Patterns of Non-Native Plants Among Native Grasslands in Alberta, Canada

by

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Abstract

Native grasslands are a fundamental part of Canada's natural heritage, but these formerly extensive ecosystems have undergone declines due to grassland conversion and fragmentation. One threat to remaining native grasslands is invasion by non-native plants, which can outcompete native flora and negatively impact grassland integrity. This study identified patterns of non-native abundance, richness, and individual species occurrences among native grasslands in the Dry Mixedgrass (DMG), Mixedgrass (MG), Northern Fescue (NF), Central Parkland (CP), and Peace River Parkland (PRP) Natural Subregions of Alberta, Canada. Species composition, environmental, and anthropogenic data were collected for 86 plots across the Subregions. Generalized additive models (GAMs) and commonality coefficient analysis were used to identify the strongest predictors for relative cover and richness of non-native plants. In general, abundance and richness of non-native plants were positively linked to moisture and nutrient availability. Aridity and soil fertility were the best predictors across all plots, with mesic loamy grasslands being the most invaded. Patterns of invasion differed between Natural Subregions. In the DMG, relative non-native richness was associated with higher soil carbon content. In the CP, non-native plant abundance and richness was highest in fine-textured fertile soil, as well as on gentle slopes. In the PRP, relative non-native cover was highest on gentle slopes with low pH levels. Kentucky bluegrass (*Poa pratensis* L.) was the most frequent and abundant non-native plant in this study. Crested wheatgrass (*Agropyron cristatum* (L.) Gaertner) and smooth brome (*Bromus inermis* Leysser) were the next most abundant, occurring in clumped distributions in the DMG and CP, respectively. With relatively low cover, dandelion (*Taraxacum officinale* F.H. Wiggers) and goat's beard (*Tragopogon dubius* Scopoli) were the next most frequent. Results suggest that environmental conditions best explain the patterns of non-native plants in Alberta grasslands. However, anthropogenic influences such as agricultural history and proximity, as well as individual species adaptations, may also play a role in the observed

patterns. Future avenues for native grassland research include teasing out soil fertility effects and assessing the roles of topography or soil texture on invasion. The patterns of non-native plants identified in this study can also be considered by land managers who are tasked with prioritizing conservation efforts.

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List of Symbols and Abbreviations

°C	Degrees Celsius
AARD	Alberta Agriculture and Rural Development
ABMI	Alberta Biodiversity Monitoring Institute
Adj-R^2	Adjusted R^2 (regression goodness of fit)
AEP	Alberta Environment and Parks
AG	Agriculture (cropland and tame pasture)
AG	Annual grass
AH	Annual herb
AHM	Annual heat:moisture index
AIC	Akaike information criterion
AICc	Corrected Akaike information criterion
AISC	Alberta Invasive Species Council
ANOVA	Analysis of Variance
AOAC	Association of Official Agricultural Chemists
ASRD	Alberta Sustainable Resource Development
BRH	Biotic resistance hypothesis
CP	Central Parkland Natural Subregion
df	Degrees of freedom
DMG	Dry Mixedgrass Natural Subregion
EC	Electrical conductivity
F	F-value
FF	Foothills Fescue Natural Subregion
FP	Foothills Parkland Natural Subregion
GAM	Generalized additive model
GoA	Government of Alberta
KB	Kentucky bluegrass
MAP	Mean annual precipitation
MAT	Mean annual temperature
MG	Mixedgrass Natural Subregion
MULTISAR	Multiple Species At Risk
n	Number of observations
NF	Northern Fescue Natural Subregion
P	P-value
PCA	Principal components analysis
PCF	Prairie Conservation Forum
PG	Perennial grass
PH	Perennial herb
PO_4-P	Phosphate

PRP	Peace River Parkland Natural Subregion
R^2	Regression goodness of fit
RNC	Relative non-native cover
RNR	Relative non-native richness
RRA	Rangeland Reference Area
SD	Standard deviation
TC	Total carbon
TN	Total nitrogen
TOC	Total organic carbon
VASCAN	Database of Vascular Plants of Canada

1 Introduction

1.1 Grasslands

The Grassland and Parkland Natural Regions in Alberta, Canada, make up the northernmost tip of the Great Plains of North America (Gauthier and Wiken 2003; Downing and Pettapiece 2006). The native grasslands within these regions are intrinsically valuable as they have never been cultivated, and therefore are important for biodiversity, carbon sequestration, livestock production, aesthetics, tourism, and recreation (PCF 2020). Today, native grassland integrity is threatened by urban expansion, cropland conversion, energy resource development, climate change, and non-native species invasions (PCF 2016). Approximately 26% of the former extent of native grasslands remains intact today, and 56% of this is under provincial ownership (MULTISAR 2019).

The grasslands in Alberta have a long history of natural disturbance (Willms, Adams, and Mckenzie 2011). Before settlement of the western prairies, seasonal movement of the plains bison (*Bison bison* L.) and naturally-occurring grassfires are believed to have maintained the prairies as grassland habitats (Moss 1955). Grazing physically removes old growth, which increases light and moisture availability and enhances plant vigour (Frank, McNaughton, and Tracy 1998). Large herbivores also fertilize and cycle nutrients (Metera et al. 2010) and transport seeds which may facilitate dispersal of zoochorous plants (Olff and Ritchie 1998). Bison roamed Alberta's dry southern grasslands in the summer and moved west and north to fescue grasslands in the winter (Morgan 1980). Bison were also managed by Indigenous people who ignited fire (Pyne 1982) to encourage prairie growth and prevent woody species encroachment (Stewart 1956). Both fire and grazing helped maintain grassland ecosystems (Bidlack and Jansky 2011).

Disturbance regimes on Alberta's prairie landscapes are much different today. Domestic livestock, mainly beef cattle, are the primary large herbivore, and instead of

large-scale ungulate movement, grazing occurs in fenced pastures (Willms, Adams, and Mckenzie 2011). With the increase in infrastructure on the landscape and the safety risk to the public, large scale fires are supressed. Fire suppression leads to shrub and aspen encroachment in parkland regions (Bailey and Wroe 1974; R. Adams et al. 2019).

Grasslands in Alberta are found primarily within the Grassland and Parkland Natural Regions, although there are also grasslands within the Foothills and Rocky Mountain Natural Regions (Downing and Pettapiece 2006). The Grassland and Parkland Natural Regions can be further differentiated into distinct Natural Subregions by changes in vegetation, climate, elevation, and latitudinal or physiographic factors.

1.1.1 Grassland Natural Region

The Grassland Natural Region is comprised of native grasslands and cultivated croplands within the southern part of Alberta (Downing and Pettapiece 2006). This Natural Region includes the Dry Mixedgrass, Mixedgrass, Foothills Fescue, and Northern Fescue Natural Subregions, which occur in concentric bands of increasing moisture moving west and north.

The Dry Mixedgrass (DMG) Natural Subregion spans roughly 47,000 km^2 and contains the warmest and driest grasslands in Alberta (Downing and Pettapiece 2006). The DMG prairie is found on Brown and Dark Brown Chernozems (Moss 1955) and features mainly drought-tolerant species such as needle-and-thread grass (*Hesperostipa comata* (Trinius & Ruprecht) Barkworth) and blue grama (*Bouteloua gracilis* (Kunth) Lagasca ex Griffiths) (Coupland 1961). It has relatively high levels of intact prairie compared to other Subregions, with 43% of the DMG remaining as non-cultivated cropland (B. Adams et al. 2013). Oil and gas exploration is extensive in the Subregion, while grazing, dryland farming, and irrigation cover about 55%, 35%, and 10% of the Subregion, respectively (Downing and Pettapiece 2006).

The Mixedgrass (MG) Natural Subregion occupies 20,072 km^2 on the slightly cooler and moister fringes of the DMG (Downing and Pettapiece 2006). Compared to the DMG, the MG features an increase in wheatgrasses (*Elymus* L.) (Coupland 1961) on Brown and Dark Brown Chernozems (Moss 1955). The MG is the most intensely cultivated Subregion with about 85% converted to annual cropland (Downing and Pettapiece 2006).

Moving north, there is a shift to moister prairies dominated by plains rough fescue (*Festuca hallii* (Vasey) Piper) and northern porcupine grass (*Hesperostipa curtiseta* (Hitchcock) Barkworth) in the Northern Fescue (NF) Natural Subregion (Coupland and Brayshaw 1953). Dark Brown Chernozems are most common in this region due to cool climatic conditions and moderate precipitation (Moss and Campbell 1964; Whalen, Willms, and Dormaar 2003). The NF occupies 14,933 km^2 with about 60% cultivated and 40% native grazing lands, and oil and gas exploration and coal mining are frequent in the region (Downing and Pettapiece 2006).

Closer to the foothills of the Rocky Mountains in southwestern Alberta, the moist prairies of the Foothills Fescue (FF) Natural Subregion are dominated by mountain rough fescue (*Festuca campestris* Rydberg) (B. Adams et al. 2015). Black Chernozems are the dominant soil (Downing and Pettapiece 2006). Approximately 30% of its 13,620 km^2 remains as native grassland (MULTISAR 2019), but the amount of cultivation varies from 80% on plains and less than 20% on hilly uplands (Downing and Pettapiece 2006).

1.1.2 *Parkland Natural Region*

The Parkland Natural Region is comprised of patches of aspen (*Populus tremuloides* Michaux), shrublands, native grasslands, and productive agricultural land (Downing and Pettapiece 2006). This Natural Region includes the Central Parkland, Foothills Parkland, and Peace River Parkland Natural Subregions.

The Central Parkland (CP) covers 53,607 km^2 and occurs at intermediate climatic conditions between the Grassland and the Boreal Natural Regions (Downing and Pettapiece 2006). Grasslands within the CP were historically dominated by plains rough fescue, but today about 80% of the plains and 65% of hummocky uplands are converted to cropland, with the remaining area left as native grazing lands (Downing and Pettapiece 2006). Aspen groves are a result of increased moisture (Kupsch et al. 2013). The region has heavy agricultural influence and is best delineated by soil characteristics (Downing and Pettapiece 2006). Plant community composition within the CP changes with soil texture, drainage, and topographic features (Kupsch et al. 2013).

The Foothills Parkland (FP) covers 3,921 km^2 and occurs at intermediate climatic conditions between Grassland and the Rocky Mountain regions, and the grasslands resemble those of the FF (Downing and Pettapiece 2006).

The Peace River Parkland (PRP) covers 3,120 km^2 in northwestern Alberta (Downing and Pettapiece 2006). Nearly all of the upland grasslands in the PRP have been cultivated, and remnant native grasslands occur mainly on steep south-facing river slopes (Wilkinson and Johnson 1983; PCF 2019). These grasslands are dominated by western porcupine grass (*Hesperostipa curtiseta* (Hitchcock) Barkworth), June grass (*Koeleria macrantha* (Ledebour) Schultes), and sedges (*Carex* L.) (Moss 1952; Stone, Willoughby, and Rosendal 2007). The spatial extent of grasslands in the PRP may have fluctuated in the past due to drought and prescribed burning by Indigenous peoples (Schwarz and Wein 1999). Unlike the FP and CP, rough fescue is absent from the PRP (Wilkinson and Johnson 1983; Stone, Willoughby, and Rosendal 2007). The grasslands within the PRP are understudied compared to other grasslands in Alberta.

