land managers considering reintroducing or expanding the existing range of bison, or removing them from areas they currently occupy, should exercise caution regarding invasive species. Protected areas of native grassland with few non-native plants and no recent history of grazing may appear to be the obvious choice for bison reintroduction sites. However, introducing bison to areas where invasive species such as *Poa pratensis* are not yet established may lead to those species being spread and established throughout the site. Alternatively, removing bison from a site also poses risks; invasive species released from grazing pressure could overwhelm native species. Land managers need to monitor reintroduction sites to ensure that any areas that become heavily dominated by *Poa pratensis* and avoided by bison are detected. Prescribed fire could be used to reduce thatch in these areas, and may induce bison to begin reoccupy them. As with the control of woody shrubs, experimental testing of this management approach is required to confirm the efficacy of combined grazing-fire approaches to prevent the dominance of this invasive species.

4.4 Final Conclusion

The purpose of this study was to examine the impact of bison on the Aspen Parkland plant community in RMNP. I found that bison serve as an agent of disturbance, with a limited short-term impact on the community. However, over the long-term, their cumulative impact results in a community that is dramatically different than would be expected to occur in their absence. The Aspen Parkland is defined by a mosaic of forest and grassland, and the ecotone between these two communities is an important component of the ecosystem. There is widespread concern over the expansion of forests into remaining grassland fragments, and bison have been posited as having a role in mitigating or reversing this process. Here, I have shown that any potential impact by bison is limited by the barrier of the tall shrub strata of these forests. Impacts by bison to the invading ecotone are likely limited to cases where the ecotone is disrupted by an alternate agent of disturbance such as fire. Outside the tall shrub strata, in rough fescue grasslands, bison alone are able to disrupt the equilibrium of the community. Over the

short-term, this results in changes to the physical structure of the grassland. These changes accumulate over time resulting in a distinct and more diverse community. The results of this study are directly applicable to the ecosystem of RMNP, and can be widely applied throughout the Aspen Parkland.

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6. APPENDICIES

Appendix A. Path coefficients, and tests of path significance for a structural equation model of the shrub and sapling community in the Lake Audy bison enclosure and its relationship with bison.

	Unstandardized coefficient	Standard Error	z-value	p	Standardized coefficient
Bison Density ~					
Current Bison	3.661	1.135	3.227	0.001	0.376
Historic Bison	-1.126	1.157	-0.974	0.330	-0.113
Ecotone Distance	0.372	0.280	1.329	0.184	0.176
Plant Height	-0.413	0.191	-2.161	0.031	-0.269
Density	-0.068	0.052	-1.295	0.195	-0.178
Canopy	2.020	3.293	0.613	0.540	0.108
Height ~					
Ecotone Distance	-0.529	0.152	-3.488	<0.001	-0.385
Density ~					
Ecotone Distance	-0.803	0.655	-1.225	0.220	-0.145
Canopy ~					
Ecotone Distance	-0.045	0.009	-5.246	<0.001	-0.399
Density	0.010	0.001	6.501	<0.001	0.477
Plant Height	0.021	0.006	3.231	0.001	0.254
Browsing ~					
Ecotone Distance	0.001	0.008	0.128	0.898	0.018
Canopy	-0.100	0.099	-1.016	0.310	-0.190
Density	-0.001	0.002	-0.816	0.414	-0.120
Plant Height	-0.005	0.006	-0.855	0.392	-0.116
Bison Density	-0.002	0.004	-0.544	0.587	-0.069
Current Bison	0.035	0.036	0.952	0.341	0.126
Historic Bison	0.039	0.035	1.127	0.260	0.140
Change in Density ~					
Bison Density	0.124	0.175	0.710	0.477	0.082

	Unstandardized coefficient	Standard Error	z-value	p	Standardized coefficient
Ecotone Distance	0.031	0.444	0.071	0.944	0.010
Canopy	-6.220	5.231	-1.189	0.234	-0.221
Density	-0.149	0.083	-1.783	0.075	-0.258
Plant Height	0.913	0.310	2.944	0.003	0.394
Browsing	-2.730	6.109	-0.447	0.655	-0.051
Covariances:					
Plant Height ~~					
Density	8.874	4.201	2.112	0.035	0.261

