

**Grassland vegetation diversity responses to the reintroduction of
Wood Bison (*Bison bison athabasca*) in Aishihik, Yukon**

by

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Abstract

In the southwest Yukon, the rain shadow effect of the Coast Mountains produces xeric south-facing slopes that support some of the most northerly grasslands in North America. These dry and nutrient poor forb-dominated grassland pockets within the vast matrix of boreal forest support distinctive plant communities that contain several rare and endemic plant species, as well as disjunct populations of prairie species such as Prairie Smoke (*Geum triflorum*) that are considered rare in the Yukon although common to the south. The unique flora of these grasslands, coupled with the fact that they occupy less than 1% of the landscape, makes them of high conservation concern. Wood bison (*Bison bison athabasca*) were reintroduced into southwest Yukon in the late 1980's as part of national recovery efforts. The Aishihik wood bison population has subsequently increased from 34 in 1988 to 1,470 individuals in 2016, prompting concerns about how they may reshape the landscape, influence other wildlife, affect traditional uses of the land, and alter these unique and rare grasslands, considered by some to be relicts of ice age steppe vegetation. Thus, there is a need to understand the potential impact of reintroduced wood bison on these native grassland communities, which do have a long-term history of grazing by large mammals.

I documented the floristic diversity of native grasslands in the Aishihik area of northwest Canada, and evaluated how current bison grazing may alter this diversity. Specific objectives were to: 1) determine whether the diversity of these grasslands has changed over the last 30+ years following wood bison reintroduction, and 2) relate grassland diversity responses to bison grazing intensity. I hypothesized that there would be little change in diversity at low levels of

bison grazing because the convergent pressures of aridity and a long history of grazing have preconditioned these grasslands to tolerate a certain amount of grazing. With increased grazing intensity, I hypothesized that diversity would decrease. Contrary to expectations, I found that richness and all other measures of diversity increased with greater bison presence, as did both forb and graminoid abundance, though not all groups were affected equally. Small upland *Carex* species increased most dramatically (i.e. species that are known to be indicators of overgrazing in the prairies), but not at the cost of forbs, which were the drivers of diversity in this system. Similarly, rare species (predominantly forbs) showed no signs of decline. Another grazer on these grasslands, the Arctic ground squirrel (*Urocitellus parryii*), was also positively associated with graminoid abundance.

The grasslands of the southwest Yukon co-evolved with a large number of mega-herbivores north of the ice sheets, in a harsh, often cold and dry, environment. The current findings suggest they may be so disturbance and aridity adapted that their diversity may be more limited by too little grazing or excess moisture, than by the reintroduction of wood bison. Supporting this hypothesis, plant community diversity decreased with increasing precipitation in these grasslands. Climate change, and the predicted increase in temperature and precipitation in this region of the Yukon, may pose a greater threat to plant diversity on these grasslands than herbivory. Results of this study have implications for reconciling wood bison and grassland conservation initiatives in the region.

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Introduction

Grasslands are some of the most plant species-rich ecosystems in the world (Martorell 2017, Wilson et al. 2012). While rainforests are considered to hold the greatest plant diversity at a large scale ($\geq 100 \text{ m}^2$; Balslev et al. 1998), following an extensive literature review, Wilson et al. (2012) found that at a small scale ($\leq 49 \text{ m}^2$) plant species richness was greatest in grasslands. Furthermore, the grasslands containing the greatest plant diversity (occurring at all tested scales below 49 m^2) were all relatively nutrient poor, had a long history of grazing or were mowed.

Grazing by both small and large mammals is one of the key factors influencing plant community structure and diversity in grasslands, although the effect is variable across ecosystems (Bakker et al. 2006, Chillo et al. 2017, Collins et al. 1998, Olff & Ritchie 1998). The presence of grazers on the landscape not only directly affects plant growth through the removal of phytomass and leaf area, but also changes ecological processes through a variety of mechanisms. The latter includes soil compaction by large herbivores such as bison and horses (Belsky & Blumenthal 1996), the creation of wallows by bison (Knapp et al. 1999) and soil aeration by burrowing small mammals like ground squirrels and prairie dogs (Huntly & Reichman 1994). Independent of size, grazers enrich the soil through dung and urine deposition (Huntly & Reichman 1994, Knapp et al. 1999).

One of the first attempts at a unifying theory to describe the disturbance-diversity relationship (grazing being one form of disturbance) was the Intermediate Disturbance Hypothesis (IDH; Connell 1978, Grime 1973). The IDH predicts that at moderate levels of disturbance the degree of competition among species is relaxed, thereby creating a balance between the abundance of disturbance-adapted species and competitively dominant species more susceptible to disturbance. In the absence of disturbance, a select group of competitively superior species dominate the community, while at high disturbance only species tolerant of disturbance survive; both situations result in reduced diversity.

But how well does this model apply to grazing in grasslands? Some grassland grazing studies show the hump-backed pattern of maximum diversity at intermediate levels of grazing (e.g. in the short grass steppe of the Great Plains [Okuda et al. 1994], in the fescue grasslands of Alberta [Willoughby 1992] and in the aspen parkland of Alberta [Vujnovic et al. 2002]), while others show a monotonic decrease in diversity (e.g. in the mountains of the Great Basin [Beever et al. 2008]), or a scale-dependent response with plot level diversity increasing minimally and landscape site level diversity not at all (e.g. in the sagebrush steppe of the Columbia Plateau and the Patagonia steppe [Adler et al. 2005] and in the American Rocky Mountain grasslands [Stohlgren et al. 1999]).

The variety of plant diversity responses to grazing in grasslands suggests that more drivers of diversity than just disturbance should be considered, and that, in at least some situations, grazing is an insignificant contributor to variation in diversity. For instance, abiotic factors such

as climate and biotic factors such as the pre-existing plant community also play an important role (Nathan et al. 2016, Wan et al. 2015). More specifically, grassland plant community diversity has been linked to the combination of grazing history and moisture regime (Mack & Thompson 1982, Adler et al. 2005). In their Generalized Model of Effects of Grazing by Large Herbivores (MSL), Milchunas et al. (1988) incorporated both these factors into the IDH, resulting in contrasting models relating different diversity-disturbance relationships across gradients of annual moisture and grazing history (Figure 1). To illustrate their model Milchunas et al. (1988) described four boundary states at the extremes of these gradients. In semi-arid grasslands with a long history of grazing only a slight decrease or no change in diversity is expected with increased grazing intensity because the grasslands have already adapted to repeated defoliation, as well as to aridity, by evolving into communities dominated by low-growing, rhizomatous grasses and sedges capable of quick regrowth after defoliation, meaning that any release from competition is short-lived.

In semi-arid grasslands with a short history of grazing, on the other hand, Milchunas et al. (1988) suggested that grassland communities would be comprised of a mix of short and intermediate grasses, as well as sedges less adapted to grazing. Within these areas, graminoid regrowth potential following defoliation would be slow and associated with vertical phytomer regrowth rather than horizontal vegetation reproduction via asexual reproduction (i.e. creeping roots or rhizomes) while forbs are likely to react more strongly to competitive release. The result would be a small increase in diversity under low levels of grazing, which would give rise

to a more marked decline in diversity under increasing grazing intensity, particularly relative to that seen in semi-arid grasslands with a long history of grazing.

Plant diversity in more productive subhumid grasslands exhibits greater variation across different levels of grazing due to greater above-ground productivity relative to below-ground productivity. Subhumid grasslands with a long history of grazing are predicted to most closely follow the IDH model because the community is composed of a mixture of short, medium and tall stature species that can differentially take advantage of varying levels of disturbance and open patches, while those with a short history are the least adapted to grazing pressure.

Milchunas et al. (1988) postulated that when the tallgrasses dominating the latter communities are grazed, even at low levels, they have poor regrowth, allowing suppressed species to increase and exotics to quickly move in, resulting in an initial increase in diversity. However, at even moderate grazing intensity, grazing-induced mortality starts to become a greater force than competitive release in regulating diversity, leading to declining diversity (Figure 1).

The Generalized Model of Effects of Grazing by Large Herbivores proposed by Milchunas et al. (1988) is one of the most widely accepted of those developed to explain disturbance-diversity relationships in grasslands, and has been shown to apply in many situations (Mack & Thompson 1982, McNaughton 1985), including in the semi-arid mixedgrass prairie of western Canada (Bai et al. 2001). However, there are other models that incorporate additional factors such as the dietary preference of grazers (Wan et al. 2015), or that utilize a non-equilibrium view of disturbance dynamics (state and transition models: Laycock 1991, Westoby et al. 1989) to

account for how grasslands may exhibit complex and unpredictable changes in composition in response to environmental stress. Additionally, while these models all focus largely on competition, there is evidence that in some systems, such as those where the main competition is belowground among root systems (Lamb & Cahill 2008), or in low- productivity systems such as those in the north (here defined as north of the 60th parallel; Grime's C-S-R (Competitor-Stress tolerator-Ruderal Triangle theory, 1977), competition may not be the primary driver of plant community composition and diversity.

Overall, empirical evidence shows that even within the most commonly studied grasslands, like those of the Great Plains of North America or the Mongolian Steppe, there is no one disturbance-diversity model that appears to account for all observed diversity responses (Cingolani et al. 2005, Hanke 2014, Wan et al. 2015). In rare and unique grasslands north of 60° latitude, such as those in the Yukon of northwest Canada, where relatively few studies have been conducted, plant diversity responses to grazing remain even more uncertain.

In the southwest Yukon, the rain shadow effect of the Coast Mountains produces xeric south-facing slopes that are home to some of the most northerly grasslands in North America (Strong 2015). While these grasslands have a shorter growing season (*ca.* 12-16 weeks) relative to their counterparts in the North American Great Plains, they experience approximately 19 hours of sunlight each day during the growing season. This amount of solar radiation, combined with a predominantly south-southwestern aspect on steep slopes, results in high insolation values that lead to elevated evaporation rates in an already moisture-limited environment. Small pockets

of grassland form on these slopes that are persistent and widespread, and occur within an otherwise vast matrix of boreal forest (Hoefs et al. 1975, Johnson & Raup 1964, Sauchyn 1987, Vetter 2000). In combination with high aridity and recurring drought, regular disturbances such as fire and grazing may have helped prevent trees and shrubs from becoming established in these grasslands in the past (Heyerdahl 2006, Knapp et al. 1999, Stebbins 1981).

The distinctive plant communities that are adapted to these dry and nutrient-poor slopes contain several rare and endemic plant species including one of only two populations worldwide (and the only Canadian population) of *Eriogonum flavum* var. *aquilinum* (see Appendix II for species authorities). It is listed as being of special concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), as is *Draba yukonensis* (COSEWIC 2011, 2017), also found within our study area. Aside from these endemics, populations of *Geum triflorum* and *Comandra umbellata*, disjunct from their southern range in the prairie grasslands of Canada and the United States, are found on these grasslands, and are considered rare in the Yukon although common to the south. The unique flora of these grasslands, coupled with the fact that they occupy less than 1% of the landscape (Caslys Consulting 2018), makes these grasslands of high conservation concern (Government of Yukon 2012).

These grasslands are also considered by many to be analogues of the Pleistocene steppe vegetation that existed in the glacial refugia (Beringia) that extended from the Mackenzie River in western Yukon through Alaska to the Lena River in northwest Russia (including the now submerged Bering and Chukchi continental shelves) during the Pleistocene (Lloyd et al. 1994,

Willerslev et al. 2014, Yurtsev 2001). Paleo-environmental reconstructions indicate that during the colder, drier glacial periods of the Pleistocene, the Beringian landscape was comprised of a mosaic of tundra and steppe vegetation known as tundra-steppe (Hibbert 1982) which co-evolved with a much wider variety of megafauna than exists there today (about 40 species of animals over 40 kg; Blinnikov 2011), many of which were grazers (Guthrie 1968, Mann et al. 2013). The steppe plant species that established themselves in Beringia during this time, some on both sides of the Bering land bridge, were adapted to a cold, arid climate and repeated grazing, i.e. they tended to be short, often rhizomatous, perennials with a high rate of regrowth following disturbance.

Although most contemporary Yukon grasslands occur in areas that were repeatedly glaciated during the Pleistocene (approximately 2.5 million years before present [ma BP] to 12 thousand years before present [ka BP]), at the last glacial maximum (around 21 ka BP), our study sites near Aishihik, Yukon were likely no more than 20 km from unglaciated terrain (Duk-Rodkin 1999) thereby facilitating migration of plant species from ice-free areas to present day grasslands as the glaciers retreated, even without obvious seed dispersal aids. Present-day Yukon grassland communities are comprised of some of the same species that existed in Beringia through the Pleistocene, and are taxonomically more similar in many cases to grasslands of northeastern Russia, Alaska (Strong 2018, Vetter 2000), and even Greenland where additional refugia are believed to have existed (Blinnikov 2011, Böcher 1954, Yurtsev 2001), than they are to the dry mixedgrass prairie and steppe of the Great Plains.

Over the course of the Pleistocene the relative abundance of different species fluctuated along with climatic and environmental fluctuations (Mann et al. 2015), however the presence of grazers would have remained constant meaning that during the Pleistocene interglacials present-day Yukon grasslands would have been subject to herbivory for many thousands of years. Fossil and genomic evidence indicates that mammoths and horses were quickly replaced by bison as the dominant grazer within the established large mammal community starting between 195,000 and 135,000 years ago, shortly after their dispersal from Asia (Froese et al. 2017). Bison then persisted within the Yukon until sometime between 325 and 490 years ago (the age of the youngest bison fossil found to date; Heintzman et al. 2016). Semi-feral horses (*Equus ferus caballus*) have been free-ranging in portions of the area for at least 125 years (Jung & Czetwertynski 2013), while domestic horses have added to their numbers at varying levels since the 1950's (Linaya Workman, pers. comm., June 29, 2012) making them the dominant grazer until wood bison (*Bison bison athabascae*) were reintroduced between 1988 and 1992 (Government of Yukon 2012).

Wood bison are presently designated as a species of special concern (COSEWIC 2013), and were reintroduced into the Nisling River valley of southwest Yukon in the 1980's as part of national recovery efforts for this species under its former endangered designation. The Aishihik wood bison herd's population has subsequently increased from 34 to 1,470 (including calves) (Jung & Egli 2014), and they have moved south into their present range, prompting concerns that bison may compete with other ungulates in the area, and alter these unique and rare grasslands that are considered by some to be relicts of ice age steppe vegetation (Lloyd et al. 1994, Vetter

2001, Yurtsev 2001). Thus, there is a need to understand the impact of wood bison on these grassland communities, and this knowledge gap was identified as a key management objective in the Aishihik wood bison herd management plan (Government of Yukon 2012).

Given the unique nature of native grasslands found in the Aishihik area of northwest Canada and their long-term history of grazing by large mammals, I set out to document the floristic diversity of these grasslands, with the further goal of evaluating how current bison grazing may alter this diversity. Specific objectives were to: 1) determine whether the diversity of these grasslands has changed over the last 30+ years following the recent reintroduction of wood bison, and 2) relate grassland diversity responses to indices of bison grazing intensity. Specific questions to be answered were 1) how well does Milchunas et al.'s MSL theory (1988) apply to this semi-arid northern grassland system, and 2) how do diversity responses to large mammal grazing compare with those in other North American grasslands? I hypothesize that there will be little change in diversity at low levels of bison grazing because the convergent pressures of aridity and a long history of grazing have preconditioned these grasslands to tolerate a certain amount of grazing. With increased grazing intensity, I expect diversity will begin to decrease. The results of this study have implications for balancing wood bison and grassland conservation initiatives in the region.

Materials and Methods

Study area

The study area is located in the Aishihik-Sekulman Lakes area in the southwest Yukon, Canada, situated between Whitehorse and Haines Junction within the Ruby Ranges and Yukon Southern Lakes ecoregions. It is bounded on the west by the Nisling and Ruby Ranges, to the north by Stevens Lake, to the east by the Nordenskjold River, and to the south by the Dezadeash River. It comprises approximately 3,300 km² centrally located within the Aishihik wood bison herd range (Figure 2), and falls within the traditional territory of the Champagne and Aishihik First Nations.

Study plots ranged from 705 meters above sea level (masl) in the southern portion of the study area, to 1047 masl in the north (Figure 3). Collectively, these sites fall within an area of both extensive and sporadic discontinuous permafrost (Bonnaventure et al. 2012). Forested sites near Aishihik village have an active layer that consistently measures about 70 cm deep, while on the south-facing slopes where grassland plots are found, the active layer can reach 2.2 m in depth (Burn 1995). The area was last glaciated *ca.* 22,000 yr BP (Duk-Rodkin 1999), and was subsequently covered by a large glacial lake, Lake Sekulmun–Aishihik. The morainal and glaciofluvial deposits left behind formed gently rolling topography at the north end of Aishihik Lake, which resulted in clusters of small south-facing slopes. The calcareous glacial parent

materials and cool, dry climate have led to primarily alkaline soils belonging to the Eutric Brunisol great group, with some Dystric Brunisol soils as well.

The climate in the region is influenced by both Pacific air masses from the west and Arctic air masses from the north. Because the area lies in the rain shadow of the Coast Mountains, it is one of the driest regions in the Yukon with a mean annual precipitation across the study sites ranging from 210-250 mm (Smith et al. 2004, Wang et al. 2012 [version 5.30]). Approximately half of the precipitation falls as rain during the growing season between June and August. The mean annual temperature across all study sites examined here ranged from -3°C to -5°C, with mean summer temperatures around 12°C, and mean winter temperatures of -16°C.

The region's landscape is primarily covered by a white-spruce (*Picea glauca*) dominated boreal forest, mixed with trembling aspen (*Populus tremuloides*) in younger stands on warmer sites. On poorly drained sites, white spruce mixes with willow, shrub birch and/or *Carex*, while on drier, south-facing slopes grasslands form that are the basis of this study. On these hillsides, the combination of moderate slopes (averaging 26 degrees from the horizontal) and a southerly aspect (ranging from southeast to southwest; Figure 3) results in relatively high insolation values that compound the limiting effects of the dry climate in preventing tree and shrub growth. A number of small upland *Carex* species, along with *Artemisia frigida* and *Penstemon gormanii*, dominate these slopes, while *Calamagrostis purpurascens*, *Koeleria asiatica* and *Poa glauca* are subdominant. These small pocket grasslands (typically about 1 ha in size each) within the boreal matrix occupy less than 1% of the Aishihik wood bison herd's core range (Caslys

2018), but provide important breeding habitat for American kestrels (*Falco sparverius*), Say's phoebes (*Sayornis saya*) and mountain bluebirds (*Sialia currucoides*) (Drury 1953), as well as grazing habitat for large mammals (primarily bison, horses and mule deer (*Odocoileus hemionus*)), along with small mammals [arctic ground squirrels (*Urocitellus parryii*) and snowshoe hare (*Lepus americanus*)].

Experimental design

Two approaches were used to examine vegetation diversity responses to bison reintroduction in the Aishihik area. First, I resampled 13 sites first surveyed by Mary Vetter in 1981 prior to the reintroduction of wood bison (hereafter referred to as the Vetter plots; Vetter 2000) in order to answer the question, "How has plant diversity changed since bison were introduced?" Second, I sampled the vegetation and measured levels of bison use through dung counts at an additional 57 sites throughout the present-day range of the Aishihik bison herd in order to study the relationship between bison and plant diversity across a range of environments, and assessed the comparative effect of environmental (grassland configuration, topographic and climatic) attributes and herbivory in accounting for this diversity.

Field sampling prior to wood bison reintroduction (1981)

In July 1981, 14 grassland sites located within an area of approximately 100 km² at the north end of Aishihik Lake were surveyed as part of research into the development of a

comprehensive conservation-lands plan for the Yukon (Sauchyn 1987). They were identified through black and white aerial photography (1979; 1:60,000). The 1981 site locations were recorded as UTM Grid numbers approximated from maps (NAD 27). At each site, the topographic and edaphic conditions were noted along with ecological processes (grazing, browsing, aspen forest invasion) that appeared to be affecting the stability and plant species composition of each grassland.

Within each grassland, a sampling area (approximately 10 m × 10 m) judged to be representative of the vegetation on the main part of the slope was selected, and cover was estimated for all vascular plant species occurring within each sampling area. Percent cover was measured at one strata that included all vascular plants, bryophytes and lichens; ground cover was not measured separately. Plot dimensions were not measured, nor were permanent markers left in place. In some of the grasslands, a minor community at the crest of the slope was recognized and described separately. Additional species that occurred outside the 10 x 10 m sampling area were noted (Vetter 2000; Mary Vetter, pers. comm., March 30, 2012).

Field sampling after wood bison reintroduction (2011-2017)

In July and August 2011, 13 of the 14 sites sampled prior to wood bison release were revisited (the fourteenth could not be located with any certainty). Locations were determined through a combination of the 1981 UTM grid coordinates, and site descriptions (aspect, slope, soils and vegetation). An additional 57 sites were visited between July and August 2011 and 2012 (13 in

2011, and 44 in 2012). Fourteen of these sites were revisited in 2013 to assess inter-annual variability. Grasslands visited by bison were first identified through aerial photography and consultation with conservation officers together with Champagne and Aishihik First Nation citizens and staff. They were then prioritized based on global position system (GPS) collar data collected between 2006 and 2009 from 13-15 wood bison (number varied by year). GPS collars collected an hourly location for each wood bison, with a spatial accuracy estimated at ≤ 30 m. Collar data were used to produce a map divided into a 2 km grid, with each grid square categorized according to the number of bison location points (Environment Yukon 2011). Based on the location point totals, the grid was classified into areas of high, medium and low levels of bison use. Sites were subsequently chosen to be representative of all 3 levels of usage in order to facilitate testing of differences among bison use levels. The sites were distributed among bison usage levels as follows: high (28 sites), medium (22 sites) and low (20 sites).

In order to remain consistent with the initial Vetter dataset predating bison reintroduction, at each of the 70 sites, a 10 x 10m plot was randomly established wherein vegetation was considered to be representative of the dominant vegetation community. No crest (i.e., hilltop ecotone) communities were surveyed in 2011 or 2012. Nine quadrats measuring 0.5m x 0.5m were nested within each plot to provide detailed subsampling of plant composition (Figure 4). Plots and quadrats were measured and GPS coordinates (WGS84) recorded. In 2011, spikes were left at all four corners of the 13 plots originally surveyed in 1981 to facilitate relocation at a later date.

A detailed site description of each grassland containing a plot was recorded along with evidence of herbivores and other disturbances. Wood bison and horse dung (over 10 cm in diameter), along with arctic ground squirrel burrows, were counted within the 100 m² macroplots, as well as within a 1 m buffer on all sides of the plot, to estimate use by the predominant large and small mammals in the area. Wood bison dung counts (ranging from 0 to 37) were used as a proxy for large mammal grazing intensity as they comprised the majority (> 99%) of large dung. Horse dung was not used in analysis as it was only found in 2 plots, although at 8 sites. Both at the 10m x 10m scale, as well as within all 9 nested quadrats, percent cover was estimated for two strata: 1) the vascular plant layer (including graminoids, forbs and woody plants), and 2) the ground layer (composed of bare ground, rock, litter, bryophytes, lichens and fecal pats).