1.2 Non-Native Plant Invasions in Grasslands

1.2.1 Impacts in Grasslands

A non-native plant refer to a species that has been introduced outside of its natural range (IUCN 2000). Non-native plants that are introduced to a new area may remain as casual if they cannot establish and reproduce successfully, but non-native plants can become naturalized if they overcome environmental and reproductive barriers, and invasive once they establish rapidly spreading populations (Richardson et al. 2000). According to VASCAN, 14% of the total richness of vascular plant species occurring in Alberta is non-native (excluding ephemeral plants not permanently established and annually cultivated plants like tomato or wheat) (Brouillet et al. 2020).

The impacts of non-native plants are a concern because grasslands have biological, aesthetic, spiritual, economic, and social values (PCF 2020). Invasive non-native plants can outcompete native species, leading to reduced native plant abundance and diversity (S. D. Wilson 1989; Vilà et al. 2011; Lyseng et al. 2018). An example of this impact in Canadian grasslands is the decline in grassland biodiversity when invaded by agronomic perennial forage grasses crested wheatgrass (*Agropyron cristatum* L. Gaertner) in semi-arid grasslands, and Kentucky bluegrass (*Poa pratensis* L.) and smooth brome (*Bromus inermis* Leysser) in mesic grasslands (Henderson and Naeth 2005; Toledo et al. 2014; Stotz, Gianoli, and Cahill 2019). In a native grassland, the displacement of native plants by invasive plants such as the rapidly senescing Kentucky bluegrass may reduce forage quality and availability for livestock (Bailey, McCartney, and Schellenberg 2010). Changes in the plant community can reduce habitat for some local fauna (Bartomeus, Vilà, and Santamaría 2008), such as abundance of upland sandpiper (*Bartramia longicauda*) and Sprague's pipit (*Anthus spragueii*) in Manitoba grasslands (S. Wilson and Belcher 1989). Invasion can also enhance habitat for other fauna, such as pollinators (Nielsen, Heimes, and Kollmann 2008). Established invasions can alter soil properties (Timsina et al. 2011) and nutrient cycling

(D'Antonio and Vitousek 1992). In southern Alberta grasslands, crested wheatgrass invasion is associated with a loss in soil quality (Dormaar et al. 1995; Lesica and Deluca 1996) and ecosystem function due to the alteration of pools and movement of energy and nutrients (Christian and Wilson 1999).

1.2.2 Potential Drivers of Invasion

Identifying patterns of non-native plants and the associated environmental conditions driving these patterns could help researchers better understand plant invasions. Empirical studies have led to several hypotheses for drivers of non-native plant establishment and spread (Richardson and Pyšek 2006).

Availability of water and nutrients on the landscape influence biodiversity patterns (Hawkins et al. 2003). In theory, adequate growing conditions that benefit native plants should also benefit non-native plants (Stohlgren et al. 2002). According to the fluctuating resources hypothesis, non-native plants may benefit more from abundant and fluctuating resources compared to native plants (Davis, Grime, and Thompson 2000) because plants may experience a pulse in growth when resources are high (Goldberg and Novoplansky 2009). In Alberta and elsewhere, studies have identified positive associations between moisture and nutrient availability and levels of non-native plants (Mcintyre and Lavorel 1994; Larson, Anderson, and Newton 2001; Blumenthal et al. 2008; Lyseng et al. 2018).

Plant community characteristics may dictate the susceptibility of habitats to invasion by non-native plants. The biotic resistance hypothesis states that ecosystems with high native diversity are resistant to non-native plant invasion due to more complete use of limiting resources (Elton 1958; Tilman 1997; Kennedy et al. 2002). However, inconsistencies among biotic resistance studies have made it the BRH a less popular hypothesis in recent years (Nunez-Mir et al. 2017).

Anthropogenic disturbance may encourage introduction of non-native plants due to elevated propagule pressure brought on by repeated introductions (Richardson and Pyšek 2006). For example, transportation corridors may accelerate introduction of non-native plants (Gifford and Otfinowski 2013). In Alberta, non-native plant richness and diversity in the CP natural subregion increased as the proportion of oil and gas disturbances increased (Vujnovic, Wein, and Dale 2002). Intentional seeding of forage plants can also increase non-native plant species presence in surrounding native communities (Scasta et al. 2015).

Grazing has varying impacts on grasslands. Under the intermediate disturbance hypothesis (Connell 1979), moderate grazing intensities enhance overall plant biodiversity due to a mosaic of heavily and lightly grazed patches (Douwes and Willms 2012; Johnston 1960; Milchunas, Sala, and Lauenroth 1988). Heavy or prolonged grazing can promote non-native plant invasion in Canadian grasslands (Willms, Smoliak, and Dormaar 1985; Willms, Adams, and Mckenzie 2011; Sinkins and Otfinowski 2012). On the other hand, prolonged protection from grazing leads to excess litter buildup (Willms, Adams, and Mckenzie 2011), which can also promote non-native plant invasion through microsite changes (Grace et al. 2001). Worldwide, grassland communities with long grazing histories may be more resistant to invasions due to intrinsic vegetative adaptations to disturbance (Alpert, Bone, and Holzapfel 2000).

Time since introduction may also influence the establishment and spread of non-native plants. Longer residence times after initial introductions may increase the spatial distributions of non-native plants (Pysek and Jarošík 2005). However, some habitats may experience invasion debt, or a lag in plant invasion, which means that invasion has not yet occurred even though there is potential for it (Rouget et al. 2016). The lag between introduction and invasion can be shortened if closer to anthropogenic disturbances due to ongoing entry of non-native propagules (Essl, Mang, and Moser 2012).

1.2.3 Non-native Plants in Alberta Grasslands

The Alberta Weed Control Regulation provides a list of invasive noxious and prohibited noxious plants threatening Alberta's landscapes (GoA 2010). A few species that are well-known invaders in grassland habitats include baby's breath (*Gypsophila paniculata* L.), cheatgrass (*Bromus tectorum* L.), leafy spurge (*Euphorbia esula* L.), Canada thistle (*Cirsium arvense* (L.) Scopoli), and yellow toadflax (*Linaria vulgaris* Miller) (AISC 2020). Besides this list, there is increasing concern about invasive non-native plants that do not appear on the Weed Control Regulation list, such as crested wheatgrass (Henderson and Naeth 2005) and cicer milkvetch (*Astragalus cicer* L.) (Le and Carlyle 2019) in southern Alberta, and smooth brome (Stotz, Gianoli, and Cahill 2019) and Kentucky bluegrass (Tannas 2011; White et al. 2013) in east-central and northern Alberta.

There is abundant research on impacts (Smoliak and Dormaar 1985; Christian and Wilson 1999; Henderson and Naeth 2005; Sanderson et al. 2017) and control (Cole et al. 2011; Otfinowski, Pinchbeck, and Sinkins 2017; Stover, Naeth, and Wilkinson 2017) of invasive non-native plants in Canadian grasslands. There is a smaller body of research that specifically addresses the drivers of invasion in Alberta grasslands (Hill, Willms, and Aspinall 2000; Tannas 2011; White et al. 2013; Bennett, Stotz, and Cahill 2014). Few studies to date have taken a multi-variable approach to quantifying patterns of non-native plants across a broad spatial scale of Alberta grasslands (but see Hill, Willms, and Aspinall 2000; Vujnovic, Wein, and Dale 2002; and Lyseng et al. 2018).

1.3 Thesis Aims

This thesis examines patterns of non-native plants across native grasslands at two spatial scales in Alberta. (1) I will first quantify patterns of non-native plants across 86 native grassland plots placed along an 800 km north-south gradient in Alberta. This broad-scale approach will test multiple environmental and anthropogenic predictors in order to identify patterns of non-native plant cover, richness, and individual species occurrence

across several native grassland types. Given the wide variation in annual precipitation, temperature, and soil fertility along this gradient, I hypothesize that these predictors will be most important for predicting patterns of non-native plants because moisture and nutrient availability strongly influence general plant biodiversity patterns (Hawkins et al. 2003). Furthermore, given the well-documented effects of anthropogenic activity on plant invasions (Henderson and Naeth 2005; Pysek et al. 2010; Essl, Mang, and Moser 2012), I hypothesize that the presence of nearby agricultural conversion of native grasslands to cropland or fragmentation by oil and gas activity, would also be important in predicting non-native plant patterns due to the increased influx of non-native plant propagules into native grasslands. (2) The second part of this thesis will involve analysis of the same predictors for plots located within the DMG, CP, and PRP Natural Subregions, respectively. This approach offers a local landscape analysis of non-native plant patterns while holding large-scale climatic influences constant. I hypothesize that topography will be an important predictor for non-native plant patterns since moisture and nutrients can vary with subtle changes in topographic relief (Moeslund et al. 2013). The results will be discussed in the context of invasion theory while also taking historical influences into account. I will then synthesize the key research results, highlight practical applications on grasslands, and identify future research needs.

2 Methods

2.1 Study sites

From June to August 2019, I sampled 86 prairie grassland plots across a 1,000 km gradient from south-east to east-central and northwestern Alberta (Appendix A). My survey included 27 plots in the Dry Mixedgrass, 4 in the Mixedgrass, 10 in the Northern Fescue, 28 in the Central Parkland, and 17 in the Peace River Parkland Natural Subregions. To achieve an even distribution of plots across the province, the number of plots surveyed within each Natural Subregion was proportionally represented by the Subregion's area. Thirty-six plots were located on grazing leases that were randomly chosen from a list of all grazing leases within each Natural Subregion (Altalis 2019). Twenty-six plots were in close proximity to Alberta Environment and Parks (AEP) Rangeland Reference Areas (RRAs), which are long term monitoring sites located on grazing leases or vacant public land with publicly available vegetation data (AEP 2020). I sampled eight plots in Alberta Parks and Protected Areas, and two on vacant public land. Before field work, I reviewed aerial imagery and interviewed grazing leaseholders (if applicable) to confirm that my potential sites had not been previously cultivated nor purposefully seeded with agronomic species. I sampled only one plot per grazing lease, except in exceptionally large grazing leases as in the Special Areas or the Peace River region where plots occasionally were placed within the same lease but not on the same quarter section. Upon arrival at the site, I used aerial imagery and visual inspection to choose a plot location that was in open grassland at least 50 m away from infrastructure such as roads or well sites. This criterion allowed me to standardize localized edge effects from localized anthropogenic disturbances. After a homogenous grassland area with minimal landscape and vegetation anomalies was identified, the exact plot location was chosen by blindly throwing an object to determine a plot corner. The observed grazing regime did not matter during sampling, as this would be impossible to quantify before arriving at the site. I aimed to sample a relatively even proportion of topographic positions

where logistically possible. Sampling began in southern Alberta and continued northwards to coincide with the phenological timing of peak vegetation growth (Caprio 1966; Beaubien 1994).