Appendix B. Species axis scores for non-metric multidimensional scaling ordination comparing unoccupied and occupied grassland communities

Species	NMDS Axis 1	NMDS Axis 2
<i>Achillia_milifolium</i>	0.260973467	0.264244454
<i>Agastache_foeniculum</i>	0.131105234	0.173701977
<i>Agropyron_trachycaulum</i>	0.132418317	-0.012756478
<i>Agrostis_scabra</i>	0.071179846	0.311486295
<i>Allium_stellatum</i>	0.246762907	-0.408431336
<i>Amelanchier_alnifolia</i>	-0.103375849	-0.773435600
<i>Androsace_septentrionalis</i>	0.214715953	0.665878487
<i>Anemone_canadensis</i>	-0.615184028	0.132673593
<i>Anemone_sp</i>	0.853415274	0.823186102
<i>Anemone_multifida</i>	0.499724575	-0.123245461
<i>Antennaria_campestris</i>	0.496227789	0.743281718
<i>Artemisia_dracunculus</i>	0.105118924	-0.876253400
<i>Artemisia_ludoviciana</i>	0.079713471	-0.253962035
<i>Asclepias_ovalifolia</i>	0.251754318	-0.070581444
<i>Aster_ciliolatus</i>	-1.813536041	0.549964988
<i>Aster_laevis</i>	0.073087726	-0.151961765
<i>Astragalus_canadensis</i>	-0.004824684	-0.357633476
<i>Astragalus_sp</i>	0.900623080	0.203746711
<i>Bromus_ciliatus</i>	-0.047478657	0.049689684
<i>Bromus_inermis</i>	-0.588024712	0.249405092
<i>Bromus_pumpellianus</i>	-0.734078762	0.575576937
<i>Campanula_rotundifolia</i>	0.559138171	0.074201158
<i>Calamagrostis_canadensis</i>	-1.624797179	0.444968269
<i>Carex_sp</i>	0.012251690	0.264302756
<i>Cerastium_arvense</i>	0.403957681	0.207285240
<i>Cirisium_arvense</i>	-1.798403453	0.034977719
<i>Cirisium_drummondii</i>	-0.038191033	1.262781449
<i>Comandra_umbellata</i>	0.258528287	-0.124473339

Species	NMDS Axis 1	NMDS Axis 2
Danthonia_spicata	0.624273431	0.342566046
Danthonia_sp	0.353739933	-0.003022186
Erigeron_glabellus	0.801122312	1.110363842
Erigeron_sp_1	0.453272313	-0.675090133
Erigeron_sp_2	0.182140831	-0.254971015
Festuca_hallii	0.369111951	-0.073467033
Fragaria_virginiana	0.084788227	-0.005370512
Gaillardia_aristata	0.349415056	0.062846685
Galium_boreale	0.065099257	-0.192263805
Geum_macrophyllum	0.706483641	1.998064121
Geum_trifolium	0.054634717	1.178924281
Hedysaurum_alpinum	0.131983310	0.034104228
Helianthus_nuttallii	0.072613915	-0.749118752
Helictotrichon_hookeri	0.653380680	0.593028981
Koleria_macanthra	0.418240208	0.197632637
Lathyrus_ochroleucus	0.021960523	0.027380877
Latuca_pullchella	-0.062425221	-0.330863857
Liatrix_ligulistylis	0.409780739	0.123947390
Linum_lewisii	0.407735308	1.223733304
Lithospermum_canescens	0.245754803	0.083346265
Sellaginella_densa	0.381006199	0.974391833
Lysimachia_cilliata	-0.433890053	0.019233310
Monarda_fistulosa	-0.001589833	-0.163163785
Muhlenbergia_sp	-0.426950114	0.299055049
Muhlenbergia_racemosa	-0.085407484	0.213514167
Muhlenbergia_richardsonis	0.417444859	-0.125481724
Oxytropis_campestris	0.636705100	0.667175391
Poa_compressa	-0.545157444	0.654844150
Poa_pratensis	-0.227386075	-0.067577843
Polygala_senega	0.426411448	0.193129470