Camera trap photos were used to examine seasonal grassland use, and to provide a crude estimate of bison stocking rates (McIlroy et al. 2011, O'Connell et al. 2011). In 2012 and 2013, motion-sensing cameras were placed at 5 of the sampling sites (2 per site). The cameras, which were positioned to focus on activity in the sampling plot, were able to detect movement 30m away, and operated with infrared at night. Photos taken from 2013-2017 were collected from the camera traps, and wildlife events were identified and characterized. Events were defined to start when the first animal was captured on camera and end when the last animal left. The number of bison recorded for each event was the number of bison seen in the photograph containing the most bison for an event, which was not necessarily the total number of bison present. From 2015 to 2017 the cameras were programmed to take a picture once a day in order to be able to accurately reflect effort, but this was not done in 2013 and 2014. As a result,

numbers of events do not perfectly reflect the actual plot visitation by bison, but give an approximation of trends. Monthly summaries of bison activity on the 5 sites with cameras were plotted as a series of bargraphs showing the number of bison events, the average duration of events, and the average number of bison per event (maximum number in a photograph). Univariate PerMANOVA was used to test for differences in the means between seasons using the ImPerm package in R (Torchiano 2019).

Data standardization for comparison of 1981 and 2011 data (13 plots)

Some data standardization was necessary to ensure consistency between the 1981 and 2011 data and facilitate analysis. Where the 1981 cover values were a range, the average value was used. Where a species cover value was "trace", it was given a cover value of 0.5%. Several woody species (*Juniperus communis*, *Populus tremuloides*, *Rosa acicularis* and *Sheperdia canadensis*) were included in the 1981 data sheets without cover values, but with a "***". For those data sheets with a legend, "***" meant these species occurred in moister swales and around the edges of the main slope. As a result, species listed with only "***" cover values were not included in the analysis as they were assumed to be outside of the principle grassland examined. Since bare ground was measured using different methods in 1981 and 2011, and there were inconsistencies and missing data from 1981, bare ground was not included in the analysis here.

The 2011 cover values observed at the 10m × 10m scale were used in the analysis to follow the same methodology as used in 1981. The 1981 species nomenclature followed Hultén (1968) and Scoggan (1978 – 79), while the final 2019 nomenclature followed the Database of Vascular Plants of Canada (VASCAN) (Brouillet et al 2019) and the Yukon Conservation Data Centre database (Environment Yukon 2019). Full details of species nomenclature for the purposes of analysis are included in Appendix I. Additionally, in 1981 only one upland sedge was identified, *Carex filifolia*. During 2011, five species of sedges were identified (*Carex duriuscula*, *Carex filifolia*, *Carex obtusata*, *Carex rossii* and *Carex supina*). As it is likely that most, if not all, of these species were also present on these sites in 1981, for comparative purposes the 1981 and 2011 vegetation upland sedge cover values were amalgamated into one group. Correspondence with Mary Vetter regarding *Carex* identifications (Mary Vetter, pers. comm. 2012) confirmed that these 4 *Carex* species may have been overlooked in 1981.

Data analysis

Three types of vegetation response variables were examined: plant diversity, abundance (cover), and community composition. Diversity and richness were examined using three indices calculated using the vegan package in R (Oksanen et al. 2017): richness, Hill's N1 and Hill's N2. These were calculated for all 70 plots sampled after wood bison reintroduction, as well as for the initial sampling of 13 plots prior to wood bison reintroduction. Hill's numbers, which represent the "effective number of species", or the number of equally common species required to give a particular value of an index (Hill 1973, Jost 2006), were used in order to allow

for comparison of different diversity measures. Hill's numbers are compound indices of richness and evenness that weight these components differently; Hill's N1 (exponential of Shannon-Weiner Index) is more sensitive to richness and rare species, while Hill's N2 (reciprocal of Simpson's Diversity Index) gives more weight to evenness and common species. Richness and abundance was also examined in relation to the following functional groups: graminoids (including sedges), forbs, legumes and woody plants (shrubs and trees). To more closely examine graminoid occurrence and abundance, richness and abundance were calculated separately for grasses and sedges, groups that differ in their stature and potential response to grazing within the study area.

Predictor variables to assess diversity responses were placed into eight classes corresponding to potential influences on the vegetation diversity observed within grasslands of the Aishihik bison herd range; these included grazing intensity, grassland size, elevation, insolation, temperature, precipitation, growing degree days (days over 5°C) and frost free days. See Appendix III for a full list of variables examined. Grazing intensity was assessed for both wood bison and arctic ground squirrels. Bison grazing intensity was estimated through 1) counts of bison dung (≥ 10 cm diameter) located within plots and a surrounding 1m buffer (144 m²), and 2) global positioning system (GPS) collar data collected between 2006 and 2009 from 13-15 wood bison (the exact number varied by year). The density of GPS location points per 2 km square grid corresponded to 7 incremental categories (26-50, 51-75, 76-100, 101-150, 151-200, 201-500, and 501-1662) (Environment Yukon, unpublished data). The number of ground squirrel burrows

in each plot and in the surrounding 1m buffer was used as a proxy measurement for ground squirrel abundance (and presumably ground squirrel grazing).

The spatial attributes examined (size class) included the area, perimeter, and ratio of area to perimeter, for each grassland containing a plot. Grassland area and perimeter were calculated in ArcMap 10.3 (ESRI 2014) from grassland polygons digitized from high resolution digital air photos (pixel size of 0.5 m) (Government of Yukon 2013). The ratio of area to perimeter was chosen as a predictor variable to examine edge effects, with a larger ratio hypothesized to lead to less edge effects and a corresponding influence (direct, or indirect via bison use patterns) on vegetation diversity. Elevation of each plot was recorded by GPS (Garmin eTrex Summit HC).

Climate variables (temperature, precipitation, growing degree days [days over 5°C], and frost free days) were derived using ClimateWNA ver5.30 (Wang et al. 2016). All values are 10 year averages (2001-2010). Annual and seasonal averages were calculated for temperature, precipitation and insolation values. Seasons for all analysis were defined based on local grassland phenology: spring: April-May; summer: June-August; fall: September-October; and winter: November-March. Monthly insolation values were calculated for 2012 using ArcMap 10.3 (ESRI 2014) using a 16m resolution digital elevation model (DEM). Two additional insolation indices were calculated: a heat load index (HLI) and a site severity index (SSI). The HLI was computed by rescaling aspect along the northwest-southeast line and transforming the data so the warmest aspect (SW or 225°) equated to 1, and the coldest aspect (NE or 45°) equated to 0 (Beers et al. 1996; as cited in Moody 2006). The SSI combines slope and aspect to

provide an insolation index that ranges between -2 (steep northeast slopes) and +2 (steep southwest slopes) (Beers et al. 1966). Aspect and slope were also considered to be insolation variables. Aspect was examined both as a continuous variable (degrees) and as a categorical variable (5 categories: east, southeast, south, southwest and west).

To identify those predictor variables that had a significant relationship with grassland plant diversity and community structure (i.e. the variables to be used in further analyses), Spearman correlations were run between all 85 response variables and all 87 predictor variables using the Hmisc package in R (Harrell 2016). Non-parametric correlations were used to account for the non-normal distributions of community data. Based on the correlation results, certain variables were omitted from further analysis due to redundancies. Monthly climate and insolation variables were excluded in favour of seasonal averages as they more concisely reflected the same results. Similarly, frost free days and degree days above 5°C were not used in further analysis as they reflected the same patterns evident in correlations with temperature. Legumes and woody species occurred in such small quantities that their abundance (and associations with diversity) were not considered an accurate reflection of ecological processes, and therefore were not used as response variables in further analysis. Only those variables to be used in further analysis are included in Tables 9 and 10.

To address the possibility that climate change may have played a role in vegetation changes since bison reintroduction, mean annual precipitation and temperature (MAP & MAT) were derived for all plots for all years from 1975 to 2012 using ClimateWNA ver5.30 (Wang et al.

2016). The sampling plot values were then averaged for each year and plotted in order to visualize trends (Figure 8).

Data analysis of Vetter sites: sampling pre- and post- bison reintroduction (1981 & 2011)

All three diversity indices were tested for normality and the Hill Indices were found to be non-normal with heterogenous variance. As a result, a univariate Permutational Multivariate Analysis of Variance (PerMANOVA; Torchiano 2019) based on a Bray-Curtis distance metric was used to test for differences in species diversity and functional group abundance before (1981) and after (2011) wood bison reintroduction ($\alpha < 0.05$). Similarly, multivariate PerMANOVA based on a Bray-Curtis distance metric was used to test the hypothesis of no difference in species composition between the two years (groups) ($\alpha < 0.05$). PerMANOVA is a non-parametric procedure for evaluating differences between two or more groups of entities that accommodates the variable distributions found in community data; a total of 999 permutations were run using the vegan package in R (Oksanen et al. 2017). Compositional change between 1981 and 2011 was also assessed by calculating a Sorensen dissimilarity index from species occurrence data for each plot using the betapart package in R (Baselga 2017).

An Indicator Species Analysis was used to determine the specific identity of those plant species preferentially associated with vegetation coinciding with periods sampled prior to and after the reintroduction of wood bison. An Indicator Value (compound index based on both exclusivity and fidelity) was calculated for each species for each sampling interval using the indicpecies

package in R (De Cáceres and Jansen 2016). In accordance with the method of Dufrêne and Legendre (1997), once the year corresponding to the highest association value of each species had been identified, 999 permutations were run to determine the statistical significance of the relationship ($\alpha < 0.05$). All statistical analyses were conducted using R version 3.3.3 (R Core Team 2017). Univariate PerMANOVAs were used to test for differences in abundance between years for species of particular interest using the *lmPerm* package in R (Torchiano 2019).

The strength and direction of plant community compositional change over time was assessed using a 2-dimensional non-metric multidimensional scaling ordination (MDS), plotted with principal components axes rotation, centering and half-change scaling so that the configurations were easier to interpret. A Wisconsin double standardization of a square root transformation of the community data was performed prior to performing the MDS.

Compositional dissimilarity of species cover was assessed using the Bray-Curtis distance measure. Twenty random starts were run to find a stable solution using the *vegan* package in R (Oksanen et al. 2017). Successional vectors plotted on the ordination were used to visualize patterns in the relative magnitude (as represented by vector length) and direction of plant community change over time (i.e., from 1981 to 2011) for each plot. Environmental and species vectors were fitted onto the ordination using the *vegan* package in R (Oksanen et al. 2017). The significance of fitted vectors that best correlated to the community dissimilarity matrix was then assessed through 999 permutations, and only those vectors with alpha values less than 0.05 were plotted on the MDS ordination.

Data analysis of sites sampled post- wood bison reintroduction (2011-2013)

The variables identified through Spearman correlations as being of interest for further analysis were included in linear mixed effects models to analyze the relationship of vegetation diversity and abundance (cover) to bison grazing intensity and environmental covariates. Location was used as a random factor to account for spatial autocorrelation among plots grouped together near helicopter landing sites, and maximum likelihood estimation was used to compare alternative models with differing numbers of fixed explanatory effects. All environmental variables were standardized into Z-scores due to widely varying scales. Analyses were conducted using the nlme package in R (Pinheiro et al. 2017). Residuals were examined to ensure normality and homogeneity of variance. A square root transformation was performed on *Carex* and grass abundance (i.e., cover) to reduce heteroscedasticity.

For each response variable, univariate linear mixed effects models were used to identify the predictor variable with the best fit (lowest AICc) within each predictor class for inclusion in multiple variable mixed effects models. The corrected Akaike Information Criterion (AICc) was used given the small sample size ($n=70$) relative to the number of parameters (Burnham and Anderson 2002). In most cases, only one variable from each predictor class was included in the same multiple regression model as they are measures of the same environmental characteristic. The two exceptions were: 1) the insolation predictor class; aspect and slope are independent variables that can be used in the same model, as they are when insolation indices

(a composite of aspect and slope) are incorporated into a model, and 2) the grazing predictor class which includes wood bison and arctic ground squirrel metrics.

Using the best fit predictor variables identified through the univariate mixed effects models, a suite of multiple variable mixed effects models for each measure of diversity and functional group abundance (i.e., cover) was developed according to the following criteria. First, the global model incorporating the variables of best fit for each predictor class was created. To avoid over-parameterization, when both categorical predictor variables were included in the global model, it was replaced by two new models, each incorporating one of the categorical variables along with the continuous variable of next best fit for the predictor class of the other categorical variable. When the fit of all seasonal variables within a predictor class was very similar ($\Delta AICc < 2$), making conclusions regarding the influence of one season over another uncertain (Burnham and Anderson 2002), then the annual average or total was used to avoid unsubstantiated inferences regarding the effect of seasonality for that environmental characteristic.

After the initial analysis of the multiple variable models (using Pinheiro et al.'s nlme package in R (2017)), if the regression coefficients of the predictor variables were found to be correlated ($|r| > 0.6$), then the model was adjusted as follows: 1) When the regression coefficients of bison dung counts were correlated with those of slope, two new models were created: one without bison dung counts but with slope, the other with bison dung counts and the best fit composite insolation index replacing slope and aspect. 2) Since the regression coefficients of elevation and temperature were highly correlated in all models, and the model fit for elevation was very

similar to that of temperature ($\Delta AICc < 2$), only one of the two variables was required; in this situation temperature, rather than elevation, was chosen as it directly effects plant growth. 3) When the regression coefficients of temperature and precipitation were correlated, two new models were built, one with temperature and the other with precipitation. Modification of the global model for each measure of plant diversity and abundance resulted in a varying number of adjusted global models for each response variable (Appendix IV).

Finally, ANOVA (R Core Team 2017) was used to calculate an F-statistic to test the predictive significance of each variable within each adjusted global mixed effects model ($\alpha < 0.05$). The MuMIn package in R (Bartoń 2018) was used to generate all possible combinations of the terms in the adjusted global models. The resulting matrix of ranked models and their component variables was examined for patterns in the AICc as variables identified as significant in the adjusted global models were eliminated or added. As a result, a list of candidate models for each response variable was created that included a) the best fit models of all possible models ($\Delta AICc < 2$), and b) the best fit model that excluded each significant predictor variable (as determined in the adjusted global model). Model-averaged coefficient estimates were then calculated for the most supported ($AICc < 2$) mixed effects models for each diversity and abundance response variable using the MuMIn package in R (Bartoń 2018).

The relationship of rare species to bison, plant functional groups and diversity was assessed using a 2-dimensional non-metric multidimensional scaling ordination (MDS), plotted with principal components axes rotation, centering and half-change scaling so that the

configurations were easier to interpret. A Wisconsin double standardization of a square root transformation of the community data was performed prior to performing the MDS. Compositional dissimilarity of species cover was assessed using the Bray-Curtis distance measure. Twenty random starts were run to find a stable solution using the vegan package in R (Oksanen et al. 2017). Environmental vectors were fitted onto the ordination using the vegan package in R (Oksanen et al. 2017). The significance of fitted vectors that best correlated to the community dissimilarity matrix was then assessed through 999 permutations, and only those vectors with alpha values less than 0.05 were plotted on the MDS ordination.

Results

Comparison of vegetation pre- and post- wood bison reintroduction (1981 & 2011)

Bison dung was found in every plot but one when sampling the Vetter plots in 2011, approximately 21 years after bison reintroduction. The median number of pieces of dung > 10 cm diameter found in each plot was 3 (IQR=4), with a maximum of 15 pieces of dung found in one outlier plot. Given this, the abundance of bison dung was considered to provide a reasonable metric to assess bison presence, and potentially their impact on plant diversity and abundance measures in 2011.

Forty-five different vascular plant species were detected in total over the two years of sampling, including pre (1981) and post (2011) bison reintroduction. This included 15

graminoids, 27 forbs and 3 shrubs/trees when all individual *Carex* determinations were included. Amalgamating all upland sedges (i.e. treating them as one species) reduced the number of species detected to 41, including 11 graminoids. Unless otherwise noted, in all further discussion of species occurrence, all sedges were considered one “species” in order to compare datasets from before and after wood bison reintroduction. Of the 41 species, 38 were detected in 2011, and 30 were detected in 1981, but the number of species occurring in more than one plot (25) was the same between years (Table 1 provides a summary of species occurrence and abundance between years). Three species were found exclusively prior to bison reintroduction, while 11 species were detected for the first time after (species detected in only one of the two survey years are listed in Table 2). Of the 11 species found only in 2011, 8 were found in a single plot, as was one of the 3 species unique to 1981. A Permutational Multivariate Analysis of Variance (PerMANOVA) indicated that 8% of plant compositional variance among plots was explained by the difference between sampling periods ($R^2 = 0.08$, $p = 0.04$).

The median cover for all functional groups (forbs, graminoids and woody species) was greater after bison were reintroduced than before, as was species richness (Table 1). The richness of woody species present increased 3-fold from 1 to 3, though the three species present still only accounted for a small percentage of total cover ($\leq 5\%$). Forbs accounted for the greatest change in species occurrence after bison reintroduction, although there was only an 18% rise in the median cover of forbs per plot relative to the median cover in 1981, while the median cover of graminoids rose proportionally by 73% (Figure 5). This reflects the fact that 20 forb species accounted for a median plot cover of 17.5% (IQR = 4) in 1981, while only 9 graminoid species

accounted for roughly the same cover (16.5%, IQR = 17.5) in the same year. The number of graminoid species (11) relative to the median graminoid cover (28.5%) in 2011 was even more disproportionate. The interquartile ranges also show the greater variability in abundance of graminoids compared to forbs. A univariate PerMANOVA showed no significant difference in forb ($F = 0.43$, $p = 0.84$) or graminoid ($F = 1.58$, $p = 0.22$) cover between years (Table 3).

Dividing graminoids further into carices and grasses revealed that the majority of the variability in cover of graminoids, both spatially within each year and temporally between years, was due to the carices (Figure 5). Grass cover remained almost the same between 1981 (6.5%, IQR = 6) and 2011 (7.1%, IQR = 4.6), and variability within each year remained relatively low as demonstrated by the interquartile ranges. On the other hand, the median cover value for carices in 2011 (20%, IQR = 14.3) was more than twice as high as the median value in 1981 (7.5%, IQR = 13). According to a univariate PerMANOVA of *Carex* abundance, there was a significant difference between years ($F = 20.2$, $p \leq 0.001$), unlike grasses ($F = 0.75$, $p = 0.40$) (Table 3).

While not consistent among all plots, the MDS ordination of plant community composition (stress = 0.182) exhibited a weak trend in the directionality of compositional change, as seen in the successional vectors drawn on the ordination depicting changes pre- and post- bison reintroduction (Figure 6). When a suite of diversity, site and environmental variables were fitted to the ordination to assess relationships between the strength and direction of this change and predictor variables, the following factors were found to have a significant ($\alpha < 0.05$)

relationship with the ordination space: elevation ($r^2 = 0.28$, $p = 0.02$), richness ($r^2 = 0.30$, $p = 0.02$), Hill's N1 diversity index ($r^2 = 0.40$, $p = 0.003$), Hill's N2 diversity index ($r^2 = 0.31$, $p = 0.009$), shrub/tree cover ($r^2 = 0.49$, $p = 0.001$), legumes ($r^2 = 0.24$, $p = 0.04$) and grassland size ($r^2 = 0.49$, $p = 0.003$) (Figure 6.a).

According to the overlain vectors depicting compositional change between pre- and post- bison sampling periods, 6 of 13 plots displayed a trend towards decreasing diversity (as measured in richness and Hill's 2 diversity indices) and decreasing elevation (see green vectors; Figure 6). Additionally, the two plots (1 and 4) that exhibited the greatest compositional change, as shown by their greater length (falling outside the standard deviation of the mean of the successional vector lengths), displayed a distinct positive relationship with increasing woody plant (shrub and tree) abundance, and a moderately negative relationship with grassland size and diversity (richness, Hill's N1 and Hill's N2). Sorensen's dissimilarity indices for all plots indicated that of the 13 plots, Plot 1 ($\beta_{\text{SOR}} = 0.43$) and Plot 4 ($\beta_{\text{SOR}} = 0.39$) exhibited the greatest dissimilarity between the 1981 and 2011 sampling times.

While there was no significant relationship between wood bison dung counts and the ordination space, it is important to remember that dung was found in every plot but one when sampling after bison reintroduction. Another environmental covariate not represented in the MDS, climate change, did not exert a significant effect on plant community composition based on interpolated temperature and precipitation values for sampling plots derived using ClimateWNA ver5.30. Mean annual temperature and precipitation showed no significant

change between 1975 and 2012 ($r^2 = 0.01$, $p = 0.54$, and $r^2 = -0.01$, $p = 0.43$, respectively) ($\alpha < 0.05$) (Figure 8).

Vascular plant species vectors were fitted to the MDS ordination of community composition, and species with statistically significant ($\alpha < 0.05$) relationships with the ordination space are displayed in Figure 6b. *Arctostaphylos uva-ursi* ($r^2 = 0.33$, $p = 0.04$), *Rosa acicularis* ($r^2 = 0.49$, $p = 0.002$) and *Populus tremuloides* ($r^2 = 0.34$, $p = 0.02$) vectors all had a significant relationship with the ordination. They are the woody species strongly associated with the trend towards shrubs and trees within plots exhibiting the greatest compositional change.

Indicator species analysis identified only 10 of 41 species as more strongly associated with the sampling period pre- bison reintroduction or the sampling period thereafter. The remainder of species were either only found in one plot (10 species), or showed no temporal association (21 species; Table 4). Most (8 of 11) graminoids were strongly associated with the combined dataset, with 2 found in only one plot in 2011 (*Anthoxanthum hirtum* and *Hordeum jubatum*), and one had a statistically insignificant association with 2011 (*Elymus trachycaulus* ssp. *subsecundus*). Woody species were either associated with 2011 (*Rosa acicularis* and *Populus tremuloides*), or found in only one plot in 2011 (*Arctostaphylos uva-ursi*). Forb species were well represented in association with 1981, 2011, and the data set from both years. *Anemone patens* was the only species identified as a significant indicator of year, and that was for 1981 ($\alpha = 0.05$).

Five species listed as critically imperiled to vulnerable (S1-S3) by the Yukon Conservation Data Centre (Environment Yukon 2017) were found in the 13 plots sampled: *Eremogone capillaris* var. *capillaris* (S3, N5, G5), *Eriogonum flavum* var. *aquilinum* (S1, N1, G5T2), *Koeleria asiatica* (S2S3, N2N3, G4), *Phlox hoodii* (S3, N5, G5) and *Phlox richardsonii* (S3, N3, GNR) (for details on the conservation status rankings in brackets see Tables 5 and 6). *Draba yukonensis* (S2S3, N2N3, G2G3), a tiny, inconspicuous plant, was found a meter from one plot, and may also grow within that plot yet remained undetected. All rare species found in 1981 were also found in 2011, although 6 of the 17 observations of rare species in Vetter's 1981 plots were not found in the same plot 30 years later in 2011. Notably, in all of these cases, these species were observed elsewhere in the same grassland. All *Phlox* were identified as *Phlox hoodii* (S3, N5, G5) in 1981, while all *Phlox* found in Vetter's plots in 2011 were identified as *Phlox richardsonii* (S3, N3, GNR). Due to uncertainty around the 1981 identifications, these two species are considered as one species in determining whether *Phlox* recurred within the same plot in 2011. Further details can be found in Tables 3 and 4. While *Koeleria asiatica* is considered imperiled/vulnerable in the Yukon, it is a subdominant species within these 13 grasslands.

Almost all species found on these grasslands in both 1981 and 2011 are considered to be increasers under grazing (Bailey et al. 1992, Tannas 2003) in Alberta and/or the Yukon. The few species known to behave as decreasers (i.e., decline in response to increasing large mammal herbivory), at least in some situations, showed no significant difference between the initial and final sampling periods representing pre- and post- wood bison introduction sampling years, according to univariate PerMANOVAs; *Bromus pumpeilianus* ($F = 0.44$, $p = 0.52$), *Calamagrostis*

purpurascens ($F = 0.54$, $p = 0.47$), *Elymus trachycaulus* ssp. *subsecundus* ($F = 0.02$, $p = 0.90$), and *Astragalus australis* only occurred in 2011. The dominant species, *Artemisia frigida* and *Carex* spp. (i.e., short upland sedges strongly dominated by *Carex duriuscula* in 2011, and also containing *Carex filifolia* and *Carex supina* in moderate quantities; in 1981 *Carex filifolia* was the only *Carex* identified) are all increasers that are highly adapted to grazing and often considered to be indicators of overgrazing.