2.2 Data Collection

2.2.1 Vegetation Survey

I recorded the percent cover of all vascular plant species within a 10 x 10 m plot, as well as separate cover values for each physiognomic group (shrubs, herbs, lichens, and bryophytes), litter, bare soil, and rock. Specimens that could not be identified in the field were collected and identified in the lab. If identification to species was not possible, plants were identified to genus (6% of all taxa in the total species list). I assigned the most recent nomenclature following VASCAN (Brouillet et al. 2020). Species not occurring in the VASCAN database for Alberta were confirmed using Flora of Alberta (Moss and Packer 1983) or Flora of North America (Flora of North America Editorial Committee 2020). Due to small taxonomic differences between native and non-native subspecies of Kentucky bluegrass (native: *Poa pratensis* subsp. *agassizensis*, non-native: subsp. *angustifolia* and subsp. *pratensis)*, I sampled Kentucky bluegrass in each plot and sent specimens for expert identification (Robert J. Soreng, National Museum of Natural History). The full species list is provided in Appendix B.

Relative non-native cover (RNC) was calculated by dividing the total non-native cover by the total vegetation cover in each plot (native + non-native). Similarly, relative non-native richness (RNR) was the number of non-native plant species divided by the total richness per plot. I chose relative measures because they improve comparability of non-native plant metrics across plots with variable total vegetation cover and richness (Catford et al. 2012).

2.2.2 Environmental Data

At each plot I recorded elevation, slope, aspect, regional landform, topographic position, site shape, and geographic coordinates. Topsoil texture was estimated by hand following Watson and Pennock (2016) at three random spots inside the 10 x 10 m plot to confirm homogeneity. I used a trowel to sample topsoil to a depth of 5 cm from three random locations within the plot. These subsamples were bulked and mixed into one topsoil sample per plot for lab analysis. Soil samples were dried in the oven at 50°C for 48 h before analyses. Soil pH was determined using a pH probe (Cole-Parmer pH/Conductivity meter) by averaging the readings obtained with distilled water $CaCl_2$ (1:2.5 soil:water ratio) (Carter and Gregorich 2008). I determined conductivity (measured in μS/cm) in distilled water using an EC probe (Cole-Parmer pH/Conductivity meter, Carter and Gregorich 2008). Total nitrogen (TN), total carbon (TC), and total organic carbon (TOC) (each measured in w/w%) were determined using the dry combustion method (Soil Science Society of America 1996; AOAC International 2000; Schumacher 2002; Thermo Fisher Scientific 2014). The Molybdenum Blue Colorimetric Analysis with Modified Kelowna Extraction was used for phosphate (PO_4-P) analysis (United States Environmental Protection Agency 1993). Climate data were generated with the ClimateAB v3.21 software package (http://tinyurl.com/ClimateAB) based on methodology described by Mbogga et al. (2010) and Alberta Environment (2005). The annual heat:moisture index (AHM) was assigned to each plot by combining mean annual temperature (MAT) and mean annual precipitation (MAP) using the formula (MAT + 10) / (MAP / 1000) (Alberta Environment 2005; Mbogga et al. 2010). Low AHM indicates low aridity (cooler, wetter climate) while high AHM indicates greater aridity.

2.2.3 Anthropogenic Impact Data

To quantify anthropogenic impact, I used the Alberta Biodiversity Monitoring Institute (ABMI) 2018 Wall-to-Wall Human Footprint Inventory (ABMI and Alberta Human

Footprint Monitoring Program 2017). Using QGIS v.3.4.5 (QGIS.org 2020), I calculated the proportion of anthropogenically-altered land within a 1 km radius of the plots. I also grouped footprints into broad categories: agricultural activity (cropland and tame pasture), oil and gas (well sites, pipelines, seismic lines, plants, miscellaneous facilities), and roads (highways, improved, unimproved). I chose these categories because of their previously documented role in the spread of invasive plants. I chose a 1 km radius because it had the strongest signals compared to other tested radii.

I estimated grazing intensity several ways because it is difficult to quantify at the local scale (Holechek et al. 1998; Holechek and Galt 2000). The first method was to count all previous-year dung pats and estimate their percent cover within the 10 x 10 m plot. The second method was to complete a Grassland Rangeland Health Assessment to get a range health score, which is a multi-question assessment that takes into account the ecological status of the plant community, plant community structure, hydrologic function and nutrient cycling, site stability, and noxious weeds (B. Adams et al. 2016). To narrow down the number of grazing variables to use in analyses, I used principle components analysis (PCA) ordination using the 'prcomp' function in R to combine the grazing variables into a single axis (R Core Team 2020). However, including the range health score in the PCA was problematic because it did not reflect the same signal in grazing intensity as dung cover or count. The final PCA axis was generated from a combination of dung count and dung cover, which together accounted for 65% of the variation; this PCA axis was used as a proxy for grazing intensity in subsequent analyses.

2.3 Data Analysis

I used R v.4.0.3 to conduct all analyses (R Core Team 2020). To capture broad-scale patterns of non-native plants across Alberta, I first pooled all 86 plots into one dataset for analyses. Trends in RNC and RNR were evaluated using generalized additive models (GAMs) from the 'mcgv' package in R (Wood 2011). I considered using zero-inflated beta regression

models (Ospina and Ferrari 2012), but model selection based on AIC found that GAMs provided a better fit. I conducted the analyses in two steps.

2.3.1 Bivariate Models

I ran simple bivariate models (one single predictor only) for the two response variables (RNC or RNR). The significance of each predictor was determined by the P-value for the overall effect (at the P≤0.05 level) and by visual inspection of the predictions. I used visual inspection to identify influential points that affected model outcomes. Several influential points were noted. Plot 45 (CP) had abnormally high conductivity and plot 15 (DMG) and plot 46 (CP) each had high phosphate levels. Plot 18 (DMG) and plot 70 (PRP) each had unusually high RNC compared to other plots. I ran analyses with and without the influential plots. In most cases, influential plots did not impact results. When results changed due to predictor variable outliers (conductivity, PO_4-P), I evaluated trends with the outlier removed, but omitted those predictors in the next step. When results changed due to RNC outliers, I evaluated trends without the influential plot and explored other contributors to this response.

2.3.2 Multiple Predictor Models

To compare the effects of multiple significant predictors, I compared models based on AIC using the 'MuMIn' package in R (Barton 2020). I then used commonality analysis in the 'yhat' package in R to account for multicollinearity among correlated significant predictors (Nimon, Oswald, and Roberts 2020). Commonality analysis is a linear model technique that can partition the variance (R^2) of a multiple regression model into unique and shared effects (Nimon et al. 2008). The analysis calculates commonality coefficients by comparing the R^2 of models with and without the effect(s) and calculates the percentage of this component relative to the R^2 of the model. Unique effects are defined as the variance that is unique to a specific variable, while shared effects are the variation that is common among groups of variables (Reio et al. 2015). Adding up the unique and common effects

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equals the total variance in the dependent variable explained by the predictor variables (Reio et al. 2015). Commonality analysis was traditionally used in the social sciences to address multicollinearity among predictors, but has more recently been used in ecology with the introduction of an R package to make computation more accessible (Nimon et al. 2008).

2.3.3 Subregion-specific Analyses

I followed the same procedure to capture patterns of non-native plants within the DMG, CP, and PRP Natural Subregions. The MG and NF Subregions were excluded from Subregion analyses because of their comparatively small number of plots. Model selection and commonality coefficient analyses were performed for the CP and the PRP, but not for the DMG because it only had a single significant predictor.

2.3.4 Influence of Kentucky Bluegrass

To test the importance of the non-native Kentucky bluegrass dominance among mesic grassland plots, I removed it from the dataset, re-ran the models, and compared model summaries. Out of the 59 *Poa pratensis* specimens collected, 51 were confirmed as the non-native *Poa pratensis* subsp. *angustifolia*, four were subsp. *pratensis*, and four were the native subsp. *agassizensis*.

3 Results

3.1 Broad patterns of native and non-native plants

Two hundred and four plant species were found in a survey of 86 grassland plots across Alberta: 183 natives and 23 non-natives (Appendix B). Out of the non-native plants there were six perennial grasses, one annual grass, seven perennial forbs, and nine annual forbs. Native vegetation associations resembled previously documented grassland communities (Downing and Pettapiece 2006). Kentucky bluegrass was the most common non-native plant, occurring in 48 out of the 86 plots, and making up 71% of the total non-native plant cover recorded in this study. Smooth brome had the next highest cover, but it occurred infrequently and mainly in the mesic grasslands (7% of total non-native cover; 6 out of 86 plots). Similarly, crested wheatgrass was the third most abundant non-native grass but occurred infrequently and mainly the semi-arid grasslands (6% of total non-native cover; 4 out of 86 plots). Meanwhile, dandelion (*Taraxacum officinale* F.H. Wiggers) and goat's beard (*Tragopogon dubius* Scopoli) occurred frequently across throughout the province (49% and 35% of plots, respectively) but at low abundances (occupying 6% and 3% of total non-native cover, respectively). Frequency and percent cover of all non-native plants are reported in Table 1.

Total plant richness (native + non-native) increased as grasslands got cooler and wetter, and as total carbon (TC) and total nitrogen (TN) increased (Figure 1). Total plant cover did not change over the aridity gradient but did decrease with slope (Figure 1). Model summaries for total plant cover and richness are provided in Appendix C.

Both the Central Parkland (CP) and the Peace River Parkland (PRP) had the highest average RNC out of all the Subregions, and the PRP had the highest average RNR (Appendix D). RNC increased as grasslands got cooler and wetter, and as TC, TN, phosphate (PO_4-P), and agricultural activity increased (Figure 2). RNC generally decreased with increasing pH and increased with conductivity, though the statistical significance of these

relationships depended on the inclusion or omission of a conductivity outlier (Appendix E; Figure 2). Gentle slopes and low slope positions also had higher RNC (Figure 2). RNR increased with TC, TN, and PO_4-P (Figure 4). TN and TC were the strongest predictors for RNC and RNR across all plots (Appendix E). Shared effects between climate and soil fertility explained variance in RNC in the following ways: 15% was explained by AHM, TN, TC, and agricultural activity; 15% was explained by AHM, TC, and TN; and 10% was explained by TC and TN (Table 2; Figure 3). Topography uniquely explained 26% of the variance in RNC (Table 2; Figure 3). For RNR, 58% of the variance was explained by shared effects TC and TN, and 32% was explained by shared effects of TN, TC, and PO_4-P (Table 3; Figure 5). When Kentucky bluegrass was removed from RNC analyses, results were insignificant (Figure 6; Appendix E). Summary statistics for RNC and RNR are provided in Appendix D, and model summaries are provided in Appendix E. For environmental variables, grasslands got cooler and wetter with increasing latitude across the province, which was positively correlated with TN, TC, PO_4-P, and agricultural activity (Appendix I).

3.2 Patterns of non-native plants within the Dry Mixedgrass

Eleven non-native plants were found in a survey of 27 plots in the Dry Mixedgrass (DMG) prairie. Goat's beard and Kentucky bluegrass were the most frequent non-native plants (each occurring in 8 of 27 plots), but crested wheatgrass invasions dominated cover estimates, making up 50% of total non-native cover in the DMG (Table 1).

RNR increased with TC (Figure 7), and there were no significant predictors for RNC in the DMG. The plot with the highest RNC was the only DMG plot located in a topographic depression and it was associated with the highest observations of TC and TN, and the second highest proportion of agriculture within 1 km (Figure 8), but other than this plot, TC, TN, nor agriculture corresponded with changes in RNC (Appendix F). For environmental variables, soil fertility (TC, TN, PO_4-P) did not vary with topographic position nor site surface shape, but TC and TN were slightly positively correlated with agricultural activity (Appendix

I). Summary statistics for RNC and RNR values are provided in Appendix D, and model summaries for the DMG are provided in Appendix F.