Species	NMDS Axis 1	NMDS Axis 2
<i>Potentilla_arguta</i>	0.506934687	0.213409959
<i>Potentilla_fruticosa</i>	0.499256595	-0.723812349
<i>Potentilla_pensylvanica</i>	0.706483641	1.998064121
<i>Prunus_virginiana</i>	-1.755243510	1.354471984
<i>Ranunculus_rhomboideus</i>	-0.137924012	0.168911691
<i>Ranunculus_sp</i>	0.357923870	0.462860728
<i>Rosa_ascicularis</i>	-0.013851220	-0.255150058
<i>Rubus_idaeus</i>	-1.442240002	0.807940952
<i>Rudbeckia_hirta</i>	0.345016825	0.243799109
<i>Schizachene_purpurescens</i>	-0.198725622	-0.149917918
<i>Sisyrinchium_montanum</i>	0.330005829	0.179746603
<i>Smilacina_stellata</i>	-0.182941726	-0.152559459
<i>Solidago_canadensis</i>	-0.957748332	0.273621969
<i>Solidago_missouriensis</i>	1.451975528	-0.240458636
<i>Solidago_rigida</i>	-0.065983437	-0.321886858
<i>Sporobolus_heterolepis</i>	0.508562913	0.101166610
<i>Stellaria_sp_1</i>	0.624946387	0.803280511
<i>Stellaria_sp_2</i>	0.200099251	-0.218338615
<i>Stellaria_longipes</i>	0.254452649	0.122667749
<i>Stipa_curtiseta</i>	0.310168664	0.371752835
<i>Stipa_richardsonii</i>	0.158700782	0.593245482
<i>Stipa_spartea</i>	0.534828311	-0.015837559
<i>Stipa_viridula</i>	0.627949751	-1.053152519
<i>Symphocarpos_occidentalis</i>	-0.564525175	-0.651770685
<i>Taraxicum_officialis</i>	0.095501243	0.365297928
<i>Thalictrum_dasy carpum</i>	-1.807114311	0.331422786
<i>Thalictrum_venulosum</i>	0.097747794	-0.093564508
<i>Tragopogon_dubius</i>	-0.450244459	1.025186654
<i>Trifolium_repens</i>	0.155854012	0.996258193
<i>Vicia_americana</i>	-0.052967624	0.012785662

Species	NMDS Axis 1	NMDS Axis 2
Viola_adunca	-0.133263147	-0.660943248
Viola_sp	-0.074687954	-0.343586598
Zygadenus_elegans	0.708090536	0.016962376
Zizia_aptera	0.304197505	0.315810335
Caryophyllaceae_sp	1.451975528	-0.240458636
Compositae_sp_1	0.755727383	-0.322127290
Compositae_sp_2	0.464785921	-0.413498975
Lichen_sp_1	0.706483641	1.998064121
Liliaceae_sp_1	0.464785921	-0.413498975
Marchantiophyta_sp	0.706483641	1.998064121
Poaceae_sp_1	0.393984405	-0.452134882
Poaceae_sp_2	0.106824491	-0.147829358
Poaceae_sp_3	0.404194266	-0.456554588
Poaceae_sp_4	0.518747653	-0.426324906
Unknown_sp_1	0.182140831	-0.254971015
Unknown_sp_2	0.218057671	-0.181706215
Unknown_sp_3	1.451975528	-0.240458636
Unknown_sp_4	0.671432660	0.002512396

Appendix C. Species axis scores non-metric multidimensional scaling ordination of south and north pasture plant communities before (2015) and after (2016) one year of experimental treatment.