Relationships between bison and plant community diversity and abundance (2011-2013)

Spearman correlations (Table 9), univariate linear mixed-effects models (Figure 10) and model-averaging of the top linear mixed effects models ($\Delta AICc < 2$) (Table 13) indicated a strong and significant ($\alpha < 0.05$) positive relationship between bison dung counts and all diversity measures, particularly richness ($\beta = 2.55$, $p < 0.0001$). Unless otherwise specified, bison ‘abundance’ refers to dung counts within regression models. Richness also showed a significant negative relationship with the ratio of area/perimeter ($\beta = -1.67$, $p \leq 0.005$); with increasing grassland edge relative to area, plant richness increases. Univariate regression models (Table 11) showed a significant negative relationship between plant community metrics (richness, diversity, cover) with slope ($\beta = -2.52$, $p < 0.0001$) and Site Severity Index ($\beta = -1.14$, $p = 0.04$). Slope was not included with bison in the same candidate models because a strong negative correlation between bison and slope introduced collinearity, and because the $\Delta AICc$ of candidate models with slope but not bison was greater than two, indicating limited benefits of including slope along with bison use. However, the best fit multiple variable model without

bison or slope showed a dramatic rise in AICc from the best fit model when containing slope but excluding bison (from 400.44 to 419.75), indicating that slope independent of bison also had a strong relationship with richness (Table 12).

Model averaging indicated a positive relationship between Hill's N1 and Hill's N2 and bison ($\beta = 1.02$, $p < 0.005$; and $\beta = 0.73$, $p < 0.005$, respectively), as well as a negative relationship with grassland area ($\beta = -0.71$, $p = 0.02$; and $\beta = -0.57$, $p = 0.03$) (Table 13). Hill's N2 also showed a significant negative relationship with summer precipitation (June-August) ($\beta = -0.90$, $p = 0.01$).

Forb cover showed a significant positive relationship with bison ($\beta = 3.44$, $p < 0.005$) (Figure 11), and while no other covariates were significant under model averaging, univariate regression indicated a significant positive relationship of forb cover with September-October precipitation ($\beta = 2.76$, $p = 0.03$) (Table 11).

Graminoid cover, and its component, grass cover, showed a positive relationship with arctic ground squirrels according to model averaging ($\beta = 0.33$, $p = 0.03$, and $\beta = 0.39$, $p < 0.005$, respectively). Graminoids also had a positive relationship with bison ($\beta = 0.36$, $p = 0.02$) (Figure 11), but a negative relationship with slope ($\beta = -0.37$, $p = 0.01$), as did grasses ($\beta = -0.36$, $p = 0.01$) (Table 13). The other component of graminoid cover, upland Carex cover, showed no significant relationship with grazing or other environmental covariates according to both model averaging and univariate regression. Additionally, the null model was one of the top candidate

models ($\Delta\text{AICc} < 2$) indicating that the environmental variables under investigation explained negligible variance in *Carex* cover.

Comparison of 2011 and 2013 data using PerMANOVA showed no significant difference between the two years ($R^2 = 0.30$, $p = 0.97$) suggesting that interannual variability was unlikely to influence the model results.

Camera traps at 5 sites (10 cameras total) captured a total of 263 bison events over 5 years (Figure 7). Forty-one percent of those events occurred in the fall (September–October), 24% in spring (April–May), 29% in summer (June –August), and the remaining 6% during the 5 months of winter (November–March). Grassland visitation by bison was very low through the winter months (November to March) and in June during the calving season. The average number of bison visible per imaging event overall was 3.6, which compared to 2.6 animals during the fall. On average, bison stayed on the sampling sites within the view of cameras for 3.8 minutes per event. During summer this duration dropped to 2.7 minutes, while in winter the average stay was 5.8 minutes. While there was a significant difference in the mean number of bison visible per event and the mean duration of each event across all seasons ($F = 4.71$, $p < 0.005$, and $F = 3.17$, $p = 0.03$, respectively), there were no significant pairwise differences in the duration of bison events detected between seasons. On the other hand, the number of bison per detection event during fall was significantly less than the number during both spring and summer ($p = 0.01$) (Table 14).

With the additional 57 plots sampled in 2011-12 along with the 13 Vetter plots in 2011 (total n=70), the number of forb species observed across all sampling plots in 2011 and 2012 more than doubled from 24 to 55, while only one additional graminoid species was found. Of the 55 forb species documented, only 19 occurred in >10% of the plots (Table 7). Despite the vastly different species richness of forbs and graminoids, the median cover/plot for each growth form was similar: 24.1% (IQR=12.48) for forbs and 21.5% (IQR=18.7) for graminoids. Carices accounted for a greater proportion of graminoid abundance than grasses on average; the median cover per plot for *Carex* spp. was 11.1% (IQR=14.68), while for grasses it was 7% (IQR=10.05). The number of woody species and legumes found overall doubled from 3 to 6 with the larger sample size, but the median vascular cover per plot remained very low: <0.05% (IQR=1.38) for woody species and 1% (IQR=2) for legumes. Woody species were only found in 29 plots, but legumes occurred in 51 plots (largely due to the dominant species, *Oxytropis splendens*).

Five dominant and 6 subdominant species were identified (Table 15) based on the following criteria. Dominant species (dom) are those that occurred in ≥ 35 plots (50%) and had a mean cover > 2.5%. Subdominant species (subdom) are those that occurred in ≥ 6 plots (35%) and had a mean cover > 2%. Collectively, 4 short upland sedges dominated the grasslands sampled: *Carex duriuscula* (dom), *Carex filifolia* (subdom), *Carex obtusata* (subdom) and *Carex supina* (subdom). Grasses were represented by *Calamagrostis purpurascens* (dom) and *Poa glauca* (subdom). The sum of the average cover per plot of the dominant and subdominant sedges was 24.5%, while that of grasses was 6.2%, and that of forbs was 23.6%. The most dominant forb

was *Artemisia frigida*, which occurred in the most plots and had the greatest average cover per plot of all species.

Nine rare species were found in the 70 100 m² vegetation plots sampled in 2011 and 2012 (Table 8). These critically imperiled to vulnerable species (S1-S3) occurred variably across 20 plots. Four plots contained 3 of these species, while there were 8 plots containing 2 species and 8 plots with one species. Six of these plots held locally critically imperiled or imperiled species (S1-S2), specifically *Comandra umbellata*, *Eriogonum flavum* var. *aquilinum* and *Geum triflorum*. The MDS ordination of plant community composition for 2011-2012 (stress = 0.193) exhibited a clear and positive relationship among rare species, richness, diversity and bison (Figure 9). The following factors (vectors) were all found to have a significant ($\alpha < 0.05$) relationship with the ordination space: bison dung counts ($r^2 = 0.37$, $p = 0.001$), richness ($r^2 = 0.84$, $p = 0.001$), Hill's N1 diversity index ($r^2 = 0.62$, $p = 0.001$), Hill's N2 diversity index ($r^2 = 0.49$, $p = 0.001$), graminoids ($r^2 = 0.13$, $p = 0.01$), grasses ($r^2 = 0.28$, $p = 0.001$), legumes ($r^2 = 0.10$, $p = 0.03$) and shrub/tree cover ($r^2 = 0.16$, $p = 0.001$) (Figure 9).

Discussion

Has plant diversity changed since wood bison were reintroduced?

Comparison of vascular plant richness, diversity and composition at the Vetter sites pre- and post- wood bison reintroduction showed very little change: neither Hill's N1, Hill's N2 nor

richness showed any significant alteration. The number of species found overall did increase slightly, however all species but one are more closely associated with both years than with either pre- or post- bison vegetation communities. This indicates there were no clear shifts in the species composition with the introduction of wood bison. The major components (i.e., the more common species) of these grassland communities have remained relatively stable as predicted by Milchunas et al. (1988) for a semi-arid plant community with a long evolutionary history of grazing. Similarly, Adler et al. (2005) found no effect of grazing at the plot scale in both sagebrush and Patagonian steppe ecosystems. Notably, in none of these systems was a decrease in diversity observed due to the loss of less grazing tolerant rare species, which was inconsistent with Milchunas et al.'s MSL theory (1988). Instead, these semi-arid systems appear resistant to the effects of grazing likely due to the convergent selection pressures of aridity and historical grazing.

While there was no significant change in diversity overall, the 8% of variability in community composition explained by changes between the two sampling periods pre- and post- wood bison reintroduction included a significant increase (> 2x) in the abundance of upland carices, the dominant species initially found within these grasslands. Because these communities are composed of plant species well adapted to grazing, composition has shifted based on changes among functional group abundance, rather than through species diversity responses. Being well-adapted to grazing, upland carices are increasers under moderate grazing pressure, and may also be indicators of overgrazing in some situations (Tannas 2003, Bailey et al. 1992). The dramatic increase in their abundance may be due to the morphological traits they possess that

help them withstand, or quickly recover from, grazing: these include a high ratio of vegetative to reproductive shoots, abundant rhizomes, low growth form, and apical meristems capable of quick regrowth following defoliation.

While this study was not intended to study functional diversity, and no measurements were made of functional traits specifically, plant growth form has been frequently used as a trait in studies of functional diversity (Adler et al. 2004, Nathan et al. 2016). This was also the case in a plant removal experiment conducted in Yukon grasslands approximately 70 km to the west of the Vetter study sites (McLaren & Turkington 2010, 2011). McLaren & Turkington (2010, 2011) chose forbs, graminoids and legumes as functional groups to manipulate based on traits that could be relevant to important ecosystem properties (e.g., C:N, stature, N-fixation ability). They found that, even though forbs dominated the plant community (similar to the Aishihik grasslands), graminoids (*Carex duriuscula* and *Poa glauca* being the dominant species) had the greatest impact on ecosystem functioning, with their removal causing an increase in soil moisture and soil nitrogen, as well as a decrease in phosphorous. While the increase in *Carex* abundance at Aishihik between 1981 and 2011 may be due to morphological adaptations to grazing, nitrogen inputs into the soil by grazers (predominantly wood bison) may also be preferentially encouraging *Carex* growth. The addition of nitrogen to soils by bison is known to strongly influence plant community structure, as in Yellowstone National Park (Knapp et al. 1999), and preferentially encourage graminoid growth in some cases (Turkington et al. 2002, Dormann & Woodin 2002).

While there was no significant change in temperature or precipitation according to interpolated sampling plot values (1 km cell size), this contradicts existing research into climate trends in the Yukon (Streicker 2016). A report specific to the Aishihik area used Scenarios Network for Alaska and Arctic Planning (SNAP) projection data (2 km cell size) to gauge present and future changes in climate (Horton 2017). Under the most conservative representative concentration pathways, the increase in temperature between the 1961-1990 mean (pre-bison to 1988), and the projected 2010-2019 mean, will be 1.35°C at Aishihik Village in the centre of the Aishihik wood bison herd range. Overall, annual precipitation is projected to increase as well, although not as consistently over time and emissions scenarios. In the Arctic, increased nutrient availability is projected to be one of the most important drivers of vegetation change under a warming climate (Dormann & Woodin 2002, McLaren 2010). Grasses and graminoids are known to respond quickly to increased nutrient availability (Turkington et al. 2002), however it is less clear how carices will respond, and it does vary by species (Shaver & Chapin 1980). Inconsistent with this theory, the upland carices surveyed in my study also showed a significant negative correlation with interpolated temperature values, however the interpolated values, themselves, are inconsistent with most climate models for the Aishihik area.

This then raises the question, are carices responding to bison grazing, nitrogen inputs by grazers, other environmental covariates, or are differences in sampling methodologies between years responsible for their increased abundance? In 2011, best efforts were made to revisit the same sites and resample the same plots initially measured in 1981 based on the site information and coordinates available (UTM Grid numbers taken from maps). While we can be

sure the right grassland was visited, without the precision of GPS coordinates we cannot know how precisely the exact 2011 plot locations corresponded to the 1981 plots. Additionally, surveying 9 quadrats within each plot in 2011 meant the sampling effort was greater, which could account for differences in diversity and abundance measures, as could different observers. Given these caveats surrounding the comparison of pre- and post- bison reintroduction sampling of Vetter's plots, greater emphasis was placed on the incorporation of a number of grazing indices for wood bison and arctic ground squirrels into the contemporary vegetation sampling.

Wood bison

Grazing was the single most important variable explaining plant diversity and abundance that I found in regression models developed using the contemporary grassland dataset. The positive relationship with bison grazing intensity (as represented by bison dung counts) exhibited by all diversity measures, was contrary to Milchunas et al.'s (1988) prediction of a small decrease in diversity as grazing intensity increased, and contrary to the results of the comparison of the Vetter sites plant abundance pre- and post- bison reintroduction. However, response patterns are ecosystem dependent as Milchunas, himself, recognized (Milchunas & Lauenroth 1993). Scale is an important, and related, aspect of diversity (Adler et al. 2005, Wilson et al. 2012). The increased sample size of the contemporary dataset (n=70 compared to 13 Vetter sites) encompassing a much large geographical area (approximately 3,300 km² compared to approximately 100 km²) examines diversity at a more regional scale, while the Vetter sites are

much more localized and therefore likely to be quite similar. Previous studies indicate that different patterns emerge at different resolutions: at finer scales niche-related variables are important, while disturbance-associated variables and heterogeneity are drivers of diversity at coarser scales (Turtureanu 2014). With this in mind, along with questions regarding the consistency of sampling methodologies between years in the Vetter plots, it becomes clear that the larger contemporary dataset, and analysis, is likely more reliable for drawing conclusions regarding the impact of bison grazing on grassland diversity.

Milchunas et al.'s (1988) Generalized Model of Effects of Grazing by Large Herbivores (MSL) assumes that the primary driver of compositional change is competition. However, there is much debate about whether competition is a primary driver of changes in diversity in nutrient poor environments. Nathan et al. (2016) found that the effects of grazing on diversity are mitigated by regional soil and climate patterns in arid systems, while Mitchell et al. (2009) found that intense competition was not important in structuring subarctic alpine plant communities such as those in southwest Yukon. Callaway et al. (2002) found that there were more facilitative interactions among plants in colder climates, and more competitive relationships in warmer climates. On the other hand, biomass compensation following experimental removals of vegetation from McLaren and Turkington's (2010, 2011) nearby study plots indicate that competition is an important explanatory mechanism in structuring the Kluane Lake grasslands. So why did grassland vascular plant diversity on the Aishihik grasslands increase as wood bison presence increased?

Forbs are the driver of diversity in these forb-dominated grasslands, accounting for 71% of total species richness between 2011 and 2013. Moreover, diversity responses to bison exhibited a positive relationship, and likely reflect forb increases with bison presence. While there are more than 3 times the number of forb species (55) than graminoid species (16) in my plots, these two functional groups had very similar median cover values per plot (24.1% and 21.5% respectively). Despite being the dominant group in these communities, Jung et al. (2015a) found that forb species comprised less than 5% of the diet of wood bison in the Aishihik herd (as determined by scat analysis; Table 16). Instead, graminoids are the primary forage for bison of the Aishihik herd, comprising approximately 90% of their diet both during summer and winter, with a much larger proportion of sedges and rushes than grasses, particularly in winter (Table 16). This raises the possibility that diversity is increasing because bison preferentially graze on graminoids, thereby providing competitive release of forbs. This would allow the latter to expand, and include new, often weedy and/or invasive, species.

Interestingly, I found only trace amounts of two weedy species on the Aishihik sites in this study, meaning that there was a very limited pool of invasive annual forbs prepared to take quick advantage of any competitive release afforded by bison grazing in this ecosystem. This is unlike North American grasslands to the south, where invasive, disturbance-adapted species are known to frequently be responsible for increases in diversity at intermediate levels of grazing, as described by Milchunas et al. (1988) in the MSL model. In addition to the above, clearly contradicting the idea that the increase in forb abundance with increasing bison is due to competitive release, is the fact that bison exhibited a positive relationship with graminoid

abundance as well, consistent with the large rise in *Carex* abundance in the Vetter plots following wood bison reintroduction.

Three main factors responsible for graminoid responses to grazing are: grazing intensity, duration of grazing, and seasonality (Trlica 2006). Camera trap photo analysis (Figure 7; Canadian Wildlife Service, unpublished data) and microhistological dung analysis (Jung et al. 2015a, unpublished data; Table 16) allow an examination of these factors and a more detailed look at bison usage of the Aishihik grasslands. How much of their time are bison spending on these grasslands, and how much of that time is actually spent grazing? Plant species identified in bison dung were used to determine where bison were grazing, and to gain a rough picture of the relative amount of time they spent in different habitats. While carices were not identified to species in the dung analysis of 2009/2010 (Jung et al. 2015a), dung collected in March 1998 (Jung 2015c) contained fragments of 9 identified species of *Carex*, of which only one (*Carex supina*) was a species found on the grasslands of south-facing slopes. *C. supina* accounted for approximately 5% of the *Carex* fragments. The only other two grassland species identified in dung samples, and occurring in more than two samples (at levels above trace amounts), were *Calamagrostis purpurascens* (more prevalent in summer and fall dung samples) and *Artemisia frigida* (found only in late winter and fall dung samples) (T.S. Jung, unpublished data). While there is no summer dung analysis identifying *Carex* to species, which would allow a clearer view of how much of their diet is coming from the Aishihik grasslands since that is when they graze there, the existing dung analysis suggests that these grasslands may provide up to 30% of their diet in the summer months. Collectively, these results indicate that bison are grazing on these

slopes and not just passing through. Moreover, although the bulk of their diet may be coming from wet sedge meadows, even in summer (Jung et al. 2015a, b, unpublished data), the small area of upland grasslands present in these landscapes, coupled with their low biomass productivity, may lead to relatively high impacts of bison while grazing within them. Further study quantifying the intensity of biomass removal within these grasslands would be advantageous.

Johansen et al. (1989) found that there was fair grazing potential (275 kg/ha) on dry grassland slopes (*Arctostaphylos uva-ursi/Calamagrostis purpurascens* communities) in the Kluane area (including one study site at Aishihik Lake), and in associated grassland parkland complexes (*Artemisia/Festuca saximontana* and *Carex obtusata/Anemone patens* communities) (450 kg/ha). In contrast, wet sedge meadows dominated by *Carex aquatilis* and *Calamagrostis canadensis* had much greater productivity (620 kg/ha). This explains why wood bison were originally released into the upper Nisling valley (to the north of their present day range; Reynolds 1982), an area dominated by wet sedge meadows with abundant forest cover, and with much fewer dry grassland slopes than their present range (Caslys Consulting 2018). The initial range assessment pre-dating bison release in the Nisling valley (Reynolds et al. 1982) calculated productivity in this area to be 1,218 kg/ha, with *Carex aquatilis* having 11.64% +/- 0.43% crude protein, and *Calamagrostis* species (likely *canadensis*) having 12% +/- 2.06% crude protein (collections made July 23-31). Crude protein values for two of the dominant species on the Aishihik grasslands, *Carex duriuscula* and *Artemisia frigida*, calculated from samples collected on the Mongolian steppe, were 14.6% and 14.1% respectively (Togtokhbayar 2006)

suggesting that the nutrient content on the Aishihik grasslands may be higher than that in the wet sedge meadows, counterbalancing their lower productivity and encouraging bison to forage in these areas. However crude protein concentrations are very context dependent, with values varying greatly by location and season (Gizachew and Smit 2012), so values for these species on the Aishihik grasslands may be quite different. Additionally, the specific grass species most prevalent in the dung analysis (Jung et al., unpublished data), *Calamagrostis purpurascens*, has been found to be rather poor in protein (Dittberner & Olson 1983). Without more precise information on the nutrient content of the various forage species found on these grasslands, and their specific utilization levels, it is hard to compare wetland and grassland values. Nevertheless, as bison are bulk feeders rather than specialists (i.e., concentrate selectors) and are more concerned with accessing adequate forage than they are with targeting high quality forage (Hoffman 1989), it follows that a greater proportion of their diet is likely to come from wet meadows. It may also be that the grasslands occupied by bison are being selected not solely for forage, but also for other reasons such as relief from mosquito predation (Belanger 2018), as they can be some of the windiest places within the boreal forest.

Bison move onto upland grasslands periodically starting in late winter (Jung et al. 2018) as they are the first areas to become free of snow, but it isn't until April that bison start visiting these grasslands regularly. This pattern then continues throughout the summer and fall, with the exception of the calving period in June (Figure 7; Canadian Wildlife Service, unpublished data). On these warm grassland slopes, upland carices are already greening up in April in preparation for flowering in May, while snow is still thick in the valleys. The young, tender leaves produced

by grasses during this period are highly palatable, particularly in comparison to other habitat types lagging behind in phenological development. If grazing occurs before these grasses have had a chance to establish sufficient leaf growth to photosynthesize and replenish carbohydrate stocks, this may reduce growth later in the season (Trlica 2006). During April and May, the cameras at each plot recorded, on average, 6.1 visits each month by 4.4 bison, but there were relatively more large herds (>10 animals) than there were in fall and winter. On average each visit also lasted considerably longer (5.1 minutes) than in summer and fall. Collectively, these observations indicate bison may be taking advantage of the first available new growth (fresh forage) of the year, which in turn, would impact grassland composition and diversity.

Summer bison visitation patterns were similar to spring, except that the time spent on grasslands was shorter relative to the other seasons (2.7 minutes), possibly due to the extreme heat likely on these slopes at that time. Additionally, grass growth slows through the hottest, driest months, reducing the plants ability to replace grazed leaves, particularly in semi-arid grasslands such as the Aishihik grasslands. Vegetation often enters a state of semi-dormancy during this moisture stressed period, meaning compensatory growth at this time of year is slow and incomplete, thereby limiting foraging opportunities for herbivores. In late summer/early fall, grasses may enter another, less intense, growing phase if there is sufficient precipitation. In September, significantly more bison visits were recorded on the Aishihik grasslands than in any other month, though they consisted of considerably smaller groups on average. Starting in late October bison start to spend most of their time in wet sedge meadows within lowland valleys (Jung et al. 2018), which would explain the very low number of visits recorded on upland

grasslands at that time. When bison did appear at that time of year, their visits were the longest on average of all the seasons.

From the camera trap data, it appears that bison grazing intensity (as represented by visitation rates and bison numbers) on these grasslands was greatest in spring when grasses were at their most vulnerable to overgrazing. Bison were recorded in moderate numbers on average, but the presence of several large herds in April and May, plus relatively long stays on the grasslands, meant that bison likely removed more foliage from the grasslands in spring than at other seasons. Regardless of the fact that it is the most intense grazing in this system, it is unclear whether this level of grazing should be considered low, medium or high intensity relative to the plant community response. Bison are not close grazers as are horses (Hoffman 1989), which means there is a greater chance they will leave behind more of the plant after grazing. With more carryover biomass on plants, the greater the chance plants will not have to draw on carbohydrate reserves to replace cropped foliage – carbohydrates that are in short supply following the production of first growth. The advantage to spring grazing is that it is a period of rapid growth, thus, if enough foliage is left to permit photosynthesis to continue, then it is actually easier to recover in spring than later in summer when growth rates can slow dramatically. The fact that grassland visitation drops considerably in June during calving may allow these upland grasslands a chance to recover while growth rates are still reasonably high, and before the hottest and driest weather further slows down plant growth. Increased visitation by smaller groups of bison in fall likely had little impact on grasses as the latter are largely dormant at that time of year, and have had the spring and summer to build up their

carbohydrate stocks. Bison grazing at this time of year may have less effect on future growth of plants unless trampling is severe enough to disturb the apical meristem and roots.