3.3 Patterns of non-native plants within the Central Parkland

Thirteen non-native plants were found in a survey of 28 plots in the Central Parkland (CP). Kentucky bluegrass was the most frequent and abundant non-native plant, occurring in 20 of 28 plots and making up 85% of the total non-native cover in the CP plots (Figure 6). Smooth brome occurred infrequently in the CP (3 of 28 plots) but had the second highest non-native plant cover (8% of total non-native cover in the CP plots) (Table 1).

Plots located on coarse-textured soils in the CP had the lowest RNC (Figure 9) and RNR (Figure 11) compared to medium- and fine-textured soils. RNC and RNR increased as TC and TN increased (Figures 9, 11). Both RNC and RNR increased with conductivity, and the statistical significance of these relationships did not change if the conductivity outlier was removed (Appendix G). RNC was highest on gentle, moderate slopes compared to steep slopes (Figure 9), and RNR was highest at the heavy grazing intensities (high dung count and cover) (Figure 11). For RNC, 19% of the variance was explained by shared effects between soil texture, TC, and TN, and 13% was explained by shared effects of soil texture, TC, TN, slope, and conductivity (Table 4; Figure 10). When Kentucky bluegrass was removed from RNC analyses, significant results were not detected (Figure 6; Appendix G). For RNR, 16% of the variance was explained by shared effects between soil texture, TC, and TN, 16% was explained by TC and TN, and 15% was unique explained by grazing (Table 5; Figure 12). For environmental variables, soil fertility (TC, TN) was higher in fine-textured soils than on coarse-textured soils, and decreased as slopes got steeper (Appendix I). Conductivity was slightly positively correlated with TC and TN, and highest on topographic plains (Appendix I). Grazing was slightly heavier on high-conductivity soils (Appendix I). Summary statistics for RNC and RNR values are provided in Appendix D, and model summaries for the CP are provided in Appendix G.

3.4 Patterns of non-native plants within the Peace River Parkland

Twelve non-native plant species were found in a survey of 17 plots in the Peace River Parkland (PRP). Kentucky bluegrass was the most frequent and dominant non-native plant, occurring in 13 of 17 plots and making up 71% of the total non-native cover in the PRP plots (Figure 6). Dandelion and goat's beard were the next most frequent (11 and 9 out of 17 plots, respectively), and smooth brome was the next most dominant, making up 12% of total non-native cover (Table 1).

RNC was highest on gentle slopes and at low pH levels (Figure 13), and effects were mostly shared between slope and pH (Table 6; Figure 14). The plot with the highest RNC (Plot 70; RNR = 0.82) occurred in a concave-shaped site. Concave sites appeared to have higher RNC levels but this relationship was insignificant when plot 70 was omitted. Plot 70 was also located at the toe of a gentle slope on a site high in TN, TC, and PO_4-P. When Kentucky bluegrass was removed from RNC analyses, concave sites still had significantly higher RNC but all other significant results were no longer detected (Figure 6; Appendix G). Relative non-native richness was highest on concave-shaped sites (Figure 15). For environmental variables, soil fertility (TN, TC) strongly decreased as slopes got steeper but did not change with topographic position nor shape (Appendix I). TN and TC decreased as pH increased (Appendix I). Summary statistics for RNC and RNR values are provided in Appendix D, and model summaries for the PRP are provided in Appendix H.

4   Discussion

Non-native plant invasion in grasslands is of interest to researchers, land managers, and conservationists because it threatens native grassland integrity (PCF 2020). This discussion will review non-native plant patterns using data collected along a 800 km latitudinal gradient of native grasslands within Alberta, Canada. Trends in non-native plant abundance and richness are examined from the perspectives of climate, soil, evolutionary history, and invasion debt (Section 4.1). Next, occurrence patterns of specific non-native plants are considered using introduction history, dispersal patterns, and competitive ability (Section 4.2). Local patterns of invasion are then examined within the Dry Mixedgrass (DMG), Central Parkland (CP), and Peace River Parkland (PRP) Natural Subregions (Section 4.3).

4.1   Broad patterns of non-native plants across Alberta

4.1.1   Climate and soil fertility

In this study, relative non-native cover (RNC) and relative non-native richness (RNR) were strongly linked to shared effects of climate and soil fertility. This means that the variance in RNC and RNR can be attributed to the influence of both climate and soil fertility simultaneously. Both response metrics increased in cooler, wetter grasslands with fertile soil. This result is consistent with two other Alberta studies that noted positive relationships between non-native plants and soil fertility (Lyseng et al. 2018; DeMaere 2019). Similarly, a study in North Dakota concluded that mesic plant communities had greater non-native plant frequencies compared to drier ones (Larson, Anderson, and Newton 2001). Climate drives plant distribution patterns and soil fertility gradients across Alberta (Hill, Willms, and Aspinall 2000; Downing and Pettapiece 2006). For example, the CP and PRP natural Subregions receive relatively higher precipitation amount than grasslands in the DMG Natural Subregion (Downing and Pettapiece 2006). The effects of climate and soil fertility were shared in the commonality analysis because abundant precipitation enhances topsoil

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thickness and nutrient availability in mesic grasslands (Whalen, Willms, and Dormaar 2003; Kupsch et al. 2013), while topsoil in the DMG Subregion has relatively less organic matter accumulation (Willms and Jefferson 1993; B. Adams et al. 2013). This gradient is reflected in the results for total plant richness, which increased with soil fertility in this study. This pattern matches results from other studies finding increases in plant productivity (Bork, Thomas, and Mcdougall 2001), diversity (DeMaere 2019), and richness (Hawkins et al. 2003; Bai et al. 2007; Palpurina et al. 2017) as soil moisture increases. Similarly, total plant richness is known to increase with soil nitrogen (Bai et al. 2007). In other words, plants generally thrive with increased resource availability, so non-native plants that are invasive likely prefer these resource-abundant habitats as well (Stohlgren et al. 2002, 2001). Under the fluctuating resources hypothesis, when resources are abundant, the most competitive non-native plants will benefit because their inherently competitive adaptations allow them to use the resources more efficiently than native plants (Grime 1973; Davis, Grime, and Thompson 2000; Goldberg and Novoplansky 2009). Therefore, the abundant moisture and nutrients in the mesic grasslands likely explains the elevated abundance and richness of non-native plants in that region. Future studies should explore a broader suite of climatic and soil fertility variables (ie. summer precipitation or soil nutrients availability at the microsite scale) to further tease out non-native plant patterns.

The result that the cooler, wetter, more diverse grasslands are more invaded in Alberta does not support the biotic resistance hypothesis (BRH), which states that diverse ecosystems are resistant to invasion due to more complete use of limiting resources (Elton 1958; Tilman 1997; Kennedy et al. 2002). Results instead align with other studies that have rejected this hypothesis (Stohlgren, Barnett, and Kartesz 2003). Spatial and temporal variability in water and nutrient availability could allow the competitive ability of non-native plants to outweigh biotic resistance of the native community (Shea and Chesson 2002). Further, the hypothesis refers to the complete use of limiting resources (Elton 1958), and

while this study did not address net resource availability nor uptake by plants, moisture and nutrient availability could vary considerably in the mesic grasslands where precipitation is abundant (Downing and Pettapiece 2006). It is also important to note that the elevated cover of non-native plants in the mesic grasslands appears to be driven by a single high-impact species, Kentucky bluegrass (see Section 4.2.1). High-impact invaders could overcome native community resistance differently than several low- or moderate-impact invaders (Nunez-Mir et al. 2017), so it would be best to test biotic resistance to invasion within an experimental setting in each Subregion.

4.1.2 Agricultural activity

In addition to climate and soil fertility, results suggest agricultural activity (proportion of cropland and tame pasture within 1 km of the plot) as an additional predictor explaining the patterns of RNC. This means that agricultural activity, climate, and soil fertility together dictate the variance in RNC across Alberta, since the influence of agriculture is expected to intensify in fertile areas. However, the agricultural influence could have more to do with the introduction of non-native plants, which is one component that contributes to the intrinsic invasibility of an area (Lonsdale 1999). Intrinsic invasibility increases if non-native plants arrive and have the ability to establish and spread past the point of introduction (Lonsdale 1999). Intentionally sown forages such as smooth brome, Kentucky bluegrass, and crested wheatgrass present a strong case for introductions of non-native plants in Alberta grasslands (Willms, Adams, and Mckenzie 2011). Since cropland and tame pasture are relatively common in the mesic grasslands and PRP, non-native species introductions are likely more common in those areas. The combination of good growing conditions and agricultural activity in the mesic grasslands may boost its intrinsic invasibility, which could explain the elevated RNC in this region. In semi-arid grasslands, reduced cropland might limit the presence of non-native plants (Lyseng et al. 2018), but the low RNC there could also be related to greater non-native species extinctions. Moisture- and

nutrient-limited growing conditions in the semi-arid grasslands could lead to increased extinction rates of potential invaders and greater resistance to invasion. Despite this prediction, the impact of agricultural activity in Alberta appears to be more strongly linked to distributions of agronomic plants, rather than their abundance or richness patterns (see Section 4.2).

4.1.3 Evolutionary history

While not directly tested in this thesis, the evolutionary history of grasslands may be important in explaining the pattern of increased RNC and RNR in the mesic grasslands because the evolutionary history of a grassland could impact its response to disturbance (Milchunas and Lauenroth 1993) and therefore, invasibility (Alpert, Bone, and Holzapfel 2000). North American grasslands evolved with grazing disturbance and regular fire, which are either supressed or altered on the landscape today (Milchunas, Sala, and Lauenroth 1988; D'Antonio and Vitousek 1992; Bork et al. 2012). Annual grazing regimes for the bison meant that the fescue grasslands were generally grazed during the fall and winter dormant season (though herbivory still occurred at all times of the year from other ungulates and straggling bison) (Willms, Adams, and Mckenzie 2011). Therefore, fescue grasslands were disturbed at a time when they were less sensitive to defoliation and as a result are less resilient than plant species in southern Alberta grasslands (Willms, Adams, and Mckenzie 2011). Today, livestock grazing practices usually involve summer grazing, even though recommendations are to delay use of native grass to late summer or fall (Alberta Sustainable Resource Development 2007; Bork et al. 2012). Summer grazing mimics historical regimes for semi-arid grasslands but is a departure from the typical regime for mesic grasslands (Morgan 1980). Maintenance of typical disturbance regimes may reduce invasibility of habitats (Alpert, Bone, and Holzapfel 2000). Therefore, mesic grasslands could be more invaded than semi-arid grasslands because their current disturbance regimes are most dissimilar from the historical regime. In other parts of the world, highly invaded

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grasslands have been consistent with those lacking long grazing histories (Seabloom et al. 2013). Degradation of bunchgrass communities after spring and summer grazing (Willms, Smoliak, and Dormaar 1985) and poorer range conditions in northern grasslands (Hill, Willms, and Aspinall 2000) provide evidence for this hypothesis in Alberta. A drawback with this hypothesis in the context of this thesis is that it is speculative and warrants further testing.