Species	South Pasture		North Pasture	
	NMDS Axis 1	NMDS Axis 2	NMDS Axis 1	NMDS Axis 2
<i>Achillia_milifolium</i>	0.4189714539	0.06221975	-0.05947635	0.54252954
<i>Agastache_foeniculum</i>	-0.0123680288	0.13599961	1.30663847	0.53345585
<i>Agimonia_striata</i>	0.2927585138	-0.92476588		
<i>Agoseris_glauca</i>	-0.1671941891	0.09806955		
<i>Agropyron_trachycaulum</i>	0.0066759592	0.09131680		
<i>Agrostis_scabra</i>	0.2035619932	-0.62966481		
<i>Allium_stellatum</i>	-0.1601983830	-0.02628019		
<i>Amelanchier_alnifolia</i>	-0.4515797106	-0.25515233		
<i>Anemone_canadensis</i>	-0.3890688869	-0.69517565	-1.07630100	-0.08399066
<i>Anemone_sp</i>	1.1530967113	0.03153323		
<i>Anemone_multifida</i>	-0.2219560458	0.54318865		
<i>Antennaria_campestris</i>	0.5970324939	0.39964835		
<i>Artemisia_dracunculus</i>	-0.4490361059	0.32515762		
<i>Artemisia_ludoviciana</i>	-0.1301395592	-0.18079224	0.39105047	-0.30975726
<i>Asclepias_ovalifolia</i>	-0.6298816337	-0.74604606		
<i>Aster_ciliolatus</i>	1.7252098363	-0.14319907	-1.16886425	-0.38204489
<i>Aster_laevis</i>	-0.0463231441	0.03582330	0.41092772	-0.25385663
<i>Aster_sp_1</i>	1.7252098363	-0.14319907		
<i>Astragalus_agrestis</i>	0.6977303449	0.14312113	0.97724322	-0.86830091
<i>Astragalus_canadensis</i>	0.0823228317	-0.25628331	0.82195321	-0.52196218
<i>Astragalus_sp</i>	0.0007111769	1.07341157		
<i>Bromus_ciliatus</i>	0.2543893459	0.26043566		
<i>Bromus_inermis</i>	-0.6660864202	-1.31104358	0.14122190	0.58770861
<i>Campanula_rotundifolia</i>	1.0232540255	0.11034074		
<i>Calamagrostis_canadensis</i>			-0.97937470	-0.03638878
<i>Calamagrostis_sp</i>			0.20037837	-0.10729838

	South Pasture		North Pasture	
Carex_sp	0.0045454786	0.10237779	-0.07164990	0.15669869
Carex_torreyi	-0.0900574198	-0.18726028		
Cerastium_arvense	0.3641985366	0.30499972		
Cirsium_drummondii	0.6568632034	-0.88499179		
Comandra_umbellata	-0.0666955189	0.12916032	0.82195321	-0.52196218
Danthonia_spicata	0.1511456460	0.71887952		
Dantonina_intermedia	0.5962563353	0.48828236		
Erigeron_glabellus	1.2764637393	-0.35127563		
Erigeron_sp_1	-0.5610509495	0.70742860		
Erigeron_sp_2	-0.0932911363	-0.33853914		
Festuca_hallii	-0.1136949149	0.20396743	0.87396486	-0.25225141
Fragaria_virginiana	-0.1739052158	0.02660797	0.81125446	-0.15278940
Galium_boreale	-0.1664757700	0.08000970	0.54300758	-0.05547867
Geum_macrophyllum	1.7632356005	-0.24015585		
Geum_trifolium	0.6354333532	-0.17474516		
Hedysaurum_alpinum	-0.0212942343	0.05035791		
Helianthus_nuttallii	-0.5636343413	0.10368597		
Helictotrichon_hookeri	0.7526360516	0.27039587		
Hieracium_umbellatum	0.3571307060	0.88643407		
Koleria_macanthra	0.4802551183	0.17889389		
Lathyrus_ochroleucus	-0.2137747981	0.23239005	0.28643185	0.46194112
Latuca_pullchella	0.0380500169	-0.02705623		
Liatrix_ligulistylis	0.1742755313	0.31717261		
Lilium_philadelphicum	-0.1942120173	-0.09897278		
Linum_lewisii	1.1893503507	-0.47858653		
Lithospermum_canescens	0.0206534091	0.03083540	0.48819675	0.10844264
Sellaginella_densa	0.4805000661	0.48902360		
Lysimachia_ciliata	0.1565227756	-0.50877135	0.63972019	-0.53950415
Monarda_fistulosa	-0.4002499267	0.06803205	-0.78501669	0.05518515
Muhlenbergia_sp			1.30663847	0.53345585