Despite the presence of grazing throughout the growing season (with a brief respite in June), graminoid and forb abundance, along with diversity, all increased with increasing bison presence on the Aishihik grasslands. There is no evidence that above-ground competition, and competitive release, is playing a role in shaping vegetation communities on these grasslands. So what unique characteristics in this ecosystem might explain these relationships? 1) The vascular plant communities on these hillsides are composed almost exclusively of forbs and graminoids considered to be increasers under grazing in Alberta and/or Yukon (Bailey et al. 1992, Tannas 2003). 2) The Aishihik grasslands are the result of several hundred thousand years of coevolution with a large collection of mega-herbivores that existed in Beringia (an isolated glacial refugium) in various configurations throughout the Pleistocene, followed by a relatively modern suite of large herbivores, including bison, that have evolved since (throughout the Holocene) (Blinnikov 2011, Willerslev 2014). 3) These grasslands exist north of the 60th parallel, in an area of discontinuous permafrost, with a mean annual temperature ranging from -3°C to -5 °C and mean annual precipitation of 210-250 mm. The combination of severe environmental conditions with a long history of grazing has resulted in communities of plant species that may not just be tolerant of grazing, but may benefit from the present levels of (presumably moderate) grazing, e.g. increased vegetative growth and reproduction (Coughenar 1985, McNaughton 1983, Owen & Wiegert 1981). Or it may be that unexplored abiotic factors such as soil moisture and chemistry are more important than grazing in structuring these grasslands. In

support of that theory, regression analysis of Hill's N2 diversity index showed a reduction in diversity with increasing summer precipitation. As Hill's N2 is more sensitive to dominant species (as opposed to rare species) within a community, does this mean that the dominant species, some of which can be indicators of overgrazing (*Carex duriuscula*, *Carex obtusata*) are so well-adapted to xeric conditions, that precipitation is detrimental to their growth, or do moister conditions introduce competition?

Arctic ground squirrels

While arctic ground squirrels showed no significant relationship with diversity, their presence was the strongest predictor of graminoid and grass abundance within my multiple variable models. Unlike prairie dog colonies, whose burrows are associated with a lack of graminoids since that is their preferred forage (Cid et al. 1991, Beals et al. 2014), arctic ground squirrel burrows in the Aishihik area were associated with increased graminoid abundance, in particular, grasses. This is consistent with studies that have found nitrogen deposition preferentially encourages graminoid growth in some cases (Turkington et al. 2002, Dormann & Woodin 2002). Similarly, McKendrick et al. (1980) found that grasses were more abundant over arctic ground squirrel burrow systems in northwest Alaska, and were associated with increased soil nitrogen assumed to come from squirrel urine deposition. They also found a decreased abundance of legumes around burrows. In a related study Batzli & Sobaski (1980) found that arctic ground squirrels had a highly varied diet primarily consisting of forbs (legumes being

preferred); graminoids were eaten mainly in the spring when food supplies were most limited. Removal of forbs in the vicinity of the burrow may provide competitive release, allowing a greater abundance of graminoids in the area; however, there is evidence that ground squirrels forage quite selectively for nutrient value and palatability, and proximity to their burrows is not a key factor in foraging decisions (Bakker 2006, Gillis et al. 2005, Zazula et al. 2006).

It is interesting to note that arctic ground squirrels have been functionally extinct in the boreal forest zone of the Kluane region since 2000 (Boonstra et al. 2018). The greater abundance of graminoids associated with ground squirrel burrows found here may be a legacy effect of a time when populations were higher. Some squirrel activity was noted while sampling the study sites, but no effort was made to confirm that the ground squirrel burrows detected in sampling plots were occupied, so it is possible some were empty. Where there were no squirrels, the churned, aerated, dropping-enriched soil would be a relatively rich environment for new plants, and due to their habit of seed caching in middens and tunnels (Zazula et al. 2007), squirrels may also leave behind an enriched seed bank from which new plants could grow. This may contribute to the increase in grass abundance.

Grassland conservation and management

When wood bison were reintroduced into the Yukon in the late 1980's, the primary concern was their conservation as an endangered species. But in the roughly 30 years since, the Aishihik herd has increased so quickly local concern has grown regarding the potential conflict between

bison and other ungulates, and the impact they are having on the landscape within their home range. On a national scale, COSEWIC recently recommended that the wood bison's status under the Species at Risk Act be revised to special concern (COSEWIC 2013). At the same time the Yukon Wood Bison Technical Team was developing the Management Plan for the Aishihik Wood Bison (*Bison bison athabascae*) Herd in Southwestern Yukon (Government of Yukon 2012), several studies were begun to address the concerns expressed by First Nations and other community members (Clark et al. 2016, Jung et al. 2015a, b, c), such as herd expansion into Kluane National Park (Markel & Clark 2012). The semi-arid grasslands found within the herd range were identified as areas of particular concern given their uniqueness and the number of rare and endemic plant species that grow on these grasslands.

When outlining their MSL theory, Milchunas et al. (1988) proposed that, in arid grasslands with a long history of grazing, as grazing intensity increased a slight decline in diversity would result from the elimination of rare species less tolerant of grazing, while the major components of the plant community would not change. Contrary to this theory, several of the rare species (*Draba yukonensis* and *Gentianopsis detonsa*) on the Aishihik grasslands showed a significant positive correlation with increased bison presence (Figure 9), while *Eremogone capillaris* showed a positive correlation with ground squirrel burrows. Similarly, comparison of the Vetter plots pre- and post- bison reintroduction showed not only no loss of rare species, but the discovery of one species not detected in 1981. As for the community as a whole, the rare species documented within these grasslands displayed no signs of decrease as a result of bison presence. In fact, most of them have been identified as increasers under grazing, at least under low levels of

grazing. It must also be noted that this bison herd is projected to keep growing in size. Between 2011 and 2014, the herd grew 6.1% per annum, and there is no sign of that abating, despite an annual harvest rate of about 10.4% during this time (Jung & Egli 2014). Thus, the impacts of bison on plant community diversity, including rare species, may change in the future.

It is interesting that among the 9 rare species found on the Aishihik grasslands there was a mixture of endemics (*Draba yukonensis*, *Eriogonum flavum* var. *aquilinum*) and species that are widely common to the more southern great plains prairies, but remain disjunct to the Yukon where they are considered rare (*Geum triflorum*, *Phlox hoodii*). These species assemblages are rare, as are the small pockets of grasslands tucked into the boreal forest. Climate change, together with shrub and tree encroachment onto these grasslands, likely remains much more of a threat than the bison at current population levels.

With the temperature in the Aishihik area predicted to rise and precipitation to increase (Horton 2017), cascading effects are expected to be seen across all plant communities. For instance, shrub encroachment is anticipated to increase under a warmer, moister climate. Using tree core samples from the same grasslands sampled for this study, as well as in nearby Kluane, Conway & Danby (2014) found that in the last 60-80 years trees have invaded an average of 30m into grasslands in southwest Yukon, and grassland size has decreased by 36% on average. The greatest degree of plant compositional change between the Vetter plots sampled in 1981 and 2011 was evident in the 2 plots associated with an increase in woody species according to the MDS ordination. This may be an indicator of future changes to be

expected in these grasslands. Bison grazing may help facilitate the encroachment by providing competitive release of woody species from herbaceous neighbors, thereby facilitating shrub and tree establishment. Alternatively, grazing may provide nutrient-rich microsites for germination (Mast et al. 1998) or bison may slow the encroachment of aspen (*Populus tremuloides*) through trampling (Bork et al. 2013), although the latter seems unlikely given that the encroachment on these Aishihik grasslands pre-dates bison reintroduction and there has been no sign of abatement since they were released.

Additionally, under a warming climate, soil nutrients in the north are expected to increase (Chapin et al. 1995, Dormann & Woodin 2002), which has the potential to change northern vegetation dramatically. Climate change is much more of a threat to the Aishihik grasslands, and the rare species they hold, than are bison under current population levels and present climatic conditions, and will only become more so as temperatures warm.

Conclusion

Yukon grasslands have been studied most frequently as analogues or relicts of the Beringian steppe, using present-day vegetation to assist in building paleo-environmental reconstructions of the steppe-tundra that supported a much more diverse host of megafauna than exists in the Yukon today. Hoefs (1975) study of the grassland vegetation of Sheep Mountain, which looked at vegetation associations as well as forage yield, is one of the few exceptions that has looked at these grasslands in the context of contemporary grazing. In comparison, I looked at studies

of grazing and diversity on similarly arid grasslands with a long history of grazing to the south, such as mixedgrass prairie and steppe, to develop a generalized working hypothesis of Yukon grassland diversity responses to increasing grazing. As a result, I hypothesized that there would be little change in diversity at low levels of bison grazing, likely because the convergent pressures of aridity and a long history of (modest) grazing have preconditioned these grasslands to tolerate a certain amount of grazing. With increased grazing intensity, I hypothesized that plant diversity would begin to decrease. Contrary to expectations, I found that plant species richness and all other measures of diversity increased with greater bison presence, as did both forb and graminoid abundance, though not all functional groups were affected equally. The small upland *Carex* species increased most dramatically (i.e. species known to be indicators of overgrazing in the prairies), but not at the cost of forbs, which instead are the principle drivers of diversity and richness in this system. Similarly, rare species (again predominantly forbs) showed no signs of decline in response to bison abundance. Another grazer on these grasslands, the Arctic ground squirrel (*Urocitellus parryii*), was also positively associated with increased graminoid abundance, although probably not due to grazing itself, but most likely due to factors such as nitrogen deposition to soils.

Grasslands of the southwest Yukon co-evolved with a large number of mega-herbivores north of the ice sheets, within a harsh, often cold and dry, environment. As a result, they may be so disturbance and aridity adapted that their diversity may be more limited by too little grazing, or excess moisture, than it is by the recent reintroduction of wood bison. Supporting this hypothesis, plant community diversity was found to decrease with increasing precipitation in

these grasslands. Ongoing climate change, and the predicted increase in temperature and precipitation in this region of the Yukon, may therefore pose a greater threat to vascular plant diversity within these grasslands than herbivory.

it has been proposed that the response of Beringian paleo-grasslands to rapid climate change in the past could provide a valuable tool for predicting and mitigating future responses of contemporary grasslands to a changing climate (Blinnikov et al. 2011, Kittel et al. 2000). As methods used in paleo-environmental reconstruction continue to evolve, and temporal and taxonomic resolution become more precise (Willerslev et al. 2014), past reconstructions are becoming more easily translatable into the present. Grassland genetic diversity and its relationship to the fragmented spatial nature of Yukon grasslands today is one avenue for future research that might elucidate past reactions to rapidly changing climates.

There are also other important abiotic factors that were not examined in this study that may be contributing to plant diversity in the Aishihik grasslands such as soil moisture and nutrients. These abiotic factors are fundamental in shaping grassland vegetation, so while it does appear that diversity is increasing under the influence of bison grazing, these covariates may be exerting an influence that has not yet been accounted for. In summary, while the Aishihik wood bison herd does not appear to pose any immediate threat to the diversity of the Aishihik grasslands in their core range, they may in the future, including when coupled with escalating threats such as a changing climate. Further study on the influence of soil moisture and nutrients

on vegetation diversity within these grasslands would increase the level of confidence in our results.

Table 1 Summary of vascular plant species occurrence and abundance (% cover) in Vetter’s Aishihik area grassland plots (Vetter 2000) between years, and among functional groups (n =26). Species numbers in square brackets include all 5 *Carex* species detected in 2011 individually, while adjacent unbracketed numbers treat all carices as one species to facilitate comparison of 1981 and 2011 values. The interquartile range (IQR) is given in brackets for each median.

Response Variable (area sampled per year = 13 plots x 100m ²)	Sampling year	Vascular plants	Forbs	Graminoids	Upland Carex spp.	Grasses	Shrubs & trees	Legumes
# Species (richness)	1981	30	20	9	1	8	1	2
	2011	38 [42]	24	11 [15]	1 [5]	10	3	3
	1981 & 2011	41 [45]	27	11 [15]	1 [5]	10	3	3
# Species in >1 plot	1981	25	16	8	1	7	2	3
	2011	25 [29]	16	7 [11]	1 [5]	6	2	2
	1981 & 2011	31 [35]	20	9 [13]	1 [5]	8	2	3
Median # spp/plot (IQR)	1981	12 (3)	8 (2)	4 (0)	1 (0)	3 (1)	0 (0)	0 (1)
	2011	13 (5)	7 (5)	6 (2)	1 (0)	3 (1)	0 (1)	1 (1)
Median vascular cover (%)/plot (IQR)	1981	39 (18.5)	17.5 (4)	16.5 (17.5)	7.5 (13)	6.5 (6)	0 (0.5)	0 (0.5)
	2011	50.7 (11.5)	20.6 (11.2)	28.5 (26.2)	20 (14.3)	7.1 (4.6)	0 (1)	0.2 (3)
Frequency of occurrence (# plots)	1981	13	13	13	12	13	4	5
	2011	13	13	13	13	13	5	8
	1981 & 2011	26	26	26	25	26	9	13

Table 2 Plant species detected in only one of 2 sampling years within grasslands of the Vetter plots, the number of plots in which they occurred, the plot numbers, and their cover averaged over the number of plots where they were found. Upland sedges were amalgamated into one upland sedge category for the purposes of statistical analysis.

Taxon	1981	2011	# of plots	Cover averaged over plots where found (%)	plot #
Graminoids					
<i>Anthoxanthum hirtum</i>	–	✓	1	0.1	8
<i>Hordeum jubatum</i>	–	✓	1	0.5	1
<i>Carex duriuscula</i> (upland sedge)	–	✓	13	14.15	all
<i>Carex obtusata</i> (upland sedge)	–	✓	7	1.37	2, 5, 9, 11, 12, 13, 14
<i>Carex rossii</i> (upland sedge)	–	✓	2	0.3	1, 9
<i>Carex supina</i> (upland sedge)	–	✓	6	4.12	5, 10, 11, 12, 13, 14
Forbs					
<i>Achillea millefolium</i>	✓	–	2	0.5	1, 5
<i>Astragalus australis</i>	–	✓	2	0.1	1, 2
<i>Boechera holboellii</i>	–	✓	4	0.2	1, 2, 4, 13
<i>Chamaenerion angustifolium</i>	✓	–	1	0.5	1
<i>Crepis tectorum</i>	–	✓	1	0.1	1
<i>Erysimum angustatum</i>	✓	–	1	0.5	1
<i>Erysimum coarctatum</i>	–	✓	1	0.1	3
<i>Linum lewisii</i>	–	✓	1	0.1	1
<i>Myosotis asiatica</i>	–	✓	1	0.1	3
<i>Plantago canescens</i>	–	✓	1	0.1	13
Shrubs/Trees					
<i>Arctostaphylos uva-ursi</i>	–	✓	1	0.1	1
<i>Populus tremuloides</i>	–	✓	2	0.75	1, 8

Table 3 Summary of univariate PerMANOVA tests of dissimilarity between vascular plant species diversity metrics pre- and post- bison reintroduction within Vetter’s Aishihik area plots (n = 13 per year) ($\alpha < 0.05$). Plots measure 10m x 10m. PerMANOVA calculated using Bray-Curtis distance measures.

Response Variable	df	Sum Sq	Mean Sq	F value	p-value
Richness	1	8.65	8.65	0.93	0.35
Hill's N1 diversity index	1	0.26	0.26	0.06	0.80
Hill's N2 diversity index	1	0.85	0.85	0.33	0.57
Forbs (% cover)	1	3.9	3.92	0.43	0.84
Graminoids (% cover)	1	431	430.52	1.58	0.22
Grasses (% cover)	1	27.4	27.42	0.75	0.40
Carex spp. (% cover)	1	16.96	16.96	20.2	<0.001

Table 4 Results of the Indicator Species Analysis for Vetter’s plots grouped by pre- and post-bison reintroduction years (1981 and 2011) (n = 13 per year) (Vetter 2000). Species are ordered first by category of strongest association, and then by strength of association. Indicator species are highlighted in blue ($\alpha < 0.05$). Dominant species (occurring in ≥ 12 plots with a mean cover/plot $\geq 8\%$ in both years) are highlighted in dark green, and subdominant species (occurring in ≥ 6 plots with a mean cover/plot $\geq 2\%$ in both years) are highlighted in light green.

Taxon	Indicator Value	p-value	Functional Group
Species associated with 1981			
<i>Anemone patens</i> L.	0.768	0.026	forb
<i>Phlox</i> spp.	0.680	0.176	forb
<i>Achillea millefolium</i> L.	0.392	0.478	forb
<i>Solidago simplex</i> Kunth	0.374	0.478	forb
Species associated with 2011			
<i>Oxytropis splendens</i> Dougl.	0.690	0.059	forb
<i>Rosa acicularis</i> Lindl. s.l.	0.578	0.187	shrub/tree
<i>Boechera holboellii</i> (Hornemann) Á. Löve & D. Löve	0.555	0.099	forb
<i>Elymus trachycaulus</i> (Link) Gould ex Shinners ssp. <i>subsecundus</i> (Link) Á. Löve & D. Löve	0.468	0.365	graminoid
<i>Populus tremuloides</i> Michx.	0.392	0.477	shrub/tree
<i>Astragalus australis</i> (L.) Lam.	0.392	0.487	forb
Species associated with the data set from both years			
<i>Artemisia frigida</i> Willd.	1	NA	forb
<i>Carex</i> spp.	0.981	NA	graminoid
<i>Poa glauca</i> Vahl.	0.961	NA	graminoid
<i>Penstemon gormanii</i> Greene	0.941	NA	forb
<i>Calamagrostis purpurascens</i> R.Br.	0.877	NA	graminoid
<i>Androsace septentrionalis</i> L.	0.832	NA	forb
<i>Potentilla pensylvanica</i> L.	0.809	NA	forb
<i>Koeleria asiatica</i> Domin	0.679	NA	graminoid
<i>Bromus pumpellianus</i> Scribn.	0.679	NA	graminoid
<i>Potentilla arenosa</i> (Turczaninow) Juzepczuk	0.650	NA	forb
<i>Bupleurum americanum</i> Coult. & Rose	0.620	NA	forb
<i>Chamaerhodos erecta</i> (L.) Bge.	0.555	NA	forb
<i>Cherleria obtusiloba</i> (Rydberg) A.J. Moore & Dillenberger	0.519	NA	forb

<i>Erigeron caespitosus</i> Nutt.	0.480	NA	forb
<i>Saxifraga tricuspidata</i> Rottb.	0.439	NA	forb
<i>Elymus lanceolatus</i> ssp. <i>psammophilus</i> (J.M. Gillett & H. Senn) Á. Löve	0.439	NA	graminoid
<i>Eremogone capillaris</i> (Poiret) Fenzl var. <i>capillaris</i>	0.392	NA	forb
<i>Elymus trachycaulus</i> (Link) Gould ex Shinners ssp. <i>trachycaulus</i>	0.340	NA	graminoid
<i>Festuca saximontana</i> Rydb.	0.340	NA	graminoid
<i>Eriogonum flavum</i> Nutt. var. <i>aquilinum</i> Reveal	0.277	NA	forb
<i>Oxytropis borealis</i> DC. var. <i>viscida</i> (Nutt.) Welsh	0.277	NA	forb
Species found in only one plot			
<i>Anthoxanthum hirtum</i> (Schränk) Y. Schouten & Veldkamp	0.277	1	graminoid
<i>Arctostaphylos uva-ursi</i> (L.) Spreng. s.l.	0.277	1	shrub/tree
<i>Chamaenerion angustifolium</i> (Linnaeus) Scopoli	0.277	1	forb
<i>Crepis tectorum</i> L.	0.277	1	forb
<i>Erysimum angustatum</i> Rydb.	0.277	1	forb
<i>Erysimum coarctatum</i> Fern.	0.277	1	forb
<i>Hordeum jubatum</i> L.	0.277	1	graminoid
<i>Linum lewisii</i> Pursh	0.277	1	forb
<i>Myosotis asiatica</i> (Vestergren ex Hultén) Schischkin & Sergievskja	0.277	1	forb
<i>Plantago canescens</i> Adams	0.277	1	forb

Table 5 Summary of rare and invasive vascular plant species richness in Vetter’s Aishihik area grassland plots sampled in 1981 and 2011 (n = 26) (Vetter 2000).

Response variable (area sampled per year = 13 plots x 100m²)	Year	Rare plants (S1-S3)^a	Rare plants (S1-S2)^a	Invasive plants
# species	1981	4	1	0
	2011	4	1	1
	1981 & 2011	4	1	1
# species in >1 plot	1981	3	0	0
	2011	3	0	0
	1981 & 2011	3	0	0
# plots	1981	9	1	0
	2011	7	1	1
	1981 & 2011	10	1	1
Sum of cover in all 13 plots (%)	1981	39	0.5	0
	2011	34.7	5	0.1
Cover averaged over # of plots where found (%)	1981	4.3	0.5	0
	2011	5.0	5	0.1

^a Conservation Status Ranks as defined by NatureServe (NatureServe, 2017):

Geographic Scale:

S = subnational (Yukon Territory)

Conservation Status:

1 = critically imperiled

2 = imperiled

3 = vulnerable

Table 6 Rare plant species found in Vetter’s Aishihik area grassland plots (n = 26) (Vetter 2000), along with their conservation status ranking as defined by the Yukon Conservation Data Centre (Environment Yukon, February 2019). Only those species ranked S1-S3 are included. All plots where each species was observed in each year are listed.

Species	Common Name	G Rank ^a	N Rank ^a	S Rank ^a	1981 Plots	2011 Plots
<i>Draba yukonensis</i>	Yukon Draba	G2G3	N2N3	S2S3	--	14* (beside plot)
<i>Eremogone capillaris</i> <i>var. capillaris</i>	Thread-leaved Sandwort	G5	N5	S3	9* , 13	10* , 13
<i>Eriogonum flavum</i> var. <i>aquilinum</i>	Umbrella Plant	G5T2	N1N2	S1S2	7	7
<i>Koeleria asiatica</i>	Oriental Junegrass	G4	N2N3	S2S3	2* , 7, 11, 12, 13, 14	7, 11, 12, 13, 14
<i>Phlox hoodii</i> ^a	Moss Phlox	G5	N5	S3	1* , 2* , 4* , 7, 11, 12, 13* , 14	--
<i>Phlox richardsonii</i> ^a	Richardson's Phlox	GNR	N3	S3	--	7, 11, 12, 14

^a listed as *Phlox sibirica* ssp. *sibirica* in 1981 field sheets, and as *Phlox hoodii* in Grasslands of the Aishihik-Sekulmum Lakes area, Yukon Territory, Canada (Vetter 2000). Since 1981 there has been debate on the relative extents and identification of *Phlox hoodii* and *Phlox richardsonii*. In 2011 both species were identified within the Aishihik wood bison core range. For the purposes of this study, the *Phlox* species recorded in the same sites in both years are considered to likely be the same species.

* sites where the species was only found in one of the two years surveyed

^a Conservation Status Ranks as defined by NatureServe (NatureServe, 2017):

Geographic Scale: G = global, N = national (Canada), S = subnational (Yukon Territory)

Conservation Status:

1 = critically imperiled

2 = imperiled

3 = vulnerable

4 = apparently secure

5 = secure

NR = unranked

T = infraspecific taxon

A numeric range rank (e.g., G2G3) is used to indicate the range of uncertainty in the status of a species.

Table 7 Summary of vascular plant species occurrence and abundance in grassland plots surveyed in 2011 & 2012, including comparisons between functional groups (n =70). The interquartile range (IQR) is given in brackets for each median.