4.1.4 Invasion debt in the Dry Mixedgrass

The low levels of RNC and RNR in the semi-arid grasslands could be due to invasion debt, or a lag phase in non-native plant invasion (Rouget et al. 2016), meaning that there is potential for invasion, but it has not happened yet or is 'lagging' behind. An example of invasion debt is in California, where the actual distribution of invasion in annual grasslands was found to be much smaller than the potential range for invasion to occur (Seabloom et al. 2003). If an area is experiencing invasion debt, the probability of future invasion increases if a species has a longer residence time in the new range (Essl, Mang, and Moser 2012). At a time when Kentucky bluegrass was already widespread throughout North America (DeKeyser, Dennhardt, and Hendrickson 2015), crested wheatgrass and downy brome, two prominent invaders in the DMG today, were first introduced in the 1930s (Rydberg 1932; Upadhyaya, Turkington, and McIlvride 1986; W. Willms, Adams, and Mckenzie 2011; ABMI 2019b). The later introduction time of these two species might be a reason for the observed non-native plant patterns in the DMG Natural Subregion, compared to Kentucky bluegrass in the mesic grasslands. Additionally, invasion lag phases can be prolonged in areas farther from anthropogenic disturbances, so the reduced cultivation in the DMG relative to the mesic grasslands might reduce the number of non-native propagules entering those native grasslands (Lyseng et al. 2018). A limitation with this hypothesis is that it is speculative and requires a closer look at non-native plant introduction times and temporal patterns of spread throughout grasslands.

4.2 Broad patterns in non-native species distributions across Alberta

4.2.1 Kentucky bluegrass

In this study, non-native Kentucky bluegrass (*Poa pratensis* subsp. *angustifolia* and to a minor extent, *Poa pratensis* subsp. *pratensis*) was by far the most common non-native plant taxon recorded in this study (74% of all non-native summed cover, 30% of all non-native frequencies). It was found in all sampled Natural Subregions, but distinctly less so in the DMG prairie. In the CP, PRP, and Northern Fescue (NF) Natural Subregions, Kentucky bluegrass made up 85%, 71%, and 76% of the combined non-native cover in the regions, respectively. Kentucky bluegrass was so dominant that it was the driver behind most of the observed significant results in the mesic grasslands. As a dominant non-native species in the northern great plains (Cully, Cully, and Hiebert 2003), the results echo the well-known spread of Kentucky bluegrass throughout mesic grasslands of western Canada and the US (Toledo et al. 2014; DeKeyser, Dennhardt, and Hendrickson 2015; Grant, Shaffer, and Flanders 2020a).

Kentucky bluegrass' highly competitive ability is one reason for its dominance in this study, as it begins photosynthesizing earlier in the spring than native grasses (DeKeyser, Dennhardt, and Hendrickson 2015), allowing it to grow taller and faster. The rhizomatous root system creates dense mats (Bonos and Murphy 1999), lowering light availability and temperature at the soil level (Weaver and Rowland 1952) which hinder native plant growth. Other soil effects include secretion of allelopathic litter leachates which prevent germination of native plants (Bosy and Reader 1995).

The elevated abundance of Kentucky bluegrass in the mesic grasslands could be due to higher precipitation amounts in that region (DeKeyser, Dennhardt, and Hendrickson 2015), which is in line with its distribution (Malyshev and Malysheva 2009) and habitat preference in the native distribution range, in Eurasia (Zvelev 1976). Examples of this pattern include a recent study from North Dakota, which noted increasing presence of

Kentucky bluegrass along a climatic gradient of increasing moisture (Grant, Shaffer, and Flanders 2020a), and a study from Alberta that noted non-native plant abundance, including Kentucky bluegrass, was highest in the cool, wet grasslands (Lyseng et al. 2018). Similarly, a study on Saskatchewan grasslands found that Kentucky bluegrass was abundant in high-rainfall areas and was associated with higher amounts of soil carbon (Bork et al. 2020). Kentucky bluegrass grows poorly in dry conditions (AARD 2009), which could explain why it was not abundant in the semi-arid grasslands. Temporal variability in precipitation could also contribute to Kentucky bluegrass invasion (DeKeyser, Dennhardt, and Hendrickson 2015). For example, data from a long-term grassland monitoring plot in southwestern Alberta show a positive correlation between annual precipitation and the cover of Kentucky bluegrass (GoA 2017). If the data are available, future studies could address the link between Kentucky bluegrass invasion and historical precipitation levels to further tease out this relationship.

Intentional seeding of Kentucky bluegrass likely contributes to its dominance across the study area. Kentucky bluegrass is intentionally sown as a forage grass (AARD 2009), and propagule pressure is multiplied due to widespread use as a lawn and turf grass (DeKeyser, Dennhardt, and Hendrickson 2015). There are approximately 250 individual commercially available cultivars of Kentucky bluegrass in the US (Honig, Bonos, and Meyer 2010). Widespread and consistent Kentucky bluegrass propagule pressure probably increases the likelihood for continual invasion into native grasslands (Richardson and Pyšek 2006; Haydu, Hall, and Hodges 2018). Further, while Kentucky bluegrass is generally considered to be of Eurasian origin, it may also be native to some parts of North America (Sather 1996). The native subspecies of Kentucky bluegrass (*Poa pratensis* subsp. *agassizensis*) was recorded four times in this study, but its native range in Alberta is largely unknown, and it is almost indistinguishable from the non-native varieties (Moss and Packer 1983). Interestingly, an early-1930s survey of Wood Buffalo National Park in northern

Alberta found that Kentucky bluegrass was the primary vegetation species in semi-open prairies (Raup 1935), though it is uncertain whether it was the native or non-native subspecies. It is possible that it was the non-native subspecies because Kentucky bluegrass was already widespread throughout the Northern Great Plains by the late 1800s (DeKeyser, Dennhardt, and Hendrickson 2015). An opportunity for future research would be to delineate the footprint of the native Kentucky bluegrass subspecies within Alberta.

The results of this study suggest that Kentucky bluegrass is a passenger of invasion because its occurrence patterns respond to environmental conditions (Macdougall and Turkington 2005). More specifically, while Kentucky bluegrass occurred throughout the mesic grasslands, its abundance was elevated in areas that collected or slowed the movement of water (see Section 4.3). However, its competitive traits, such as the ability to shade out native species using light-blocking litter and foliage (Macdougall and Turkington 2005), suggest that it could also be a driver of invasion. It is not known from these thesis results whether the observed patterns between Kentucky bluegrass abundance and moisture or soil fertility are a cause or an effect of Kentucky bluegrass invasion. For example, White et al. (2013) found that Kentucky bluegrass responded positively to nitrogen application, which suggests that it responds well to soil fertility, but Bork et al. (2020) found that Kentucky bluegrass invasion was associated with higher soil carbon levels, possibly its invasion led to increased soil carbon levels. White et al. (2013) suggest that Kentucky bluegrass is a 'back-seat driver', a concept devised by Bauer (2012). In this subset of the driver model, Kentucky bluegrass initially invades with suitable environmental conditions, and takes over the role of driver once established (Bauer 2012). Kentucky bluegrass' long residence time and ability to act as both a passenger and driver of invasion likely explain why it was so abundant and frequent in this study. Realistically, Kentucky bluegrass' ability to seek out the best environmental conditions and then outcompete the established native vegetation could mean that it might not ever be contained.

4.2.2 *Crested wheatgrass and smooth brome*

Crested wheatgrass made up 50% of all non-native cover in the DMG Subregion of southern Alberta but occurred in only 3 out of 27 plots. The results reflect well-documented crested wheatgrass invasion throughout southern Alberta and Saskatchewan (Dormaar et al. 1995; Henderson and Naeth 2005; Willms, Adams, and Mckenzie 2011). Crested wheatgrass was observed here because it was purposely seeded in the 1930s to assist with recovery of eroded lands (Willms, Adams, and Mckenzie 2011) as it can tolerate drought (Knowles and Kilcher 1983) and establish rapidly (Willms, Adams, and Mckenzie 2011). The qualities that make it a desirable agronomic grass also make it strong competitor against native grassland flora (Willms, Adams, and Mckenzie 2011). For similar reasons, crested wheatgrass was recommended for use in oil and gas reclamation plans even until the late 1980s (Hardy BBT Ltd 1989). Repeated introductions over space and time likely drive crested wheatgrass invasion via intense propagule pressure in this region (Richardson and Pyšek 2006). Farther north, smooth brome made up 8% and 12% of total non-native plant cover in the CP and PRP, respectively. However, its frequency was relatively low compared to Kentucky bluegrass (3 out of 28 CP plots and 3 out of 17 plots in the PRP). Smooth brome is best adapted to the black soil climatic zone and is commonly used for hay production (AARD 2009). However, smooth brome invasion is known to promote homogenization and negative impacts on native plant communities in the parkland (Stotz et al. 2017; Stotz, Gianoli, and Cahill 2019). Interestingly, a broad-scale study by Hill, Willms, and Aspinall (2000) found that smooth brome was the dominant agronomic grass in Alberta, not Kentucky bluegrass. Since Kentucky bluegrass was the dominant species in this study, this discrepancy could reflect a true considerable increase in Kentucky bluegrass invasion in the last two decades, or it could also be because the Hill, Willms and Aspinall (2000) study sampled tame pastures, which would increase the smooth brome occurrences in that study. Given the widespread evidence of both crested wheatgrass and smooth brome invasion in native grasslands, they were observed infrequently in this study. The clumped distribution

patterns of both species might explain the low frequencies but high abundances noted in this study (Larson, Anderson, and Newton 2001). More specifically, the single plot study design likely under-sampled these patchy distributions, which may have contributed to the zero-inflation in the dataset.

4.2.3 Dandelion and goat's beard

Dandelion and goat's beard occurred throughout all the natural Subregions at low abundances but relatively high frequencies (occurring in 49% and 35% of plots, respectively). The thesis results support previous documentation for dandelion being a common non-native plant throughout Alberta's Subregions (Lyseng et al. 2018; ABMI 2019a), and goat's beard is common in Alberta grassland and parkland (Moss and Packer 1983), and throughout the rest of Canada (Clements, Upadhyaya, and Bos 1999). In North Dakota, goat's beard was recorded as sparsely but evenly distributed on the prairie (Larson, Anderson, and Newton 2001), which mimics its distribution in this study. The observed occurrence patterns for both species are probably due to their adaptation for a broad range of habitats and passive dispersal patterns. Dandelion can tolerate a wide range of climatic conditions, habitats, and soil types (Stewart-Wade et al. 2002). Similarly, goat's beard can grow in most vegetation types from semi-arid grasslands to mesic forests (Novak, Soltis, and Soltis 1991). This suitability for a wide range of habitats likely explains its ability to distribute evenly across Alberta's grasslands. Dandelion is not known as a competitive plant, so even small increases in surrounding vegetation height can shade it out, leading to decreased densities (Mølgaard 1977). Goat's beard has an extensive root system that can compete with native grass species, and are a concern on rangelands in British Columbia (Upadhyaya et al. 1993). Despite this concern, goat's beard has not yet been added to any provincial noxious weed lists in western Canada. Even though both species are wind-dispersed via aerodynamic pappi (Clements, Upadhyaya, and Bos 1999; Stewart-Wade et al. 2002) and produce many seeds with high germination rates, optimal conditions are

required for establishment (Gross 1984; Stewart-Wade et al. 2002). For wind-dispersed seeds this can be difficult to find because obstacles and varying surface textures of the soil may reduce germination success (Cousens, Dytham, and Law 2008). This passive spread of propagules is a contrast from the purposefully seeded agronomic perennial grasses and may explain the overall lower abundance of dandelion and goat's beard.