	South Pasture		North Pasture	
Muhlenbergia_racemosa	0.3720894640	0.10312326	1.30663847	0.53345585
Muhlenbergia_richardsonis	0.0979516244	0.16170388		
Orthocarpus_luteus	1.7252098363	-0.14319907		
Oxytropis_campestris	0.8123990802	0.17096545		
Oryzopsis_canadensis	0.6543980112	0.35733106		
Poa_annua	0.0066643484	0.11633581		
Poa_compressa	-0.7418470293	0.14637931	1.30663847	0.53345585
Poa_pratensis	0.0333661698	-0.25233973	-0.22466161	-0.08034170
Polygala_senega	0.1760171644	0.45194163		
Potentilla_fruticosa	-0.9189252742	0.55846074		
Potentilla_pensylvanica	1.7711109942	-0.26023626		
Ranunculus_rhomboideus	0.1510076006	0.37438179		
Ranunculus_sp	0.3256487213	-0.03311305		
Rosa_ascicularis	-0.2427805577	-0.54726106	1.09536346	0.45436480
Rubus_idaeus			-0.25102620	0.97775618
Rudbeckia_hirta	0.1194831307	0.18158701	0.91088796	0.38530618
Schizachene_purpurescens	0.3398332988	-0.27397041	0.14818932	-0.31233917
Sisyrinchium_montanum	0.1370481490	0.10019952		
Smilacina_stellata	0.0806043102	-0.07713850		
Solidago_canadensis	-0.6786151808	0.21547482	-0.49394008	0.05362905
Solidago_rigida	0.0800628627	-0.55396965		
Sphenopholis_intermedia	0.0917940384	0.28922423		
Sporobolus_heterolepis	0.1060353866	0.47169455		
Stachys_palustris	0.2927585138	-0.92476588		
Stellaria.1	1.2091140065	-0.55060691		
Stellaria.2	-0.0932911363	-0.33853914		
Stellaria_longipes	0.0372475696	0.00133814	0.76130833	0.32931087
Stipa_curtisetata	0.3371687783	0.16759203		
Stipa_spartea	-0.1279532270	0.35522262		
Stipa_viridula	-1.0730519160	0.49139378		

	South Pasture		North Pasture	
<i>Symphocarpos_occidentalis</i>	-0.5864699693	0.28794536	0.93098497	-0.76513248
<i>Taraxicum_officialis</i>	0.3983236633	-0.37096966		
<i>Thalictrum_dasycarpum</i>			-1.10774432	-0.50230199
<i>Thalictrum_venulosum</i>	-0.0943790228	-0.00171004	0.80856377	0.18934611
<i>Trifolium_repens</i>	0.6568632034	-0.88499179		
<i>Trifolium_hybridum</i>	0.6782277915	-0.33449294		
<i>Vicia_americana</i>	-0.2193364690	0.13541484	-0.27033637	-0.03567703
<i>Viola_pedatifida</i>	0.2541526664	0.03004753		
<i>Viola_sp</i>	0.4654663951	-0.01826299		
<i>Zygadenus_elegans</i>	-0.1239379196	0.62176799		
<i>Zizia_aptera</i>	0.3004385935	0.06880805		
<i>Caryophyllaceae_sp</i>	-0.2245617771	-0.01808801		
<i>Compositae_sp</i>	-0.5296185581	0.45927943		
<i>Poaceae_sp_1</i>	-0.4179629437	0.22405828		
<i>Poaceae_sp_2</i>	-0.0877614906	-0.10551896		
<i>Poaceae_sp_3</i>	-0.4179629437	0.22405828		
<i>Poaceae_sp_4</i>	0.0647702448	0.93137378		
<i>Lichen_sp_1</i>	1.8170121520	-0.37727345		
<i>Liliaceae_sp_1</i>	-0.5296185581	0.45927943		
<i>Marchantiophyta_sp</i>	1.8170121520	-0.37727345		
<i>Unknown_sp_1</i>	-0.0932911363	-0.33853914		
<i>Unknown_sp_3</i>	0.0007111769	1.07341157		