Response Variable (area sampled = 70 plots x 100m²)	Vascular plants	Forbs	Graminoids	Upland Carex spp.	Grasses	Shrubs & trees	Legumes
# Species (richness)	77	55	16	5	11	6	6
# Species in > 10% of plots (> 7 plots)	33	19	11	4	7	3	2
# Species in > 20% of plots (> 14 plots)	23	14	9	4	5	0	1
Median # spp/plot (IQR)	15 (7)	9.5 (6)	5 (2)	2 (1)	3 (2)	0 (1)	1 (1)
Median vascular cover (%)/plot (IQR)	50 (21.25)	24.1 (12.48)	21.5 (18.7)	11.1 (14.68)	7 (10.05)	0 (1.38)	1 (2)
Frequency of occurrence (# plots)	70	70	70	65	70	29	51

Table 8 Rare species found in grassland plots surveyed in 2011 and 2012 (n = 70), along with their conservation status ranking as defined by the Yukon Conservation Data Centre (Environment Yukon, February 2019), and the number of plots in which they were found. Only those species ranked S1-S3 are included.

Species	Common Name	G Rank ^a	N Rank ^a	S Rank ^a	# Plots
<i>Comandra umbellata</i>	Pale Comandra	G5	N5	S2	1
<i>Draba yukonensis</i>	Yukon Draba	G2G3	N2N3	S2S3	2
<i>Eremogone capillaris</i> <i>var. capillaris</i>	Thread-leaved Sandwort	G5	N5	S3	6
<i>Eriogonum flavum</i> var. <i>aquilinum</i>	Umbrella Plant	G5T2	N1	S1	3
<i>Gentianopsis detonsa</i>	Sheared Gentian	G3G5	N4	S3	2
<i>Geum triflorum</i>	Prairie Smoke	G5	N5	S2	2
<i>Koeleria asiatica</i>	Oriental Junegrass	G4	N2N3	S2S3	10
<i>Phlox hoodii</i>	Moss Phlox	G5	N5	S3	1
<i>Phlox richardsonii</i>	Richardson's Phlox	GNR	N3	S3	9

^a **Conservation Status Ranks as defined by NatureServe (NatureServe, 2017):**

Geographic Scale:

G = global, N = national (Canada), S = subnational (Yukon Territory)

Conservation Status:

1 = critically imperiled

2 = imperiled

3 = vulnerable

4 = apparently secure

5 = secure

NR = unranked

T = infraspecific taxon

A numeric range rank (e.g., G2G3) is used to indicate the range of uncertainty in the status of a species.

Table 9 Spearman correlations of plant diversity metrics with grazing and environmental variables ($\alpha < 0.05$). Different measures of the same potential source of influence on diversity are grouped into predictor classes of that name (grazing, size, elevation, insolation, temperature and precipitation).

Predictor Variable	Richness	Hill's N1	Hill's N2
<i>Grazing</i>			
Bison Dung Counts	0.54***	0.43***	0.32*
Ground Squirrel Burrow Count	0.04	-0.03	-0.08
<i>Size</i>			
Area	-0.15	-0.11	-0.06
Perimeter	-0.08	-0.05	-0.01
Area/Perimeter Ratio	-0.26*	-0.17	-0.13
<i>Elevation</i>			
Elevation	0.1	0.02	0.02
<i>Insolation</i>			
Aspect	0.07	0.09	0.11
Slope	-0.43***	-0.25*	-0.16
Heat Load Index	0.1	0.11	0.1
Site Severity Index	-0.14	-0.02	0.05
Insolation – Apr-May (16m DEM)	-0.28*	-0.34***	-0.33***
Insolation – Jun-Aug (16m DEM)	-0.28*	-0.33*	-0.31*
Insolation – Sep-Oct (16m DEM)	-0.32*	-0.38***	-0.37***
Insolation – Nov-Mar (16m DEM)	-0.31*	-0.37***	-0.37***
<i>Temperature</i> (10 year average: 2001-2010)			
Temperature – annual average	-0.08	-0.07	-0.09
Temperature – April-May average	-0.14	-0.15	-0.16
Temperature – June-Aug average	-0.06	-0.08	-0.11
Temperature – Sept-Oct average	-0.1	-0.1	-0.12
Temperature – Nov-Mar average	-0.08	-0.07	-0.09
<i>Precipitation</i> (10 year average: 2001-2010)			
Precipitation - annual	0.05	0	-0.03
Precipitation – Apr-May	0.33*	0.16	0.06
Precipitation – Jun-Aug	0.11	-0.04	-0.13
Precipitation – Sep-Oct	-0.04	-0.09	-0.12
Precipitation – Nov-Mar	0.09	0.04	0

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table 10 Spearman correlations of plant functional group cover values with grazing and environmental variables ($\alpha < 0.05$). Different measures of the same ecological or environmental characteristic are grouped into predictor classes of that name (grazing, grassland size, elevation, insolation, temperature and precipitation).

Predictor Variable	Forbs	Graminoids	Carex spp.	Grasses	Shrubs/Trees
<i>Grazing</i>					
Bison Dung Counts	0.32*	0.11	0.15	0.01	0.04
Ground Squirrel Burrow Counts	-0.13	0.27*	0.19	0.15	-0.06
<i>Size</i>					
Area	-0.08	-0.3*	0.12	-0.33*	-0.12
Perimeter	-0.06	-0.29*	-0.11	-0.32*	-0.12
Area/Perimeter Ratio	-0.13	-0.22	-0.1	-0.25*	-0.09
<i>Elevation</i>					
Elevation	-0.19	0.31*	0.37***	0.08	-0.21
<i>Insolation</i>					
Aspect	0.09	0.05	-0.07	0.16	-0.2
Slope	-0.13	-0.28*	-0.23	-0.28*	-0.29*
Heat Load Index	0.11	0	-0.04	0.05	-0.21
Site Severity Index	-0.21	-0.2	0.04	-0.4***	-0.06
Insolation – Apr-May (16m DEM)	-0.2	-0.07	-0.01	-0.14	0.12
Insolation – Jun-Aug (16m DEM)	-0.19	-0.06	0.03	-0.15	0.08
Insolation – Sep-Oct (16m DEM)	-0.19	-0.07	-0.07	-0.12	0.13
Insolation – Nov-Mar (16m DEM)	-0.19	-0.07	-0.07	-0.11	0.14
<i>Temperature</i> (10 year average: 2001-2010)					
Temperature – annual average	0.18	-0.25*	-0.24*	-0.18	0.19
Temperature – April-May average	0.1	-0.81***	-0.35***	0.14	0.2
Temperature – June-Aug average	0.15	-0.73***	-0.28*	0.22	0.26
Temperature – Sept-Oct average	0.11	-0.82***	-0.35***	0.13	0.26
Temperature – Nov-Mar average	0.08	-0.61***	-0.38***	0.07	0.22

Precipitation (10 year average: 2001-2010)

Precipitation - annual	0.21	-0.04	-0.11	0.01	0.15
Precipitation – Apr-May	0.19	-0.04	0.01	-0.11	0.36*
Precipitation – Jun-Aug	0.24	-0.1	-0.16	-0.04	0.24
Precipitation – Sep-Oct	0.17	-0.51***	-0.32*	-0.06	0.12
Precipitation – Nov-Mar	0.12	-0.46***	-0.23	-0.15	0.14

*** p < 0.001, ** p < 0.01, * p < 0.05

Table 11 Results of univariate linear mixed effects models examining the relationship of diversity and abundance (cover) with grazing and environmental variables. Z-scores were used for all predictor variables. Location was the random term. The model of best fit (lowest AICc) for each predictor class is bolded. Additional variables used in multiple mixed effects models are italicized.

Response variable	Predictor class	Predictor variable	AICc	β	SE	F	p	
Richness	Grazing	Bison dung counts	404.87	2.46	0.49	25.25	<0.0001	
		Bison collar data	434.69	-	-	0.77	0.60	
		Ground squirrel burrows	425.90	0.54	0.55	1.01	0.32	
	Size	Area	425.92	-0.60	0.60	0.99	0.32	
		Ratio of Area/Perimeter	422.46	-1.30	0.61	4.49	0.04	
	Elevation	Elevation	424.32	1.60	1.00	2.58	0.11	
	Insolation	Slope	400.77	-2.52	0.45	31.73	<0.0001	
		<i>Aspect (direction)</i>	<i>422.99</i>	-	-	<i>2.81</i>	<i>0.03</i>	
		Aspect (°)	425.94	-0.57	0.58	0.98	0.33	
		Heat Load Index (HLI)	423.96	-0.99	0.57	3.04	0.09	
		<i>Site Severity Index (SSI)</i>	<i>422.39</i>	<i>-1.14</i>	<i>0.53</i>	<i>4.62</i>	<i>0.04</i>	
		Insolation Apr-May	425.53	-0.67	0.57	1.39	0.24	
		Insolation Jun-Aug	426.02	-0.54	0.57	0.90	0.35	
		Insolation Sep-Oct	424.63	-0.86	0.57	2.31	0.13	
		Insolation Nov-Mar	424.59	-0.86	0.56	2.35	0.13	
		Temperature	<i>Temperature (annual av.)</i>	<i>425.40</i>	<i>-1.22</i>	<i>0.99</i>	<i>1.51</i>	<i>0.22</i>
			Temperature Apr-May	425.05	-1.41	1.04	1.85	0.18
			Temperature Jun-Aug	424.96	-1.40	1.00	1.97	0.17
	Temperature Sep-Oct		425.10	-1.39	1.03	1.81	0.18	
	Temperature Nov-Mar		425.72	-1.05	0.97	1.19	0.28	
	Precipitation	Precipitation (annual)	426.88	0.19	0.89	0.05	0.83	
		Precipitation Apr-May	424.17	1.31	0.79	1.31	0.79	
		Precipitation Jun-Aug	426.88	0.17	0.83	0.04	0.83	
		Precipitation Sep-Oct	426.81	-0.32	0.92	0.12	0.73	
		Precipitation Nov-Mar	426.84	0.27	0.94	0.08	0.77	

Hill's N1	Grazing	Bison dung counts	330.25	0.93	0.28	11.06	0.001
		Bison collar data	344.15	-	-	1.51	0.19
		Ground squirrel burrows	340.77	0.03	0.15	0.01	0.91
	Size	Area	337.51	-0.57	0.31	3.29	0.08
		Ratio of Area/Perimeter	337.94	-0.56	0.33	2.82	0.10
	Elevation	Elevation	339.88	0.57	0.60	0.89	0.35
	Insolation	Slope	335.04	-0.67	0.28	5.83	0.02
		Aspect (direction)	341.72	-	-	1.54	0.20
		<i>Aspect (°)</i>	<i>340.58</i>	<i>-0.14</i>	<i>0.31</i>	<i>0.20</i>	<i>0.66</i>
		HII	339.20	-0.38	0.31	1.59	0.21
		SSI	339.26	-0.35	0.29	1.51	0.22
		Insolation Apr-May	337.65	-0.52	0.30	3.13	0.08
		Insolation Jun-Aug	338.20	-0.48	0.30	2.56	0.12
		Insolation Sep-Oct	336.81	-0.59	0.30	4.01	0.05
		<i>Insolation Nov-Mar</i>	<i>336.74</i>	<i>-0.59</i>	<i>0.29</i>	<i>4.08</i>	<i>0.05</i>
		Temperature	<i>Temperature (annual av.)</i>	<i>339.86</i>	<i>-0.57</i>	<i>0.60</i>	<i>0.90</i>
	Temperature Apr-May		339.19	-0.81	0.65	1.57	0.22
	Temperature Jun-Aug		339.90	-0.56	0.60	0.87	0.35
	Temperature Sep-Oct		339.65	-0.68	0.64	1.11	0.30
	Temperature Nov-Mar		340.10	-0.48	0.58	0.67	0.42
	Precipitation	<i>Precipitation (annual)</i>	<i>339.96</i>	<i>-0.47</i>	<i>0.52</i>	<i>0.81</i>	<i>0.37</i>
		Precipitation Apr-May	340.73	0.10	0.45	0.05	0.82
		Precipitation Jun-Aug	339.21	-0.58	0.46	1.56	0.22
Precipitation Sep-Oct		340.00	-0.48	0.55	0.77	0.38	
Precipitation Nov-Mar		340.42	-0.34	0.56	0.36	0.55	
Hill's N2	Grazing	Bison dung counts	309.97	0.58	0.25	5.57	0.02
		Bison collar data	318.56	-	-	1.65	0.15
		Ground squirrel burrows	315.38	-0.07	0.25	0.08	0.78

Size	Area	312.81	-0.43	0.26	2.65	0.11
	Ratio of Area/Perimeter	313.55	-0.39	0.28	1.89	0.17
Elevation	Elevation	314.97	0.33	0.48	0.49	0.49
Insolation	Slope	313.31	-0.35	0.24	2.12	0.15
	Aspect (direction)	317.21	-	-	1.34	0.27
	Aspect (°)	315.41	-0.06	0.26	0.05	0.82
	HLI	314.34	-0.27	0.26	1.12	0.29
	SSI	314.87	-0.19	0.25	0.59	0.45
	Insolation Apr-May	312.88	-0.40	0.25	2.58	0.11
	Insolation Jun-Aug	313.43	-0.36	0.25	2.02	0.16
	Insolation Sep-Oct	311.97	-0.47	0.25	3.53	0.07
	Insolation Nov-Mar	311.85	-0.48	0.25	3.67	0.06
	Temperature	<i>Temperature (annual av.)</i>	<i>314.25</i>	<i>-0.52</i>	<i>0.47</i>	<i>1.20</i>
Temperature Apr-May		313.84	-0.63	0.50	1.60	0.21
Temperature Jun-Aug		314.83	-0.37	0.47	0.62	0.43
Temperature Sep-Oct		314.29	-0.53	0.50	1.15	0.29
Temperature Nov-Mar		314.41	-0.47	0.46	1.05	0.31
Precipitation	Precipitation (annual)	313.29	-0.60	0.41	2.16	0.15
	Precipitation Apr-May	315.18	-0.19	0.37	0.28	0.60
	Precipitation Jun-Aug	311.80	-0.71	0.37	3.70	0.06
	Precipitation Sep-Oct	313.88	-0.54	0.43	1.58	0.21
	Precipitation Nov-Mar	314.31	-0.47	0.44	1.14	0.29

Forbs	Grazing	Bison dung counts	515.49	3.41	1.11	9.39	0.003
		Bison collar data	535.94	-	-	0.14	0.99
		Ground squirrel burrows	524.47	0.21	1.16	0.03	0.86
Size	Area	524.50	-0.06	1.22	0.00	0.96	
	Ratio of Area/Perimeter	523.81	-1.03	1.24	0.69	0.41	
Elevation	Elevation	524.40	-0.51	1.49	0.12	0.74	
Insolation	Slope	519.57	-2.49	1.11	4.99	0.03	
	Aspect (direction)	529.44	-	-	0.53	0.71	

		<i>Aspect (°)</i>	524.34	0.48	1.20	0.16	0.69
		HLI	524.44	0.29	1.21	0.06	0.81
		SSI	524.50	0.03	1.16	0.00	0.98
		Insolation Apr-May	523.57	-1.13	1.18	0.91	0.34
		Insolation Jun-Aug	523.64	-1.09	1.18	0.85	0.36
		Insolation Sep-Oct	523.40	-1.22	1.18	1.08	0.30
		<i>Insolation Nov-Mar</i>	523.31	-1.27	1.17	1.16	0.29
Temperature		Temperature (annual av.)	522.79	1.94	1.37	2.02	0.16
		Temperature Apr-May	523.90	1.16	1.46	0.64	0.43
		Temperature Jun-Aug	524.48	-0.20	1.48	0.02	0.89
		Temperature Sep-Oct	524.05	1.03	1.46	0.49	0.48
		Temperature Nov-Mar	521.97	2.32	1.32	3.12	0.08
Precipitation		<i>Precipitation (annual)</i>	521.39	2.40	1.31	3.37	0.07
		Precipitation Apr-May	522.44	1.96	1.37	2.04	0.16
		Precipitation Jun-Aug	522.63	1.85	1.33	1.92	0.17
		Precipitation Sep-Oct	520.39	2.76	1.27	4.70	0.03
		Precipitation Nov-Mar	521.30	2.46	1.31	3.52	0.07
sqrt (Graminoids)	Grazing	<i>Bison dung counts</i>	241.42	0.31	0.15	4.06	0.04
		Bison collar data	241.53	-	-	2.90	0.02
		Ground squirrel burrows	238.78	0.38	0.15	6.34	0.01
Size		Area	242.02	-0.29	0.16	3.23	0.08
		Ratio of Area/Perimeter	243.10	-0.24	0.17	2.07	0.16
Elevation		Elevation	240.77	0.46	0.17	7.41	0.01
Insolation		Slope	237.52	-0.41	0.15	7.96	0.01
		Aspect (direction)	249.81	-	-	0.58	0.68
		<i>Aspect (°)</i>	245.01	0.02	0.16	0.01	0.92
		HLI	245.01	0.01	0.16	0.01	0.94
		SSI	244.98	-0.03	0.16	0.04	0.85
		Insolation Apr-May	244.25	-0.14	0.16	0.75	0.39
		Insolation Jun-Aug	244.35	-0.13	0.16	0.65	0.42

		<i>Insolation Sep-Oct</i>	244.22	-0.14	0.16	0.78	0.38
		Insolation Nov-Mar	244.32	-0.13	0.16	0.69	0.41
Temperature		<i>Temperature (annual av.)</i>	242.20	-0.35	0.20	3.25	0.08
		Temperature Apr-May	241.51	-0.40	0.19	4.38	0.04
		Temperature Jun-Aug	242.13	-0.35	0.20	3.15	0.08
		Temperature Sep-Oct	241.81	-0.38	0.19	4.03	0.05
		Temperature Nov-Mar	242.74	-0.32	0.20	2.55	0.12
	Precipitation		<i>Precipitation (annual)</i>	244.54	-0.14	0.20	0.48
		Precipitation Apr-May	244.47	-0.15	0.20	0.55	0.46
		Precipitation Jun-Aug	244.97	0.04	0.20	0.05	0.83
		Precipitation Sep-Oct	243.91	-0.22	0.20	1.10	0.30
		Precipitation Nov-Mar	243.41	-0.26	0.20	1.63	0.21
sqrt (Carex spp.)		Grazing	Bison dung counts	260.62	0.28	0.18	2.63
	Bison collar data		266.18	-	-	1.51	0.19
<i>Ground squirrel burrows</i>	262.77		0.11	0.17	0.42	0.52	
Size		Area	262.34	-0.17	0.19	0.84	0.36
		Ratio of Area/Perimeter	263.03	-0.08	0.20	0.17	0.68
Elevation		Elevation	259.39	0.52	0.26	4.09	0.05
Insolation		Slope	260.57	-0.28	0.17	2.61	0.11
		<i>Aspect (°)</i>	262.58	-0.14	0.18	0.62	0.44
		Aspect (direction)	262.96	-	-	1.84	0.13
		HLI	263.15	0.04	0.18	0.05	0.83
		<i>SSI</i>	263.08	-0.06	0.17	0.11	0.74
		Insolation Apr-May	263.20	0.01	0.18	0.00	0.97
		Insolation Jun-Aug	263.19	0.02	0.18	0.01	0.91
		Insolation Sep-Oct	263.20	0.00	0.18	0.00	0.98
		Insolation Nov-Mar	263.20	0.01	0.18	0.00	0.97
	Temperature		<i>Temperature (annual av.)</i>	260.34	-0.46	0.25	3.47
		Temperature Apr-May	260.60	-0.44	0.26	2.83	0.10
		Temperature Jun-Aug	261.60	-0.34	0.27	1.58	0.21

		Temperature Sep-Oct	260.90	-0.41	0.26	2.53	0.12
		Temperature Nov-Mar	260.43	-0.45	0.24	3.54	0.06
	Precipitation	<i>Precipitation (annual)</i>	262.83	-0.16	0.25	0.41	0.52
		Precipitation Apr-May	263.20	0.00	0.24	0.00	1.00
		Precipitation Jun-Aug	263.04	0.10	0.25	0.18	0.67
		Precipitation Sep-Oct	261.29	-0.36	0.24	2.14	0.15
		Precipitation Nov-Mar	261.89	-0.30	0.25	1.45	0.23
sqrt(Grasses)	Grazing	Bison dung counts	235.09	0.17	0.15	1.27	0.26
		Bison collar data	240.99	-	-	1.24	0.30
		Ground squirrel burrows	227.03	0.43	0.14	9.75	0.00
	Size	Area	232.74	-0.30	0.15	3.91	0.05
		Ratio of Area/Perimeter	232.09	-0.32	0.15	4.34	0.04
	Elevation	Elevation	235.55	0.16	0.17	0.95	0.33
	Insolation	Slope	230.02	-0.36	0.14	6.49	0.01
		Aspect (direction)	237.19	-	-	1.69	0.16
		<i>Aspect (°)</i>	235.37	0.14	0.15	0.90	0.35
		HLI	236.22	-0.03	0.15	0.04	0.83
		SSI	236.26	-0.01	0.15	0.00	0.96
		Insolation Apr-May	233.97	-0.23	0.15	2.39	0.13
		Insolation Jun-Aug	234.20	-0.22	0.15	2.15	0.15
		Insolation Sep-Oct	233.68	-0.24	0.15	2.68	0.11
		<i>Insolation Nov-Mar</i>	233.62	-0.25	0.15	2.73	0.10
	Temperature	Temperature (annual av.)	235.47	-0.16	0.18	0.78	0.38
		Temperature Apr-May	234.53	-0.23	0.17	1.95	0.17
		Temperature Jun-Aug	232.67	-0.32	0.15	4.70	0.03
		Temperature Sep-Oct	234.66	-0.22	0.17	1.74	0.19
		Temperature Nov-Mar	235.86	-0.11	0.18	0.40	0.53
	Precipitation	Precipitation (annual)	235.95	-0.10	0.17	0.30	0.58
		Precipitation Apr-May	234.09	-0.25	0.16	2.25	0.14
		Precipitation Jun-Aug	235.99	-0.09	0.17	0.27	0.60

Precipitation Sep-Oct	236.18	-0.05	0.18	0.08	0.77
Precipitation Nov-Mar	235.96	-0.10	0.18	0.30	0.59

Table 12 Summary of the top-ranked ($\Delta AICc < 2$) candidate linear mixed effects models examining the relationship of vascular plant diversity and abundance with bison grazing and environmental covariates. Also included are the models of best fit that excluded each significant predictor variable, or combination of significant variables ($\alpha < 0.05$; as identified in adjusted global models) (yellow highlighted). Location was included as a random effect in all models. Top models are highlighted in green. Italicized models are adjusted global models.