4.3 Local patterns of non-native plants in three Natural Subregions

4.3.1 Dry Mixedgrass

The only significant predictor in the DMG was total carbon (TC), which increased with RNR. Environmentally, TC was strongly positively correlated with total nitrogen (TN) and slightly positively correlated with agricultural activity, though TN and agricultural activity each did not significantly predict RNR. This subtle link between non-native richness and soil fertility is echoed in other studies (Stohlgren et al. 1998; Bai et al. 2007). In the DMG, soil fertility is relatively low compared to other grasslands further north and west in Alberta (B. Adams et al. 2013), so it is possible that even slight increases in soil carbon may trigger noticeable peaks in species richness. Furthermore, increased TC may also be associated with greater water-holding capacity because of higher organic matter content. According to the fluctuating resources hypothesis, abundant and fluctuating nutrients and water benefit competitive non-native plants the most (Grime 1973; Davis, Grime, and Thompson 2000), contributing to higher non-native richness.

Contrary to expectations, there were no significant predictors for variability in RNC in the DMG Subregion. However, interestingly, one plot with exceptionally high RNC in the DMG (RNC = 0.67) was associated with unusually high TC and TN observations. This plot was also the only plot located in a topographic depression, which suggests a potential but undetected link between topography, soil fertility, and non-native plant abundance. The relationship would not be unexpected, as low, wet areas within the DMG are known to be more invaded (L. Schroeder, pers. comm.), and other studies have found elevated invasion

levels at low elevations and in areas of topographic wetness (Stohlgren et al. 1998; Kumar et al. 2006; Szymura et al. 2018). The RNC values in the DMG were relatively low compared to more northern Subregions, so it is possible that there were not enough data to show a topographic relationship. It is also possible that changes in topographic relief are too subtle in the DMG, and such relationships would be more detectable in areas with more extreme changes in relief, such as in the hummocky Central Parkland or the steep slopes of the Peace River valley. Future studies on invasion in the DMG should implement more specific measures of soil fertility and finer-scale topographic sampling.

4.3.2 Central Parkland

In the mosaic of the CP, both RNC and RNR here highest in fine-textured, loamy soils, which had high TC, TN, and conductivity levels. Alternatively, dry sandy plant communities had very low RNC and RNR. These results echo a landscape study in North Dakota which found that mesic plant communities were more invaded than dry plant communities (Larson, Anderson, and Newton 2001). A more recent study from the Dakotas concluded that loamy and clayey ecological sites were more invaded than sandy sites (Grant, Shaffer, and Flanders 2020b). In Alberta, so far there are no studies that have identified a relationship between soil texture and invasion in the CP grasslands. The link to soil texture is most likely related to nutrient and water retention. Fine-textured loamy soils hold water and nutrients readily, which would benefit the most competitive non-native plants (Grime 1973), such as Kentucky blue grass and smooth brome. On the other hand, sandy soils drain quickly, have low organic matter accumulation, and are generally vegetated by native plants that are adapted to stressful growing conditions (Kupsch et al. 2013). Therefore, a secondary reason for lower RNC and RNR on sandy soils could be that non-native plants are less competitive in moisture- and nutrient-stressed conditions (Macdougall and Turkington 2005). For example, Kentucky bluegrass, which is widespread throughout the mesic grasslands in the CP, is growth-inhibited in moisture-stressed

conditions (AARD 2009). However, some non-native plants with specific physiological and morphological traits can allow them to thrive in low-resource communities (Funk and Vitousek 2007; Funk 2013). Species like leafy spurge are particularly adapted to sandy soils (Selleck, Coupland, and Frankton 1962), and are already a rising issue on sandy sites in the CP (P. Porter, pers. comm.). Future research could look at how soil texture influences distributions of individual non-native species within the variable communities of the CP. A third texture-related explanation for the elevated abundance and richness of non-native on loamy soils could be the closer proximity to cultivation and heightened propagule pressure of non-native plants (Seabloom et al. 2013). While proximity to agriculture was not a significant predictor in the CP, fine-textured loamy soils are more commonly converted to cropland and tame pasture compared to sandy soils, which have poor cropping potential and are more likely left as grazing land (Pyle, Hall, and Bork 2019). With repeated introductions of non-native species, the heightened propagule pressure in the fertile soils in the CP may contribute to higher RNC and RNR in those areas (Richardson and Pyšek 2006).

Among the variable topography in the CP, gentle slopes had the highest RNC. Gentle slopes also had the highest levels of TC and TN, which have already been positively linked to abundance and richness of non-native plants in this study. The results match a recent study from North Dakota which found that gentle slopes had the fewest native plants across a broad-scale study (Grant, Shaffer, and Flanders 2020b). The invasion link with gentle slopes was also found in the PRP in this study (see Section 4.3.3). In a Subregion with diverse landscape heterogeneity (Downing and Pettapiece 2006), slope is likely a predictor for RNC because it alters water drainage patterns by slowing it down, and leading to greater water availability (Moeslund et al. 2013). This combined with the elevated TC and TN on gentle slopes would contribute to greater resource availability due to greater infiltration and less nutrient runoff, leading to higher non-native plant abundance (Davis, Grime, and

Thompson 2000). Future studies should implement a more rigorous sampling design that accounts for local variability in topography, texture, and soil moisture levels.

RNR was highest at elevated grazing intensities in the CP, which is in line with other research finding that overgrazing leads to invasion by weedy species (Willms, Adams, and Mckenzie 2011; Sinkins and Otfinowski 2012). The thesis results also align with a recent study in Alberta grasslands that found non-native richness increased in the presence of grazing (Lyseng et al. 2018), though intensity of grazing was not assessed in that study. In fescue grasslands specifically, heavier grazing pressure can lead to declines in grassland health (Willms, Smoliak, and Dormaar 1985; Douwes and Willms 2012). According to the intermediate disturbance hypothesis, moderately grazed grasslands are expected to have the greatest diversity, implying that heavily grazed grasslands would have low diversity (Connell 1979; Milchunas, Sala, and Lauenroth 1988). However, this hypothesis applies to overall diversity, and not non-native plants specifically, though moderate grazing intensities can facilitate non-native plant establishment (Milchunas, Sala, and Lauenroth 1988). The positive relationship between non-native richness and grazing intensity in the CP is likely caused by the low grazing resilience of fescue grasslands, which are easily degraded under heavy grazing pressure (Bailey, McCartney, and Schellenberg 2010; B. Adams et al. 2015). The evolutionary history of fescue grasslands likely makes them more invasible under current management regimes (see Section 4.1.3). A limitation with the grazing variables in this study is that it unknown whether dung count and cover actually represent a full range of grazing intensity, particularly for heavy intensities. This thesis sampled primarily on grazing leases (public land), which generally have lower stocking rates than owned private grazing land (Pyle, Hall, and Bork 2017). Furthermore, estimating grazing intensity in this way may not be accurate as the places where cattle defecate may not necessarily be where they graze or bed down (Oudshoorn, Kristensen, and Nadimi 2008). Though there is some difficulty in accurately estimating grazing intensity (Jasmer and Holechek 1984), future

studies should try to incorporate other grazing proxies such as stocking records, or examine temporal changes in invasion as it relates to grazing.

Throughout the CP, Kentucky bluegrass was the dominant non-native plant. In fact, the results noted above were no longer significant once Kentucky bluegrass was removed from the dataset. Kentucky bluegrass abundance was elevated in loamy, fine-textured soils, on gentle slopes, and in heavier grazed areas, indicating that while non-native plant abundance was the responding variable in these results, Kentucky bluegrass was the primary vegetative component behind these conclusions. Future research within the CP should note this dominance of Kentucky bluegrass when creating study designs, particularly if the goal is to capture other non-native species.

4.3.3 Peace River Parkland

Non-native plant invasion within the PRP was most strongly linked to topography. RNR was elevated on concave-shaped sites, and RNC was highest on gentle slopes and low-pH soils. Environmentally, gentle slopes had the highest TC and TN levels, which corresponded to low-pH soils. The results are consistent with other studies that found higher levels of invasion at lower elevations (Stohlgren et al. 1998; Kumar et al. 2006), concave sites (Szymura et al. 2018), and gentle slopes (Kumar et al. 2006; Grant, Shaffer, and Flanders 2020b). The link to topography is not surprising in the PRP, since a majority of the remnant grasslands occur on the slopes of the Peace River valley. Topography-driven changes in soil moisture are one driver for grassland diversity patterns (Moeslund et al. 2013) since they influence the distance to water table and impacts local drainage patterns (Moeslund et al. 2013). In dry habitats, soil moisture can effect nitrogen availability (Rodriguez-Iturbe et al. 1999) and transport of dissolvable cations, which can affect soil pH (Zinko et al. 2006). Based on these generalities, topographic features that collect (concave sites and low slope positions) or slow (gentle slopes) the movement of water likely have higher moisture and nutrient availability for plants. According to the fluctuating resources

hypothesis, these areas of topographic wetness have higher RNC and RNR because of greater resource availability for competitive non-native plants (Grime 1973; Davis, Grime, and Thompson 2000). The localized boost in resources could explain the higher RNC noted on gentle slopes, and the higher RNR on concave sites. Interestingly, the proxies of soil fertility (TN, TC) were strongly correlated with slope, but not topographic position nor shape. However, these categorical predictors were also unevenly sampled (8 upper slopes, 5 middle slopes, 4 lower slopes; and 3 concave sites, 4 convex sites, and 10 straight sites). Even though there was no apparent link between topographic position or shape, the highest RNC occurrence was associated with a plot which was located on a concave site, at the toe of a slope, and on soil with high soil fertility metrics. This highlights a future research opportunity that could further examine interactions between topographic, fertility, and moisture variables in the PRP. Future studies should also sample topographic positions more evenly, collect localized and finer-scale soil fertility data.

5 Synthesis & Conclusion

Assessing the patterns of non-native plant abundance, richness, or individual species' distributions can give insight to the drivers of invasion on grassland landscapes. In this study, moisture and nutrient availability were most distinctly associated with non-native plant patterns across all studied grassland types, as well as on the local landscape. From a broad perspective, the grasslands with elevated soil fertility and precipitation amounts were the most invaded, supporting theory that abundant resources boost invasion (Davis, Grime, and Thompson 2000). However, the pattern of mesic grasslands being more invaded than semi-arid grasslands could also be attributed to other factors. Contrasting evolutionary histories may influence how Alberta grasslands respond to disturbance (Milchunas and Lauenroth 1993), including resistance to invasions (Alpert, Bone, and Holzapfel 2000). Furthermore, the mesic grasslands are more suitable for conversion to cropland and tame pasture, so propagule pressure from agronomic species could boost non-native plant establishment in these areas.

Moisture and nutrient availability were also important on a local scale. Topography is a promising predictor for non-native plants, as the most non-native species abundant and rich areas within heterogeneous landscapes appeared to be zones of topographic wetness. This signal was weak in the semi-arid plains in southern Alberta but strengthened with latitude towards the hummocky Central Parkland and slope-dominated Peace River valley. The topographic driver could be investigated further by implementing a more rigorous sampling design that captures nutrient and soil moisture at all topographic positions. Soil texture was also a promising predictor for invasion, but this was only apparent in the Central Parkland, where texture was more variable than in the Dry Mixedgrass or Peace River Parkland. Topographic and soil texture information could be used in future research that predicts where non-native plant invasions are likely to occur on the local landscape.

Interestingly, anthropogenic activities such as oil and gas did not appear to have a strong effect on non-native plant patterns. This probably due to limitations of the sampling design. Plots were placed consistently far enough from infrastructure so that anthropogenic effects were somewhat standardized. The lack of significant anthropogenic predictors in this study should not minimize their previously documented impacts on grassland landscapes (Nasen, Noble, and Johnstone 2011), or the measures in place to mitigate those effects (Lancaster et al. 2017; AEP 2018).

The study design might also explain why several well-known invaders in Alberta grasslands were sampled infrequently or not at all. Since the plots were placed in open grasslands away from road edges or pipelines, they likely under-sampled the non-native plants present among grasslands invaded by smooth brome (Stotz, Gianoli, and Cahill 2019) or crested wheatgrass (Henderson and Naeth 2005), which have often been seeded along transportation corridors. The non-random placement of these plots 50 m away from infrastructure edges is thus a conservative measure of invasions in Alberta grasslands and likely left many non-native plants associated with roadside disturbance and propagule pressure undetected. Additionally, the single-plot sampling protocol probably contributed to low detection rates, particularly for species with clumped distribution patterns (Larson, Anderson, and Newton 2001). Therefore, the results generated in this study represent a more conservative estimate of the local abundance and frequency of non-native plants. Future non-native plant assessments and mapping at the regional scale could help monitor existing and emerging non-native plant patterns, particularly for invasive plants.

One species that defied the sampling design limitation was Kentucky bluegrass, which was so dominant in this study that its removal from the dataset made results insignificant. This prompts a reminder for future studies to consider how invasion is assessed, as a study that calculated only non-native richness would not have captured the effect of this high-impact invader.

Intentionally sown agronomic plants dominated cover estimates in this study, implying that they may have larger footprints throughout native grasslands compared to most provincially-regulated invasive plants (GoA 2010). Adding to the complexity, agronomic species hold an important economic value in the forage industry (AARD 2009). Future studies could look at ways to find balance between preserving the integrity of native grasslands, while maintaining existing agronomic systems sustainably. Future research could also explore how the categorization and management of invasive species is prioritized from social, economic, or ecologic perspectives. For instance, what is the threshold for deciding whether a non-native plant should be controlled in Alberta? Why should grassland managers control leafy spurge but not Kentucky bluegrass? For example, in the case of aggressive non-native Kentucky bluegrass, it might be that control is not an option because it is already widespread and spreading unaided throughout the grasslands. Given that Kentucky bluegrass is palatable to livestock and wildlife, it may be more valuable on the landscape than leafy spurge, which has limited palatability (Walker et al. 1995). The decisions perhaps depends on management goals and the feasibility of achieving them.

Non-native plant invasions are just one of many threats to native grassland integrity (PCF 2020). Few studies in Alberta have quantified patterns of non-native plants over a large spatial scale. The broad approach of this thesis was to identify patterns of non-native plants throughout prairie and parkland grasslands in Alberta, Canada. The results related to moisture and nutrient availability are in line with a large body of research with similar conclusions, while specific links to topography and soil texture are relatively novel among grassland literature in Alberta. The study also clearly shows the dominance of agronomic grasses in native grasslands across all climatic conditions. These patterns outline opportunities for future invasion research in native grasslands, as well as some direction for the prioritization of conservation efforts. Understanding patterns of non-native plants in grasslands can help preserve the integrity of these globally endangered ecosystems.

Table 1. List of non-native species by A) total number of observations and B) total percent cover across Natural Subregions.[1]

Scientific Name	Life Form[2]	A) Total # of Observations out of 86 Plots						B) Total Summed % Cover					
		DMG	MG	NF	CP	PRP	All Plots	DMG	MG	NF	CP	PRP	All Plots
Agropyron cristatum	PG	3	-	-	1	-	4	53	-	-	0.5	-	53.5
Axyris amaranthoides	AH	-	-	-	3	-	3	-	-	-	2	-	2
Bromus inermis	PG	-	-	-	3	3	6	-	-	-	38	31	69
Bromus japonicus	AG	1	-	-	-	-	1	0.5	-	-	-	-	0.5
Bromus riparius	PG	1	-	-	-	1	2	1	-	-	-	0.5	1.5
Camelina microcarpa	AH	1	1	-	-	-	2	0.5	3	-	-	-	3.5
Chenopodium album	AH	-	-	1	2	1	4	-	-	0.5	1	0.5	2
Cirsium arvense	PH	-	-	-	1	-	1	-	-	-	1	-	1
Crepis tectorum	AH	2	-	1	1	1	5	1	-	0.5	1	0.5	3
Descurainia sophia	AH	2	2	-	1	-	5	3	2	-	1	-	6
Salsola sp.	AH	-	1	-	-	-	1	-	0.5	-	-	-	0.5
Linaria vulgaris	PH	-	-	-	-	3	3	-	-	-	-	1.5	1.5
Medicago sativa	PH	2	-	-	-	1	3	2	-	-	-	1	3
Phleum pratense	PG	-	-	-	-	1	1	-	-	-	-	0.5	0.5
Poa pratensis subsp. *angustifolia*	PG	8	1	6	20	13	48	19	13	62	409.5	177.5	681
Poa pratensis subsp. *pratensis*	PG	-	1	1	1	1	4	-	1	10	10	2	23
Polygonum aviculare subsp. *aviculare*	AH	-	-	-	1	-	1	-	-	-	0.5	-	0.5
Rumex crispus	PH	-	-	1	-	-	1	-	-	0.5	-	-	0.5
Sisymbrium loeselii	AH	-	-	-	1	-	1	-	-	-	2	-	2
Taraxacum erythrospermum	PH	5	-	-	-	-	5	9.5	-	-	-	-	9.5
Taraxacum officinale	PH	7	4	6	9	11	37	13	3	6.5	20	13.5	56
Tragopogon dubius	AH	8	2	4	7	9	30	4	1	2	4	20.5	31.5
Trifolium sp.	PH	-	-	-	-	3	3	-	-	-		1.5	1.5

[1] DMG = Dry Mixedgrass, MG = Mixedgrass, NF = Northern Fescue, CP = Central Parkland, PRP = Peace River Parkland
[2] PG = perennial grass, AG = annual grass, PH = perennial herb, AH = annual herb

Table 2. Summary of the commonality coefficient analysis for relative non-native cover across all plots. Coefficient refers to the partitioning of the variance (R^2), and percent total refers to the percentage of variance that is contributed by the predictor combination (Nimon et al. 2008). Refer to Figure 3 for a visual summary of the summed effects.

Predictor combinations[1,2]	Coefficient	% Total
Unique to topographic position	0.1256	26.18
Common to AHM, TN, and TC	0.0749	15.61
Common to AHM, TN, TC, and agriculture	0.0733	15.28
Common to TN, and TC	0.0482	10.04
Unique to agriculture	0.0429	8.95
Unique to slope	0.0323	6.74
Common to slope, TN, and TC	0.0287	5.98
Common to TN, TC, and agriculture	0.0264	5.5
Unique to TN	0.0263	5.49
Unique to AHM	0.0186	3.88

[1] Only the top 10 effects are reported in order to streamline table length
[2] AHM = annual heat:moisture index, TN = total nitrogen, TC = total carbon

Table 3. Summary of the commonality coefficient analysis for relative non-native richness across all plots. Coefficient refers to the partitioning of the variance (R^2), and percent total refers to the percentage of variance that is contributed by the predictor combination (Nimon et al. 2008). Refer to Figure 5 for a visual summary of the summed effects.

Predictor combinations[1]	Coefficient	% Total
Common to TC, and TN	0.0629	58.63
Common to TC, TN, and PO_4-P	0.0349	32.49
Unique to PO_4-P	0.0064	5.97
Unique to TC	0.0031	2.86
Unique to TN	0.0005	0.42
Common to TC, and PO_4-P	-0.0002	-0.16
Common to TN, and PO_4-P	-0.0002	-0.2
Total	0.1073	100

[1] TN = total nitrogen, TC = total carbon, PO_4-P = phosphate

Table 4. Summary of the commonality coefficient analysis for relative non-native cover in the Central Parkland. Coefficient refers to the partitioning of the variance (R^2),and percent total refers to the percentage of variance that is contributed by the predictor combination (Nimon et al. 2008). Refer to Figure 10 for a visual summary of the summed effects.

Predictor combinations[1,2]	Coefficient	% Total
Common to soil texture, TC, and TN	0.0986	19.26
Common to slope, soil texture, conductivity, TC, and TN	0.0651	12.72
Common to conductivity, and TN	0.0436	8.52
Unique to TN	0.0389	7.59
Common to conductivity, and TC	0.0384	7.5
Common to soil texture, conductivity, and TN	0.0349	6.81
Common to soil texture, conductivity, TC, and TN	0.0316	6.16
Unique to TC	0.0282	5.51
Common to slope, conductivity, and TN	0.0282	5.51
Common to slope, and conductivity	0.0266	5.2
Common to slope, conductivity, and TC	0.0218	4.26

[1] Only the top 10 effects are reported in order to streamline table length
[2] TN = total nitrogen, TC = total carbon

Table 5. Summary of the commonality coefficient analysis for relative non-native richness in the Central Parkland. Coefficient refers to the partitioning of the variance (R^2), and percent total refers to the percentage of variance that is contributed by the predictor combination (Nimon et al. 2008). Refer to Figure 12 for a visual summary of the summed effects.

Predictor combinations[1,2]	Coefficient	% Total
Common to soil texture, TC, and TN	0.0815	16.39
Common to TC, and TN	0.0782	15.71
Unique to grazing	0.0745	14.97
Common to grazing, and TC	0.0616	12.38
Common to soil texture, conductivity, TC, and TN	0.0598	12.02
Common to grazing, and TN	0.0456	9.16
Common to soil texture, grazing, conductivity, TC, and TN	0.0419	8.43
Common to grazing, and conductivity	0.0387	7.78
Common to soil texture, and grazing	0.0371	7.46
Common to grazing, conductivity, TC, and TN	0.0334	6.72
Common to soil texture, grazing, TC, and TN	0.032	6.44

[1] Only the top 10 effects are reported in order to streamline table length
[2] TN = total nitrogen, TC = total carbon

Table 6. Summary of the commonality coefficient analysis for relative non-native cover in the Peace River Parkland. Coefficient refers to the partitioning of the variance (R^2), and percent total refers to the percentage of variance that is contributed by the predictor combination (Nimon et al. 2008). Refer to Figure 14 for a visual summary of the summed effects.