Model	Model Complexity (K)	AICc	Delta AICc	Akiake weight (w_i)	logLik	Best fit model excluding specified predictor variable
Richness						
					-	
bisdung + aspdire + areaper	9	395.82	0	0.17	187.41	
bisdung + aspdire + areaper + tmpAnn	10	396.25	0.43	0.13	-186.26	
bisdung + areaper + tmpAnn	6	396.26	0.44	0.13	-191.46	
bisdung + SSI + areaper	6	396.33	0.51	0.13	-191.5	
bisdung + areaper	5	396.43	0.61	0.12	-192.75	
bisdung + SSI + areaper + tmpAnn	7	396.61	0.79	0.11	-190.4	
bisdung + areaper + pptApMay + tmpAnn	7	396.82	1	0.1	-190.51	
<i>bisdung + SSI + areaper + pptApMay + tmpAnn</i>	8	397.08	1.26	0.09	-189.36	
slope + pptApMay + tmpAnn	6	400.44	4.61	0.02	-193.55	bisdung or areaper
areaper + aspdire	8	419.75	23.93	<0.01	-200.7	both slope and bisdung
NULL MODEL	3	424.68	28.86	<0.01	-209.16	
Hill's N1 (exponential of Shannon Index)						
					-	
bisdung + area + pptAnn	6	326.66	0	0.38	156.66	
bisdung + area	5	326.93	0.26	0.33	-157.99	
bisdung + area + tmpAnn	6	327.82	1.16	0.21	-157.25	
bisdung	4	330.25	3.59	0.06	-160.82	area
slope + area	5	334.41	7.75	0.01	-161.74	bisdung

area	4	337.5	10.84	<0.01	-164.44	both slope and bisdung
NULL MODEL	3	338.53	11.87	<0.001	-166.08	

Hill's N2 (inverse of Simpson's index)

					-	
bisdung + pptJunAu + area	6	303.9	0	0.88	145.28	
bisdung + area	5	308.33	4.43	0.1	-148.7	pptJunAu
pptJunAu + area	5	310.76	6.86	0.03	-149.91	bisdung
NULL MODEL	3	313.21	9.31	<0.01	-153.42	

Forbs

					-	
bisdung + tmpNoMar + areaper	6	515.09	0	0.19	250.88	
bisdung + tmpNoMar	5	515.47	0.38	0.16	-252.27	
bisdung	4	515.49	0.4	0.15	-253.44	
bisdung + pptAnn	5	515.92	0.83	0.12	-252.49	
bisdung + areaper	5	516.06	0.97	0.12	-252.56	
bisdung + aspect	5	516.83	1.74	0.08	-252.95	
bisdung + aspect + tmpNoMar	6	516.88	1.79	0.08	-251.78	
bisdung + pptAnn + areaper	6	516.89	1.8	0.08	-251.78	
slope + pptAnn	5	519.29	4.2	0.02	-254.17	bisdung
pptAnn	4	521.39	6.3	0.01	-256.38	both bisdung and slope
NULL MODEL	3	522.25	7.16	0.01	-257.94	

sqrt(Graminoids)

slope + squirrel	5	234.30	0.00	0.21	-111.68	bisdung
slope + squirrel + elev	6	234.80	0.50	0.16	-110.74	
slope + squirrel + area	6	235.48	1.18	0.11	-111.07	
slope + squirrel + tmpAnn	6	235.62	1.32	0.11	-111.15	
squirrel + bisdung	5	235.81	1.51	0.10	-112.44	slope

slope + squirrel + aspect	6	236.08	1.78	0.08	-111.37	
slope + squirrel + elev + area	7	236.12	1.82	0.08	-110.16	
squirrel + bisdung + area	6	236.22	1.92	0.08	-111.44	
slope + elev	5	237.05	2.75	0.05	-113.06	squirrel
bisdung + tmpAnn + area	6	239.55	5.25	0.01	-113.11	both squirrel and slope
NULL MODEL	3	242.77	8.47	0.00	-118.20	

sqrt(*Carex* spp.)

					-	
tmpAnn + bisdung	5	260.11	0	0.14	124.59	
tmpAnn + slope	5	260.23	0.12	0.13	-124.65	bisdung
tmpAnn	4	260.34	0.23	0.13	-125.86	
slope	4	260.57	0.46	0.11	-125.98	
bisdung	4	260.62	0.51	0.11	-126.00	
NULL MODEL	3	260.95	0.83	0.09	-127.29	
tmpAnn + bisdung + area	6	261.15	1.03	0.09	-123.91	
bisdung + area	5	261.61	1.50	0.07	-125.34	
tmpAnn + area	5	261.76	1.65	0.06	-125.41	
tmpAnn + slope + area	6	261.88	1.77	0.06	-124.27	

sqrt(Grasses)

					-	
squirrel + slope + pptApMay + aspect	7	222.11	0	0.28	103.15	bisdung
squirrel + slope + aspect	6	222.87	0.76	0.19	-104.77	
squirrel + slope	5	223.54	1.44	0.14	-106.3	
squirrel + slope + areaper + pptApMay + aspect	8	223.6	1.49	0.13	-102.62	
squirrel + slope + pptApMay	6	223.67	1.56	0.13	-105.17	
squirrel + slope + tmpJunAu + pptApMay + aspect	8	224	1.9	0.11	-102.82	
squirrel + areaper + pptArMay	6	227.54	5.43	0.02	-107.1	slope

slope + area_ha + pptApMay + aspect	7	229.01	6.9	0.01	-106.6	squirrel
NULL MODEL	3	234.01	11.9	0	-113.82	

codes used within multiple variable mixed effects models:

bisdung = bison dung counts

biscolr = bison collar data

squirrel = ground squirrel burrows

area = grassland area

areaper = ratio of grassland area to perimeter

elev = elevation

aspect = aspect (degrees)

aspdir = aspect (direction)

slope = slope

SSI = site severity index

tmpAnn = temperature (annual av.)

tmpJunAu = temperature Jun-Aug

tmpNoMar = temperature Nov-Mar

pptAnn = precipitation (annual)

pptApMay = precipitation Apr-May

pptJunAu = precipitation Jun-Aug

pptNoMar = precipitation Nov-Mar

Table 13 Summary of model-averaged coefficient estimates for the most supported ($AIC_c < 2$) mixed effects models for each diversity and abundance response variable. Location was included as a random effect in all models. ($\alpha < 0.05$)

Response Variable	Model Structure	β	SE	z value	Pr(> z)
Richness	bisdung	2.55	0.46	5.37	<0.0001
	aspdire.SE	-1.06	1.99	0.53	0.56
	aspdire.S	-1.66	2.75	0.60	0.55
	aspdire.SW	-1.09	2.01	0.54	0.59
	aspdire.W	-0.83	1.83	0.45	0.66
	areaper	-1.67	0.51	3.21	0.00
	tmpAnn	-0.76	0.91	0.82	0.41
	SSI	-0.22	0.40	0.54	0.59
	pptApMay	0.18	0.48	0.38	0.71
Hill's N1 (exponential of Shannon index)	bisdung	1.02	0.27	3.68	0.00
	area	-0.71	0.29	2.40	0.02
	pptAnn	-0.31	0.47	0.64	0.52
	tmpAnn	-0.15	0.38	0.39	0.70
Hill's N2 ¹ (inverse of Simpson's index)	bisdung	0.73	0.24	3.08	0.00
	pptJunAu	-0.90	0.34	-2.66	0.01
	area	-0.57	0.25	-2.29	0.03
Forbs	bisdung	3.44	1.12	3.00	0.00
	tmpNoMar	0.94	1.32	0.71	0.48
	areaper	-0.66	1.09	0.60	0.55
	pptAnn	0.35	0.89	0.39	0.70
	aspect	0.18	0.61	0.29	0.77
sqrt(Graminoids)	slope	-0.37	0.14	2.52	0.01
	squirrel	0.33	0.15	2.17	0.03
	elev	0.31	0.20	1.50	0.13
	area	-0.19	0.16	1.17	0.24
	tmpAnn	-0.24	0.22	1.11	0.27
	bisdung	0.36	0.15	2.39	0.02
	aspect	0.12	0.15	0.76	0.45
sqrt(Carex spp.)	tmpAnn	-0.29	0.30	0.98	0.33
	bisdung	0.11	0.18	0.64	0.53
	slope	-0.11	0.17	0.62	0.54

sqrt(Grasses)	squirrel	0.39	0.13	2.86	0.00
	slope	-0.36	0.14	2.61	0.01
	pptApMay	-0.18	0.18	0.99	0.32
	aspect	0.19	0.17	1.13	0.26
	areaper	-0.02	0.08	0.27	0.79
	tmpJunAu	-0.01	0.07	0.21	0.83

codes used within multiple variable mixed effects models:

bisdung = bison dung counts	SSI = Site Severity Index
squirrel = ground squirrel burrows	tmpAnn = temperature (annual av.)
area = grassland area	tmpJunAu = temperature Jun-Aug
areaper = ratio of grassland area to perimeter	tmpNoMar = temperature Nov-Mar
elev = elevation	pptAnn = precipitation (annual)
aspect = aspect (degrees)	pptApMay = precipitation Apr-May
asmdir = aspect (direction)	pptJunAu = precipitation Jun-Aug
slope = slope	

¹ As there was only one candidate model for Hill's N2, the coefficient values, and associated standard error, t (as opposed to z-value) and p values are not averaged values

Table 14 Summary of seasonal variation in camera trap event duration and the number of bison observed per event. Results of a Tukey test of the difference of means between seasons ($\alpha < 0.05$). The adhoc test was based on a univariate PerMANOVA . Events are strings of consecutive photos depicting one group of bison on the sampling site at one time.

Season pairs	diff	lwr	upr	p adj
Number of bison/event				
spring-fall	1.80	0.33	3.27	0.01
summer-fall	1.66	0.28	3.04	0.01
winter-fall	1.11	-2.06	4.29	0.80
summer-spring	-0.14	-1.71	1.42	1.00
winter-spring	-0.69	-3.94	2.57	0.95
winter-summer	-0.54	-3.76	2.67	0.97
Duration of event				
spring-fall	1.58	-0.77	3.92	0.31
summer-fall	-0.82	-3.03	1.38	0.77
winter-fall	3.67	-1.44	8.78	0.25
summer-spring	-2.40	-4.92	0.12	0.07
winter-spring	2.09	-3.16	7.35	0.73
winter-summer	4.49	-0.70	9.68	0.12

Table 15 Dominant and subdominant plant species occurring in plots sampled in 2011 and 2012 (n=70). Dominant species are those that occur in ≥ 35 plots (50%) and have a mean cover $> 2.5\%$. Subdominant species are those that occur in ≥ 6 plots (35%) and have a mean cover $> 2\%$. Average cover/plot = cover averaged over plots in which the species occurred.

Species	# plots	Average cover/plot (%)	Functional group
Dominant			
<i>Artemisia frigida</i>	68	9.7	forb
<i>Calamagrostis purpurascens</i>	62	4.2	grass
<i>Carex duriuscula</i>	57	8.4	sedge
<i>Oxytropis splendens</i>	41	4.4	forb
<i>Penstemon gormanii</i>	62	4.5	forb
Subdominant			
<i>Carex filifolia</i>	32	4.9	sedge
<i>Carex obtusata</i>	25	5.2	sedge
<i>Carex supina</i>	33	6.0	sedge
<i>Chamaerhodos erecta</i>	30	2.9	forb
<i>Poa glauca</i>	54	2.0	grass
<i>Potentilla pensylvanica</i>	44	2.1	forb

Table 16 Means and SE of percent diet composition of 4 broad forage classes and composite diet indices for wood bison occurring at low elevation (≤ 1000 masl) sites during summer (15 May – 14 October) and winter (14 October - 15 May) in southwestern Yukon, Canada. Standard error in brackets.

Sample Set	Forbs	Sedges & Rushes	Grasses	Shrubs
Winter	1.9 (0.7)	75.6 (2.7)	16.4 (2.3)	3.4 (2)
Summer	3.7 (0.6)	55.9 (5.4)	32.9 (3.4)	6.3 (2.3)

Adapted from Tables 3 and 4 of Appendix A: Dietary Overlap and Potential Competition in a Dynamic Ungulate Community in Northwestern Canada (Jung et al. 2013).

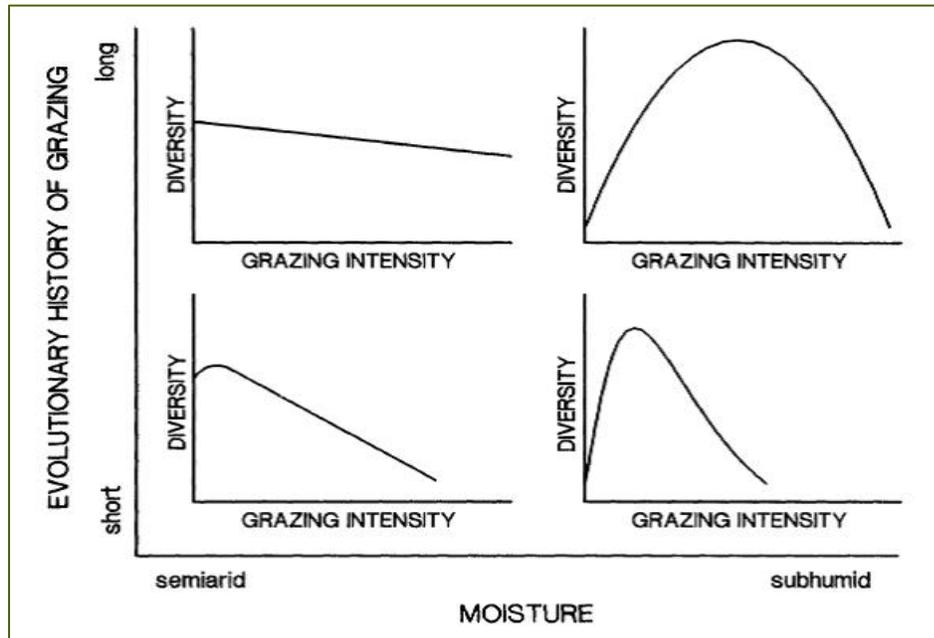


Figure 1 Milchunas' generalized model of effects of grazing by large herbivores on diversity. (Milchunas et al. 1988)

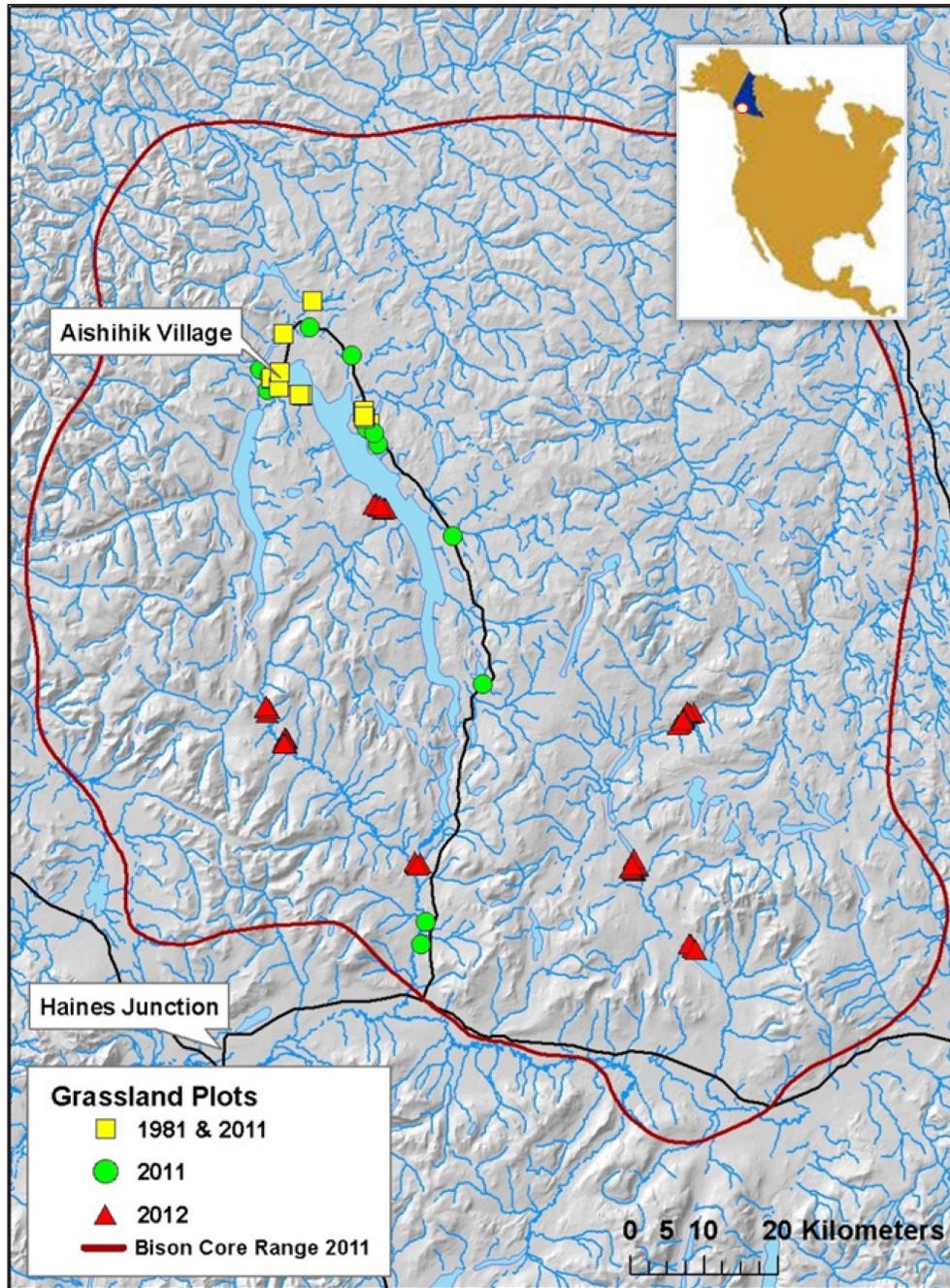


Figure 2 Map of study sites within the Aishihik wood bison herd's 2011 core range. Inset shows the location of the study area in relation to Yukon Territory and North America.

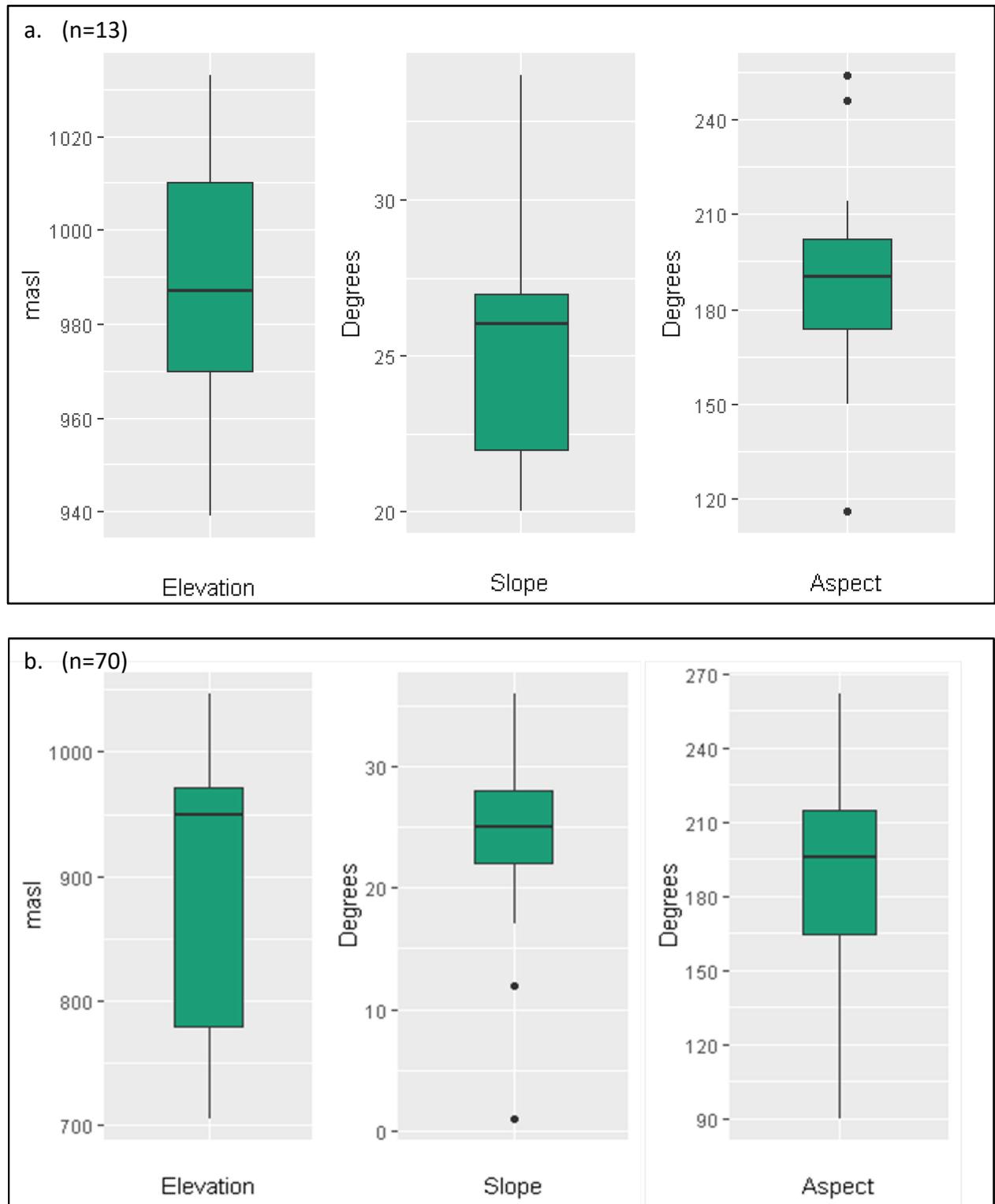


Figure 3 Variation in environmental variables (elevation, slope and aspect) a) across the 13 sites first sampled in 1981 prior to bison reintroduction (Vetter 2001), and b) across the 70 sites sampled in 2011 & 2012 post bison reintroduction (includes the 13 sites first sampled in 1981 and resampled in 2011). With respect to aspect, 90° is east, 180° is south, and 270° is west.

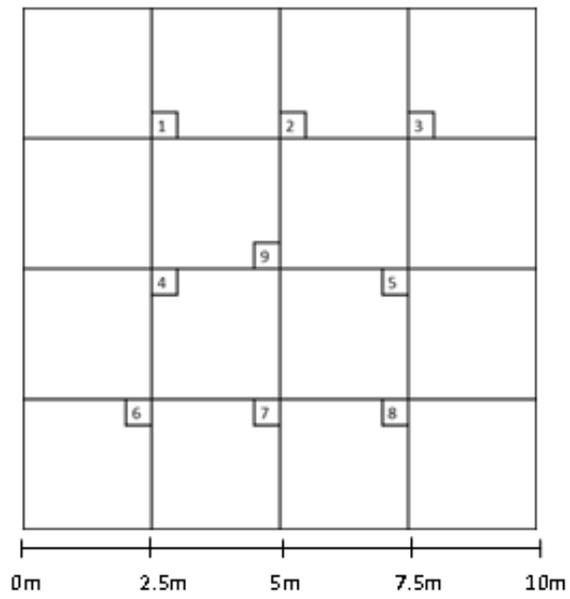


Figure 4 Sampling plot measuring 10m x 10m, containing 9 nested quadrats, each 0.5m x 0.5m.

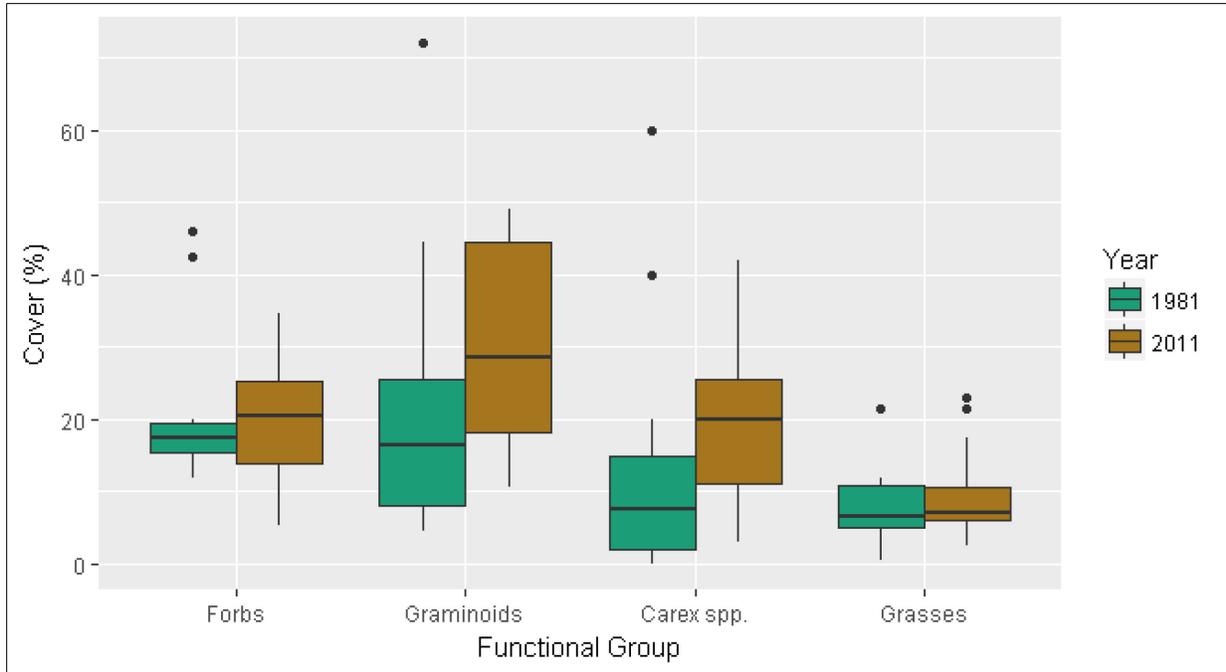


Figure 5 Mean vegetative cover for 4 functional groups (Forbs, Graminoids, Carex, Grasses) prior to bison reintroduction (1981) and after bison reintroduction (2011) (n = 13 for each year).

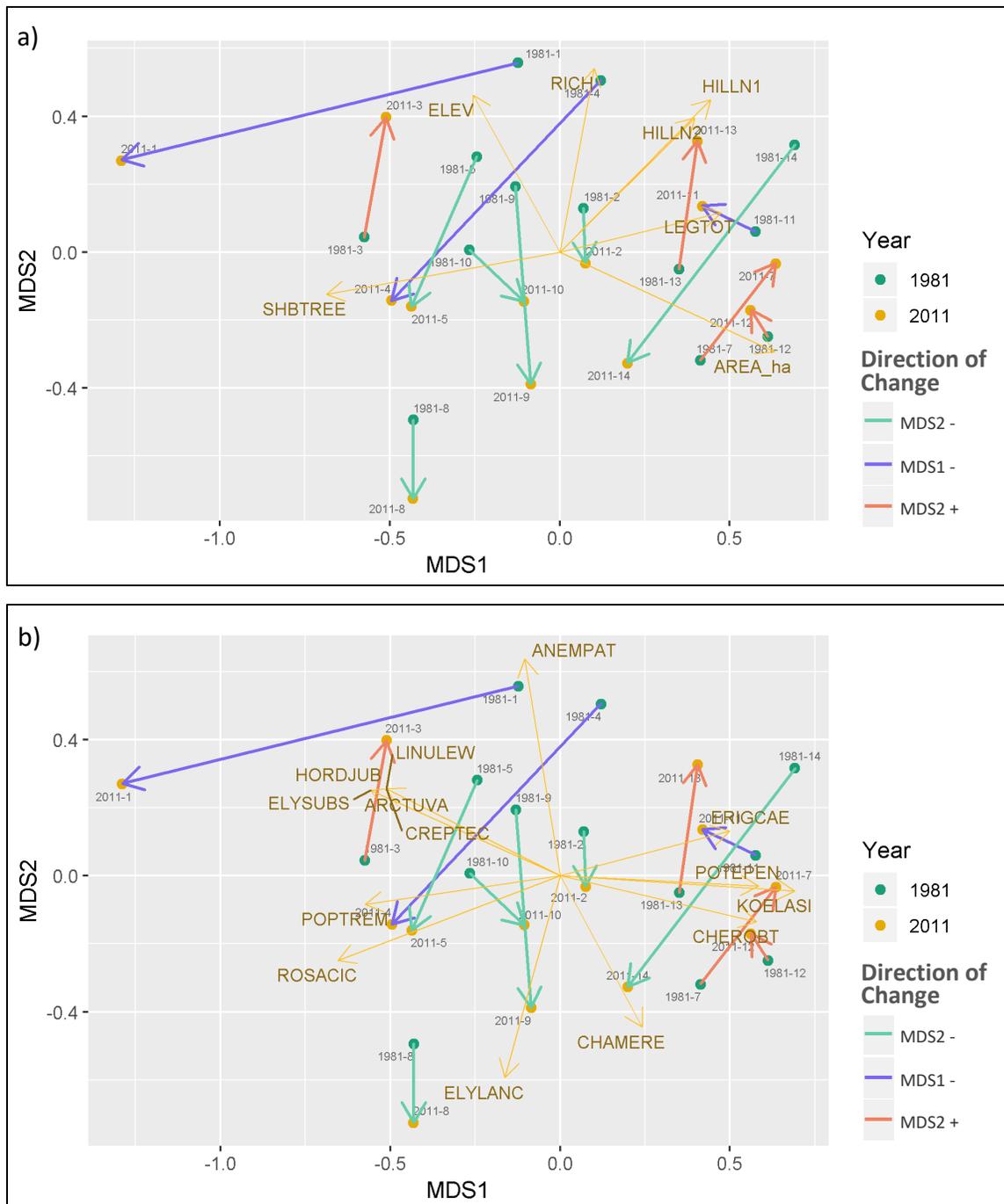


Figure 6 Two-dimensional nonmetric multidimensional scaling ordination of the vascular plant community presented with i) vectors for each plot that indicate by angle and length the direction and strength of plant compositional change between 1981 and 2011 (vectors are colour coded to represent general directional change; $n=13$ for each year); and ii) fitted vectors (gold) representing environmental, site and diversity variables (Plot a), and plant species (Plot b). Only environmental, site, diversity and species vectors that had a significant ($\alpha < 0.05$) relationship to the ordination are shown (see Appendix II for species code descriptions).

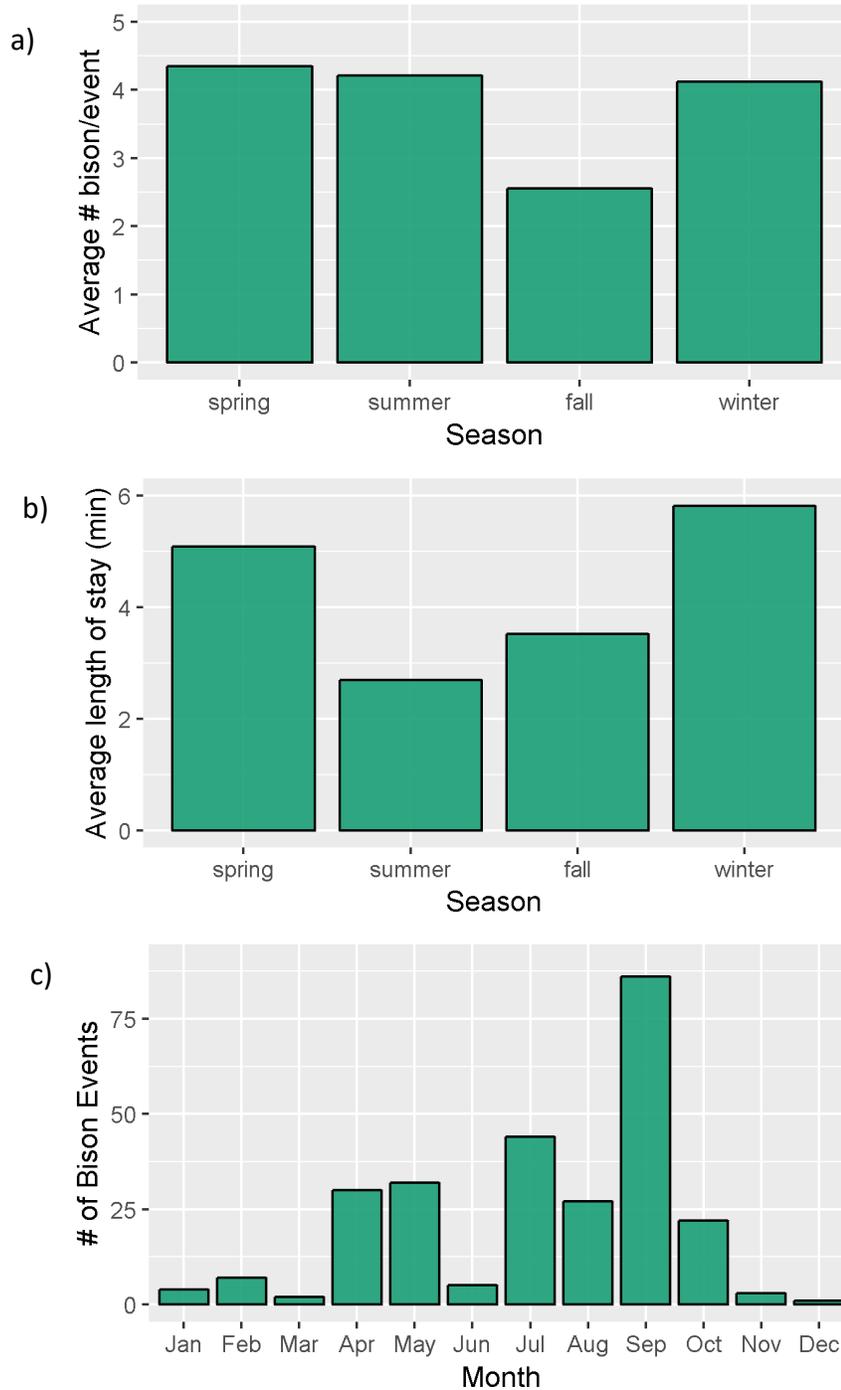


Figure 7 Summary of bison visitation at 5 plots based on camera trap data collected from 10 cameras (2 at each site) from 2013-2017. 3 bar graphs show: a) the average number of bison per event each season (number of bison is the maximum number seen in an event photograph), b) the average amount of time each event lasted each season, and c) the number of bison events per month. Events are strings of consecutive photos picturing one group of bison on the sampling site at one time.

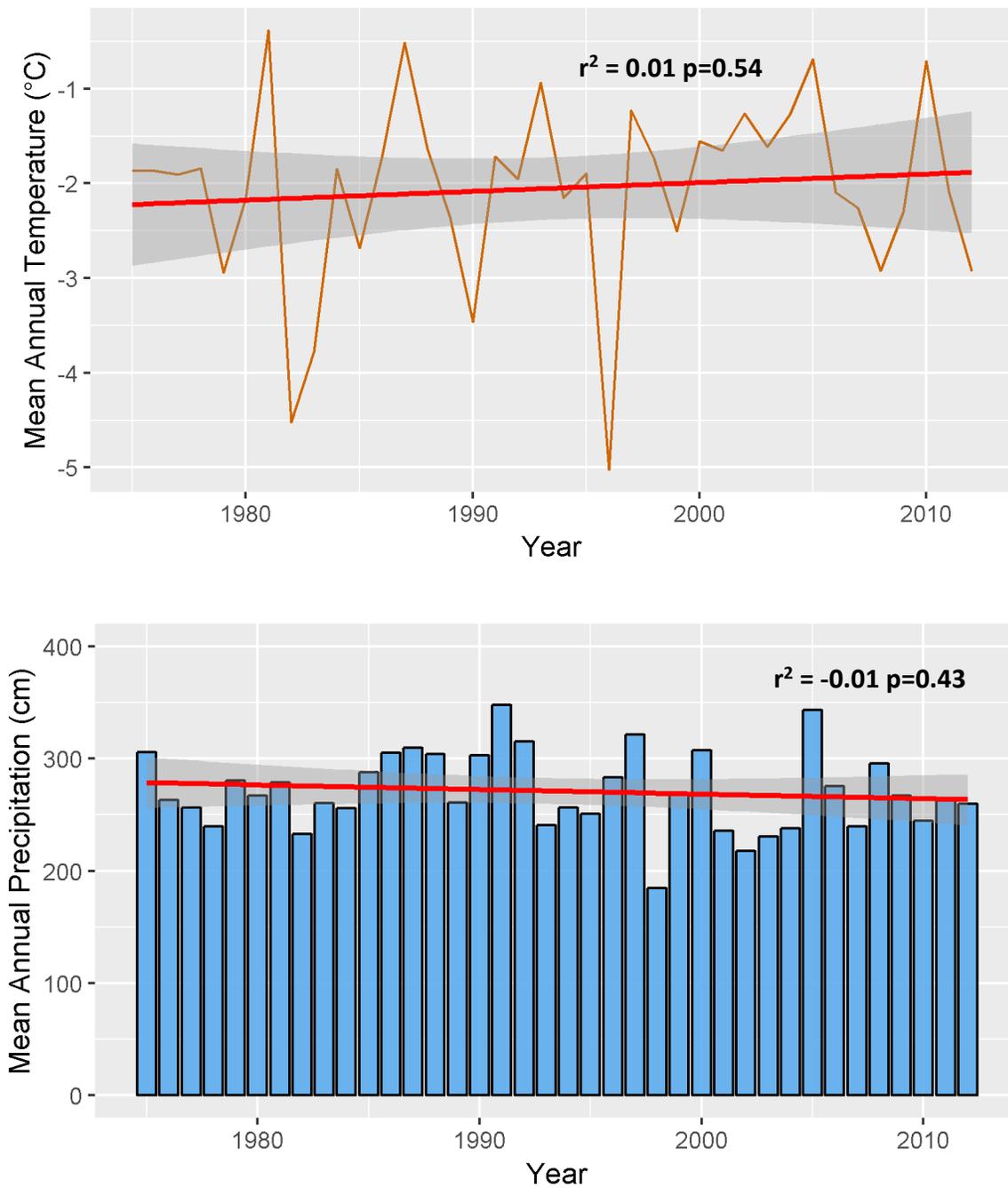


Figure 8 Mean annual precipitation (MAP) and temperature (MAT) from 1975-2012, including more than 10 years both pre- and post- bison reintroduction. Trend lines are shown for both temperature and precipitation values are the average of interpolated plot values derived using ClimateWNA ver5.30 (Wang et al. 2016) (n=70).

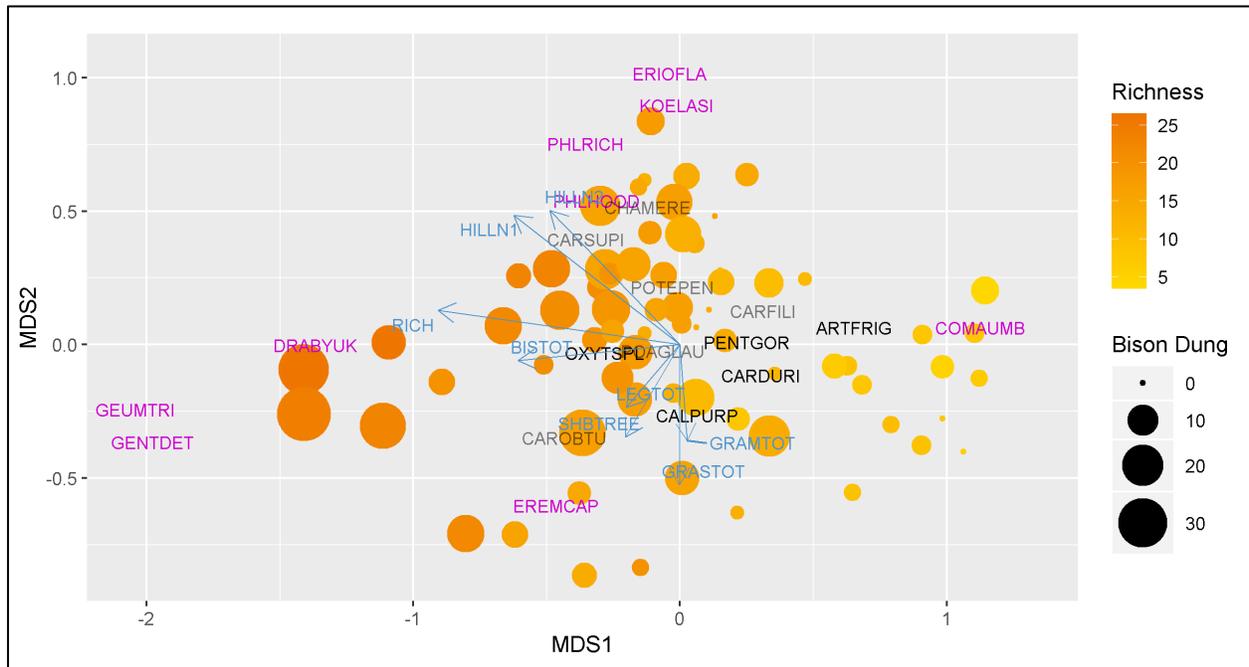


Figure 9 Two-dimensional nonmetric multidimensional scaling ordination of the vascular plant community surveyed in 2011-2012 showing rare (purple), subdominant (grey) and dominant species (black) (n=70; see Appendix II for species code descriptions). Richness, diversity, bison and plant functional group vectors illustrate relationships with plant species ($\alpha < 0.05$). Bison dung counts are represented by size and richness by colour (see legend).

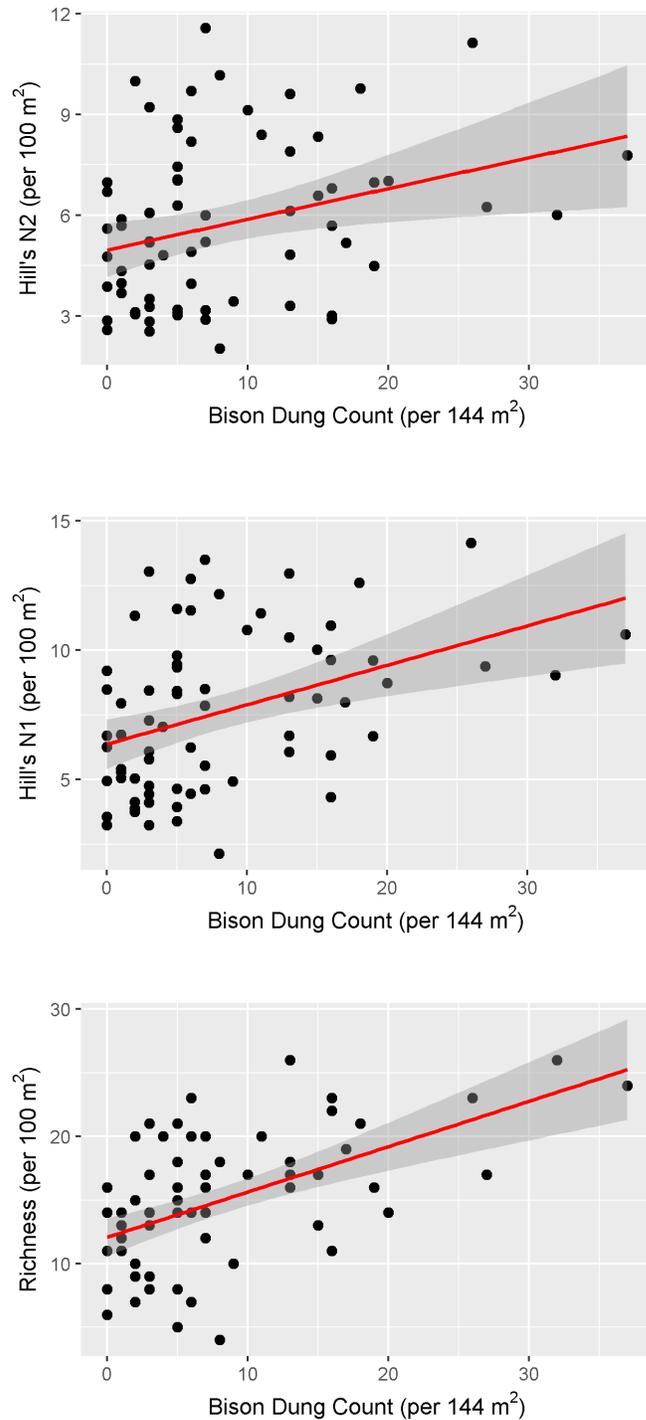


Figure 10 Univariate linear mixed effects models examining the relationship of richness and diversity with bison grazing. Location was the random term. The regression line from the results of the mixed effects model analysis is shown. All relationships are significant ($\alpha < 0.05$).

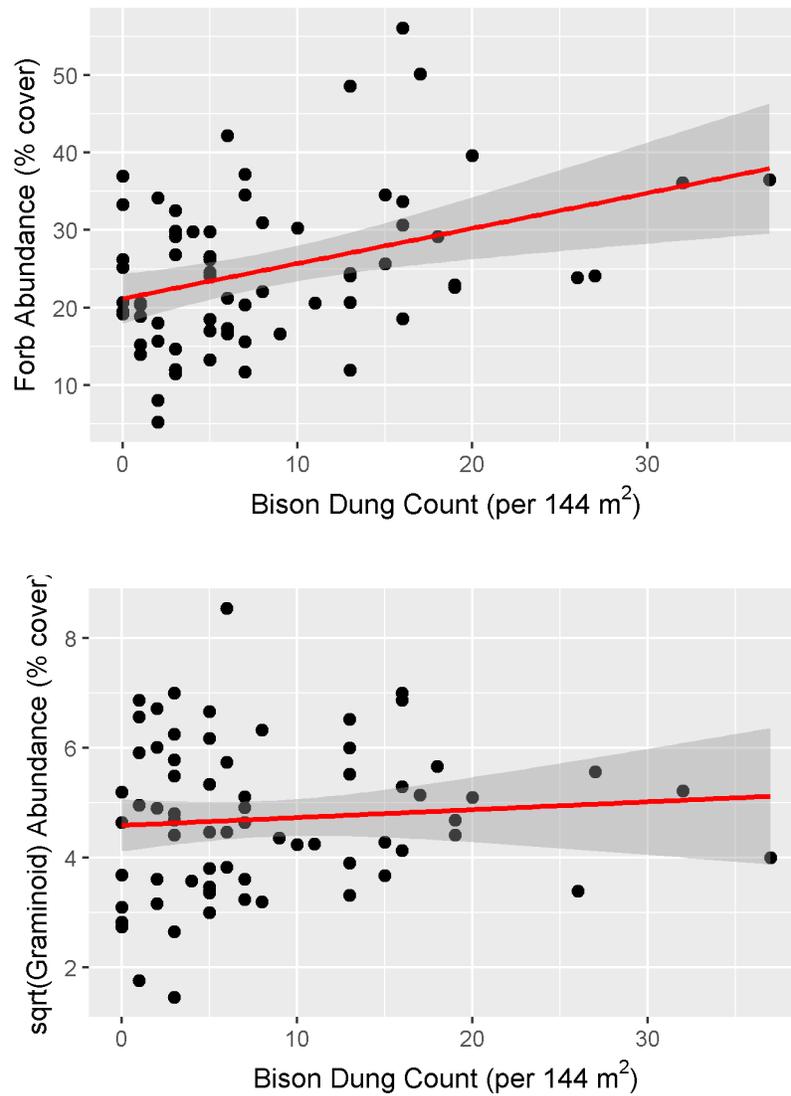


Figure 11 Univariate linear mixed effects models examining the relationship of graminoids and forbs with bison grazing. Location was the random term. The regression line from the results of the mixed effects model analysis is shown. All relationships are significant ($\alpha < 0.05$)

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Appendix I Vascular plant nomenclature for species originally surveyed in 1981 that are referred to by a different name in this study.

Vetter 1981 field sheets	Vetter 2000 paper in Arctic^d	Schroeder 2011 field sheets	Schroeder 2019 final
<i>Achillea borealis</i>	<i>Achillea millefolium</i> ssp. <i>Borealis</i>	<i>Achillea millefolium</i>	<i>Achillea millefolium</i>
<i>Arenaria capillaris</i>	<i>Arenaria capillaris</i>	<i>Arenaria capillaris</i>	<i>Eremogone capillaris</i>
<i>Bupleurum triradiatum</i> ssp. <i>arcticum</i>	<i>Bupleurum americanum</i>	<i>Bupleurum americanum</i>	<i>Bupleurum americanum</i>
<i>Epilobium angustifolium</i> ssp. <i>angustifolium</i>	<i>Epilobium angustifolium</i> ssp. <i>angustifolium</i>	<i>Epilobium angustifolium</i>	<i>Chamaenerion</i> <i>angustifolium</i>
<i>Linum perenne</i> ssp. <i>lewisii</i>	<i>Linum lewisii</i>	<i>Linum lewisii</i>	<i>Linum lewisii</i>
<i>Minuartia arctica</i>	not included	<i>Minuartia obtusiloba</i>	<i>Cherleria obtusiloba</i> ^a
<i>Oxytropis viscida</i>	<i>Oxytropis viscida</i>	<i>Oxytropis viscida</i>	<i>Oxytropis borealis</i> var. <i>viscida</i>
<i>Phlox sibirica</i> ssp. <i>sibirica</i>	<i>Phlox hoodii</i>	<i>Phlox richardsonii</i>	<i>Phlox</i> spp. ^b
<i>Potentilla hookeriana</i> ssp. <i>hookeriana</i> var. <i>hookeriana</i>	<i>Potentilla nivea</i>	<i>Potentilla arenosa</i>	<i>Potentilla arenosa</i> ^c
<i>Potentilla virgulata</i>	<i>Potentilla pensylvanica</i>	<i>Potentilla pensylvanica</i>	<i>Potentilla pensylvanica</i>
<i>Pulsatilla patens</i> ssp. <i>multifida</i>	<i>Pulsatilla ludoviciana</i>	<i>Pulsatilla ludoviciana</i>	<i>Anemone patens</i>
<i>Solidago decumbens</i> var. <i>oreophila</i>	<i>Solidago simplex</i>	<i>Solidago simplex</i>	<i>Solidago simplex</i>
<i>Agropyron trachycaulum</i> var. <i>unilaterale</i>	<i>Elymus trachycaulus</i> ssp. <i>subsecundus</i>	<i>Elymus trachycaulus</i> ssp. <i>subsecundus</i>	<i>Elymus trachycaulus</i> ssp. <i>subsecundus</i>
<i>Agropyron violaceum</i> ssp. <i>andinum</i>	<i>Elymus trachycaulus</i> ssp. <i>Andinus</i>	<i>Elymus trachycaulus</i> ssp. <i>trachycaulus</i>	<i>Elymus trachycaulus</i> ssp. <i>trachycaulus</i>
<i>Agropyron yukonense</i>	<i>Elymus calderi</i>	<i>Elymus calderi</i>	<i>Elymus lanceolatus</i> ssp. <i>psammophilus</i>

Appendix I contd.

Vetter 1981 field sheets	Vetter 2000 paper in Arctic ^d	Schroeder 2011 field sheets	Schroeder 2019 final
<i>Bromus pumpellianus</i> var. <i>arcticus</i>	<i>Bromus pumpellianus</i> var. <i>pumpellianus</i>	<i>Bromus pumpellianus</i>	<i>Bromus pumpellianus</i>
<i>Calamagrostis purpurascens</i> ssp. <i>purpurascens</i>	<i>Calamagrostis</i> <i>purpurascens</i>	<i>Calamagrostis purpurascens</i>	<i>Calamagrostis</i> <i>purpurascens</i>
AUTHORITY: Scroggan (78-79) Hulten (68)	AUTHORITY: Cody (96)	AUTHORITY: Cody (96) Flora of North America Bruce Bennett (pers. comm.)	AUTHORITY: Database of Vascular Plants of Canada (VASCAN) Yukon Conservation Data Centre

^a *Minuartia arctica* was the only *Minuartia* species detected by Mary Vetter in 1981 (in plots 11, 12 and 13). *Minuartia obtusiloba* was the only *Minuartia* detected in 2011 (in plots 7, 11, 12 and 13). The 2011 identification for plot 11 was verified by Bruce Bennett. Since they occurred in the same plots, and *Minuartia arctica* is much more likely to occur further north on alpine snowbed slopes or stony tundra, the *Minuartias* were amalgamated together as *Minuartia obtusiloba* which was revised to *Cherleria obtusiloba* in 2018.

^b Within the 13 plots surveyed in 1981 and 2011, *Phlox hoodii* was the only *Phlox* detected in 1981 (plot 1, 2, 4, 7, 11, 12, 13, 14) while only *Phlox richardsonii* was detected in 2011 (plots 7, 11, 12, 14). Both *Phlox* species were detected in 2011 in other sites in the region. Given that there has been debate on the relative extents and identification of *Phlox hoodii* and *Phlox richardsonii* since 1981, I have amalgamated the 1981 and 2011 *Phlox* together under *Phlox* spp.

^c There are some discrepancies in *Potentilla* identifications within Vetter's 2000 paper published in Arctic. As well, *Potentilla* section *niveae* has been much revised over the last few years. The final determination is based on a combination of Tables 1 and 2 within Vetter's 2000 paper and 2011 observations.

^dVetter, M. 2000. Grasslands of the Aishihik-Sekulmum Lakes area, Yukon Territory, Canada. Arctic 53: 165-173.

Appendix II List of species and taxa for vascular plants sampled during the study, and years in which they occurred. 1981 (Vetter 2000) sampling occurred prior to wood bison reintroduction, 2011 (Vetter plots only) sampling occurred after wood bison reintroduction in the Vetter plots established in 1981, and the 2011 & 2012 (all species) includes all species in all plots sampled after wood bison reintroduction.

Code	Taxon	Common name	Growth form	1981 (Vetter 2000) (n=13)	2011 (Vetter plots only) (n=13)	2011 & 2012 (all species) (n=70)
ACHMILL	<i>Achillea millefolium</i> L.	yarrow	forb	✓	–	✓
ANDSEPT	<i>Androsace septentrionalis</i> L.	fairy candelabra	forb	✓	✓	✓
ANEMPAT	<i>Anemone patens</i> L.	prairie crocus	forb	✓	✓	✓
ANEMULT	<i>Anemone multifida</i> Poiret	cut-leaved anemone	forb	–	–	✓
ANTROSE	<i>Antennaria rosea</i> Greene	rosy pussytoes	forb	–	–	✓
ANTHHR	<i>Anthoxanthum hirtum</i> (Schrank) Y. Schouten & Veldkamp	sweet grass	graminoid	–	✓	✓
ANTIELE	<i>Anticlea elegans</i> (Pursh) Rydberg	mountain death camas	forb	–	–	✓
APHYFAS	<i>Aphyllon fasciculatum</i> (Nuttall) Torrey & A. Gray	clustered broomrape	forb	–	–	✓
ARABup	<i>Arabis</i> spp.	rockcress	forb	–	–	✓
ARCTUVA	<i>Arctostaphylos uva-ursi</i> (L.) Spreng. s.l.	bearberry	shrub/tree	–	✓	✓
ARTFRIG	<i>Artemisia frigida</i> Willd.	pasture sage	forb	✓	✓	✓
ASTEALP	<i>Aster alpinus</i> Linnaeus	alpine aster	forb	–	–	✓
ASTRAUS	<i>Astragalus australis</i> (L.) Lam.	indian milk-vetch	forb	–	✓	✓
ASTRLAX	<i>Astragalus laxmannii</i> Jacquin	Laxmann's milk-vetch	forb	–	–	✓
ASTRTEN	<i>Astragalus tennelus</i> Pursh	loose-flowered milk-vetch	forb	–	–	✓
BOECHOL	<i>Boechera holboellii</i> (Hornemann) Á. Löve & D. Löve	Holboell's rockcress	forb	–	✓	✓
BROPUMP	<i>Bromus pumpellianus</i> Scribn.	northern awnless brome	graminoid	✓	✓	✓

Appendix II contd.

Code	Taxon	Common name	Growth from	1981 (Vetter 2000) (n=13)	2011 (Vetter plots only) (n=13)	2011 & 2012 (all species) (n=70)
BUPLAME	<i>Bupleurum americanum</i> Coult. & Rose	thoroughwort; thorrow wax	forb	✓	✓	✓
CALPURP	<i>Calamagrostis purpurascens</i> R.Br.	purple reed grass	graminoid	✓	✓	✓
CARDURI	<i>Carex duriuscula</i> C.A. Meyer ^a	low sedge	graminoid	–	✓	✓
CARFILI	<i>Carex filifolia</i> Nutt. ^a	thread leaf sedge	graminoid	✓	✓	✓
CAROBTU	<i>Carex obtusata</i> Liljeb. ^a	blunt sedge	graminoid	–	✓	✓
CARROSS	<i>Carex rossii</i> Boott. ^a	Ross' sedge	graminoid	–	✓	✓
CARSUPI	<i>Carex supina</i> Wahl. ^a	weak arctic sedge	graminoid	–	✓	✓
CERARV	<i>Cerastium arvense</i> Linnaeus	field chickweed	forb	–	–	✓
CHAMANG	<i>Chamaenerion angustifolium</i> (Linnaeus) Scopoli	fireweed	forb	✓	–	✓
CHAMERE	<i>Chamaerhodos erecta</i> (L.) Bge.	Chamaerhodos	forb	✓	✓	✓
CHEROBT	<i>Cherleria obtusiloba</i> (Rydberg) A.J. Moore & Dillenberger	sandwort/alpine stitchwort	forb	✓	✓	✓
COMAUMB	<i>Comandra umbellata</i> (Linnaeus) Nuttall	pale comandra	forb	–	–	✓
CREPTEC	<i>Crepis tectorum</i> L.	annual hawksbeard	forb	–	✓	✓
DANINTE	<i>Danthonia intermedia</i> Vasey	intermediate oat grass	graminoid	–	–	✓
DRABCAN	<i>Draba cana</i> Rydberg	hoary draba	forb	–	–	✓
DRABYUK	<i>Draba yukonensis</i> A.E. Porsild	Yukon draba	forb	–	–	✓
ELYLANC	<i>Elymus lanceolatus</i> ssp. <i>psammophilus</i> (J.M. Gillett & H. Senn) Á. Löve	Yukon wheatgrass	graminoid	✓	✓	✓

Appendix II contd.

Code	Taxon	Common name	Growth from	1981 (Vetter 2000) (n=13)	2011 (Vetter plots only) (n=13)	2011 & 2012 (all species) (n=70)
ELYSUBS	<i>Elymus trachycaulus</i> (Link) Gould ex Shinnars ssp. <i>subsecundus</i> (Link) Á. Löve & D. Löve	awned wheatgrass	graminoid	✓	✓	✓
ELYTRAC	<i>Elymus trachycaulus</i> (Link) Gould ex Shinnars ssp. <i>trachycaulus</i>	slender wheatgrass	graminoid	✓	✓	✓
EREMCAP	<i>Eremogone capillaris</i> (Poiret) Fenzl var. <i>capillaris</i>	thread-leaved sandwort	forb	✓	✓	✓
ERIGCAE	<i>Erigeron caespitosus</i> Nutt.	tufted fleabane	forb	✓	✓	✓
ERIGCOM	<i>Erigeron compositus</i> Pursh	cutleaf fleabane	forb	–	–	✓
ERIOFLA	<i>Eriogonum flavum</i> Nutt. var. <i>aquilinum</i> Reveal	yellow umbrella plant; yellow buckwheat	forb	✓	✓	✓
ERYSANG	<i>Erysimum angustatum</i> Rydb.	Dawson wallflower	forb	✓	–	✓
ERYSCOA	<i>Erysimum coarctatum</i> Fern.	crowded wormseed mustard	forb	–	✓	✓
EURYSIB	<i>Eurybia sibirica</i> (Linnaeus) G.L. Nesom	Siberian aster	forb	–	–	✓
FESSAXI	<i>Festuca saximontana</i> Rydb.	rocky mountain fescue; sheep fescue	graminoid	✓	✓	✓
FRAGVIR	<i>Fragaria virginiana</i> Miller	wild strawberry	forb	–	–	✓
GALIBOR	<i>Galium boreale</i> Linnaeus	northern bedstraw	forb	–	–	✓
GENTPRO	<i>Gentiana propinqua</i> Richardson	four-parted gentian	forb	–	–	✓
GENTDET	<i>Gentianella detonsa</i> Rottbøll	sheared gentian	forb	–	–	✓
GEUMTRI	<i>Geum triflorum</i> Pursh	prairie smoke	forb	–	–	✓
HEDBORE	<i>Hedysarum boreale</i> Nuttall	northern sweet-vetch	forb	–	–	✓

Appendix II contd.

Code	Taxon	Common name	Growth from	1981 (Vetter 2000) (n=13)	2011 (Vetter plots only) (n=13)	2011 & 2012 (all species) (n=70)
HORDJUB	<i>Hordeum jubatum</i> L.	foxtail barley	graminoid	–	✓	✓
JUNIHOR	<i>Juniperus horizontalis</i> Moench	creeping juniper	shrub/tree	–	–	✓
KOELASI	<i>Koeleria asiatica</i> Domin	oriental junegrass	graminoid	✓	✓	✓
LAPPSQU	<i>Lappula squarrosa</i> (Retzius) <i>Dumortier</i>	bristly stickseed	forb	–	–	✓
LINULEW	<i>Linum lewisii</i> Pursh	wild blue flax	forb	–	✓	✓
MERTPAN	<i>Mertensia paniculata</i> (Aiton) G. Don	tall bluebells	forb	–	–	✓
MYOSASI	<i>Myosotis asiatica</i> (Vestergren ex Hultén) Schischkin & Sergievskja	alpine forget-me-not	forb	–	✓	✓
OXYTBOR	<i>Oxytropis borealis</i> DC. var <i>viscida</i> (Nutt.) Welsh	sticky locoweed	forb	✓	✓	✓
OXYTSPL	<i>Oxytropis splendens</i> Dougl.	showy locoweed	forb	✓	✓	✓
PENTGOR	<i>Penstemon gormanii</i> Greene	Gorman's beardtongue	forb	✓	✓	✓
PHLHOOD	<i>Phlox hoodii</i> Richards.	moss phlox	forb	✓	✓	✓
PHLRICH	<i>Phlox richardsonii</i> Hook.	Richardson's phlox	forb	✓	✓	✓
PICGLAU	<i>Picea glauca</i> (Moench) Voss	white spruce	shrub/tree	–	–	✓
PLANCAN	<i>Plantago canescens</i> Adams	hairy plantain	forb	–	✓	✓
POAGLAU	<i>Poa glauca</i> Vahl.	glaucous bluegrass	graminoid	✓	✓	✓
POLEPUL	<i>Polemonium pulchellum</i> Hooker	showy Jacob's ladder	forb	–	–	✓
POPTREM	<i>Populus tremuloides</i> Michx.	trembling aspen	shrub/tree	–	✓	✓
POTEARE	<i>Potentilla arenosa</i> (Turczaninow) Juzepczuk	bluff cinquefoil	forb	✓	✓	✓
POTEPEN	<i>Potentilla pensylvanica</i> L.	prairie cinquefoil	forb	✓	✓	✓

Appendix II contd.

Code	Taxon	Common name	Growth from	1981 (Vetter 2000) (n=13)	2011 (Vetter plots only) (n=13)	2011 & 2012 (all species) (n=70)
POTEVIL	<i>Potentilla villosula</i> Jurtzev	villous cinquefoil	forb	–	–	✓
ROSACIC	<i>Rosa acicularis</i> Lindl. s.l.	prickly rose	shrub/tree	✓	✓	✓
SAXTRIC	<i>Saxifraga tricuspidata</i> Rottb.	prickly saxifrage	forb	✓	✓	✓
SEDULAN	<i>Sedum lanceolatum</i> Torrey	stonecrop	forb	–	–	✓
SHEPCAN	<i>Shepherdia canadensis</i> (Linnaeus) Nuttall	soapberry	shrub/tree	–	–	✓
SILEOST	<i>Silene ostenfeldii</i> (A.E. Porsild) J.K. Morton	Ostenfeld's catchfly	forb	–	–	✓
SOLIMUL	<i>Solidago multiradiata</i> Aiton	northern goldenrod	forb	–	–	✓
SOLISIM	<i>Solidago simplex</i> Kunth	mountain goldenrod	forb	✓	✓	✓

^a the upland sedges were amalgamated into one upland sedge category for the purposes of statistical analysis

Appendix III Predictor and response variables with their corresponding codes (as shown in MDS plots) and type. Different measures of bison grazing and environmental covariates are grouped into predictor classes of that name (grazing, size, elevation, insolation, temperature, precipitation, frost-free days and growing degree days).

Variable type (A)	Predictor Class	Variable type (B)	# of variables	Code	Variable
Response (85 variables)		continuous	1	RICH	Richness
		continuous	1	SHAN_HILL	Hill's N1 (exponential of Shannon Index)
		continuous	1	SIMP_HILL	Hill's N2 (inverse of Simpson's index)
		continuous	1	GRAMTOT	Graminoid abundance (% cover)
		continuous	1	GRASTOT	Grass abundance (% cover)
		continuous	1	FORBTOT	Forb abundance (% cover)
		continuous	1	LEGTOT	Legume abundance (% cover)
		continuous	1	SHBTREE	Shrub/tree cover (% cover)
		continuous	77	see App. II	Vascular plant abundance (% cover per species) (77 species)
Predictor (87 variables)	Grazing	continuous	1	BISTOT	Bison dung count (within each 10m x 10m plot and surrounding 1m buffer)
		categorical	1	COLR	Bison Collar data (7 categories based on the density of location points per 2km grid square: 26-50, 51-75, 76-100, 101-150, 151-200, 201-500, 501-1662)
		continuous	1	GDSQTOT	Ground Squirrel burrows (number found within each 10m x 10m plot and surrounding 1m buffer)
	Size	continuous	1	area_ha	Grassland area (ha)
		continuous	1	area_perim	Ratio of grassland area to perimeter length
	Elevation	continuous	1	ELEV	Elevation (masl)
	Insolation	continuous	1	ASPECT	Aspect (degrees)

	categorical	1	ASPDIR	Aspect direction (5 categories: E, SE, S, SW, W)
	continuous	1	SLOPDEG	Slope (degrees)
	continuous	16	INSN_ (prefix followed by month/s and 16DEM to indicate data source for calculations)	Insolation (WH/m ²) - monthly and seasonal ¹ averages
	continuous	1	HLI	Heat Load Index: 0 (coldest) to 1 (warmest)
	continuous	1	SSI	Site Severity Index: -2 (steep NE slopes) to +2 (steep SW slopes)
Temperature	continuous	17	Tave_ (prefix followed by time period and 10yr to indicate 10 year average)	Temperature (°C) – 10 year (2001-2010) monthly, seasonal ¹ and annual averages
Precipitation	continuous	17	PPT_ (prefix followed by time period and 10yr to indicate 10 year average)	Precipitation (mm) – 10 year (2001-2010) monthly, seasonal ¹ and annual averages
Frost-free days	continuous	13	NFFD_ (prefix followed by time period and 10yr to indicate 10 year average)	Frost-free days – 10 year (2001-2010) monthly and annual averages

Growing degree days	continuous	13	DD5_ (prefix followed by time period and 10yr to indicate 10 year average)	Growing degree days (# of days over 5°C) – 10 year (2001-2010) monthly and annual averages
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¹ Seasons: April-May, June-August, September-October and November-December

Appendix IV Summary of global, and adjusted global, linear mixed effects models examining the relationship of vascular plant diversity and abundance with bison grazing and environmental covariates. Location was included as a random effect in all models. The global model comprised of the best fit predictor variables for each predictor class (as identified through univariate mixed effects models) is shown in italicized bold type.

Model	AICc
Richness	
<i>rich ~ slope + bisdung + aspdire + areaper + pptApMay + tmpAnn + squirrel</i>	401.85
rich ~ bisdung + SSI + areaper + pptApMay + tmpAnn + squirrel	399.04
rich ~ slope + aspdire + areaper + pptApMay + tmpAnn + squirrel	408.97
Hill's N1	
<i>HillN1 ~ bisdung + slope + area + tmpAnn + pptAnn + aspect + squirrel</i>	336.71
HillN1 ~ bisdung + insnNoMar + area + pptAnn + squirrel	331.68
HillN1 ~ bisdung + insnNoMar + area + tmpAnn + squirrel	332.75
HillN1 ~ slope + area + aspect + pptAnn + squirrel	339.74
HillN1 ~ slope + area + tmpAnn + aspect + squirrel	340.42
Hill's N2	
<i>HillN2 ~ bisdung + pptJunAu + insnNoMar + area + tmpAnn + squirrel</i>	311.11
Forbs	
<i>forbs ~ bisdung + slope + pptAnn + tmpNoMar + areaper + aspect + squirrel</i>	524.53
forbs ~ bisdung + tmpNoMar + areaper + insnNoMar + squirrel	521.83
forbs ~ bisdung + pptAnn + areaper + insnNoMar + squirrel	520.00
forbs ~ slope + tmpNoMar + areaper + aspect + squirrel	526.22
forbs ~ slope + pptAnn + areaper + aspect + squirrel	525.70
sqrt(Graminoids)	
<i>sqrt(gram) ~ slope + squirrel + elev + bisdung + tmpAnn + area + pptAnn + aspect</i>	245.70
sqrt(gram) ~ slope + squirrel + tmpAnn + area + aspect	238.70
sqrt(gram) ~ slope + squirrel + area + pptAnn + aspect	239.44
sqrt(gram) ~ squirrel + bisdung + tmpAnn + area + insnSepOc	238.97
sqrt(gram) ~ squirrel + bisdung + area + pptAnn + insnSepOc	239.36
sqrt(Carex spp.)	
<i>sqrt(Carex) ~ tmpAnn + slope + bisdung + pptAnn + area + aspect + squirrel + ecolmst</i>	270.80
sqrt(Carex) ~ tmpAnn + slope + area + aspect + squirrel	266.59
sqrt(Carex) ~ slope + pptAnn + area + aspect + squirrel	268.54
sqrt(Carex) ~ tmpAnn + bisdung + area + aspect + squirrel	265.62

sqrt(Carex) ~ bisdung + pptAnn + area + aspect + squirrel 267.52

sqrt(Grasses)

sqrt(grass) ~ squirrel + slope + areaper + tmpJunAu + pptApMay + bisdung + aspect **228.19**

sqrt(grass) ~ squirrel + slope + areaper + tmpJunAu + pptApMay + aspect 225.88

sqrt(grass) ~ squirrel + areaper + tmpJunAu + insnNoMar + pptApMay + bisdung 230.30

codes used within multiple variable mixed effects models:

bisdung = bison dung counts

biscolr = bison collar data

squirrel = ground squirrel burrows

elev = elevation

area = grassland area

areaper = ratio of grassland area to perimeter

aspect = aspect (degrees)

asmdir = aspect (direction)

slope = slope

insnSepOc = insolation Sep-Oct

insnNoMar = insolation Nov-Mar

SSI = site severity index

tmpAnn = temperature (annual av.)

tmpJunAu = temperature Jun-Aug

tmpNoMar = temperature Nov-Mar

pptAnn = precipitation (annual)

pptApMay = precipitation Apr-May

pptJunAu = precipitation Jun-Aug

pptNoMar = precipitation Nov-Mar