Predictor combinations	Coefficient	% Total
Common to slope, and pH	0.1745	46.21
Unique to pH	0.1318	34.89
Unique to slope	0.0714	18.9
Total	0.3777	100
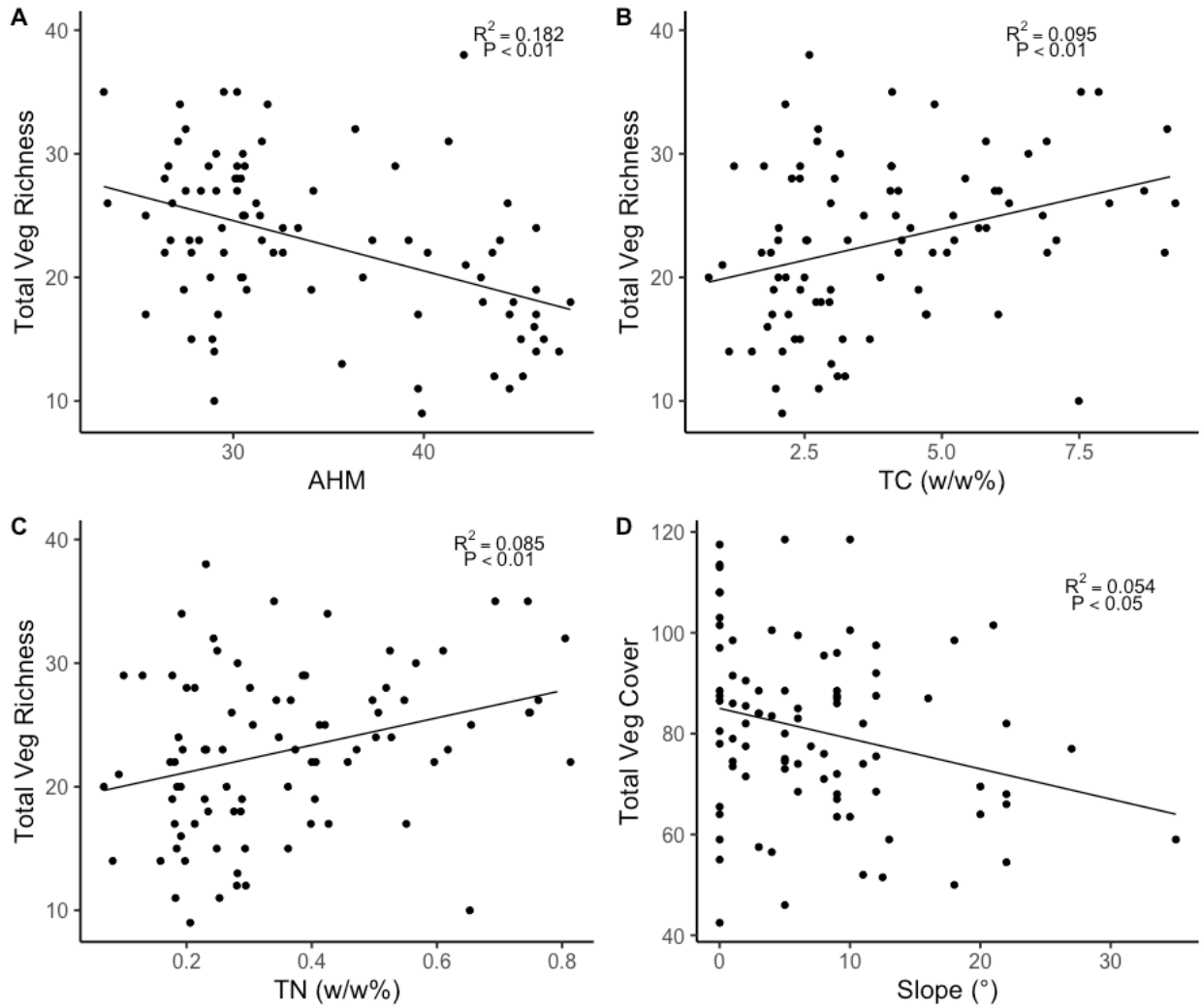
Figure 1. Relationship between total vegetation richness within a 10 x 10 m plot and the significant (P<0.05) predictors A) annual heat:moisture index (AHM), B) total carbon (TC), and C) total nitrogen (TN), and between total vegetation cover and D) slope. Lines were fitted using generalized additive models (GAMs; n = 86 plots).
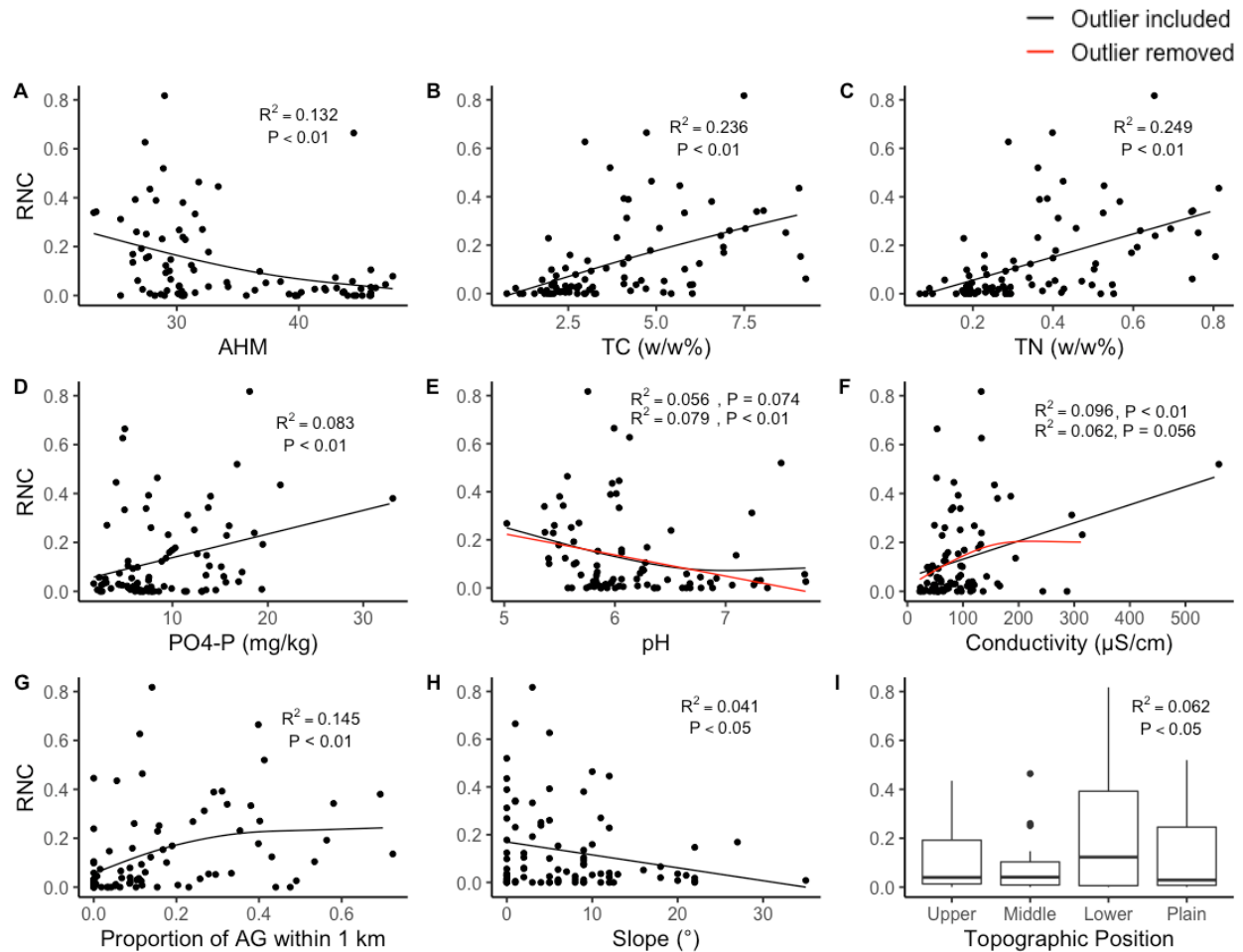
Figure 2. Relationship between relative non-native cover (RNC) within a 10 x 10 m plot and the significant (P<0.05) predictors A) annual heat:moisture index (AHM), B) total carbon (TC), C) total nitrogen (TN), D) phosphate (PO$_4$-P), E) pH, F) conductivity, G) proportion of agriculture (AG) within 1 km, H) slope, and I) topographic position. Lines were fitted using generalized additive models (GAMs; n = 86 plots). Lines for pH and conductivity were plotted using the full dataset (black line) and with an outlier removed (red line) to illustrate the influence of an outlier that altered model significance.
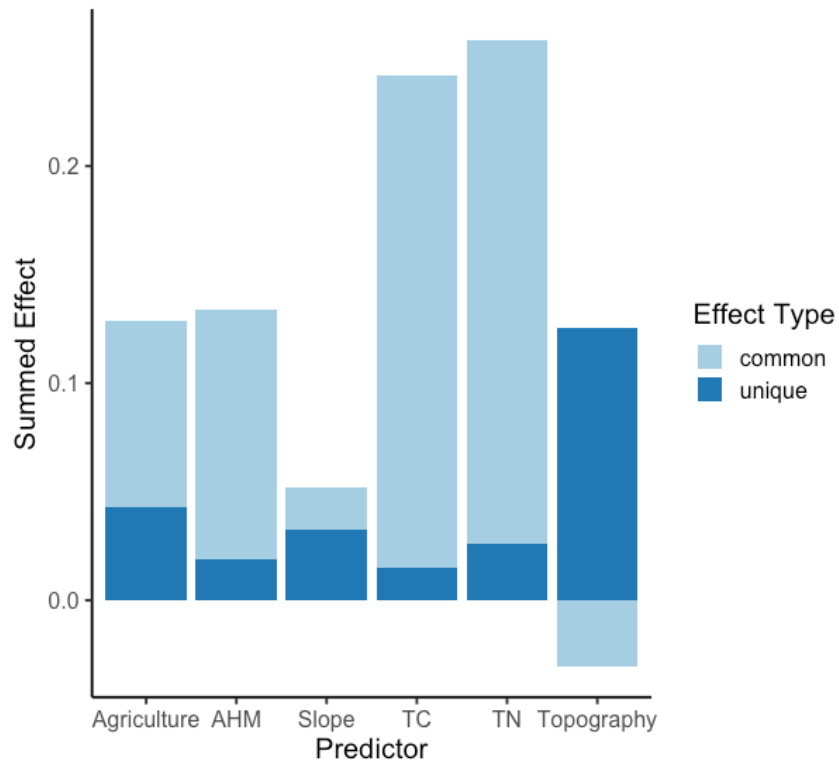
Figure 3. Summed effects from the commonality coefficient analysis for relative non-native cover across all plots. Common effects indicate how much variance (R^2) is common to groups of variables, and unique effects indicate how much variance is unique to a single variable (Reio et al. 2015). Negative values indicate a suppression effect on the variance. Refer to Table 2 for the effect combinations. AHM = annual heat:moisture index, TC = total carbon, TN = total nitrogen.

Figure 4. Relationship between relative non-native richness (RNR) within a 10 x 10 m plot and the significant (P<0.05) predictors (A) total carbon (TC), (B) total nitrogen (TN), and (C) phosphate (PO$_4$-P) across all plots. Lines were fitted using generalized additive models (GAMs; n = 86 plots). Phosphate was plotted using the full dataset (black line) and with an outlier removed (red line) to illustrate that the potential outlier did not actually influence model significance.

Figure 5. Summed effects from the commonality coefficient analysis for relative non-native richness across all plots. Common effects indicate how much variance (R^2) is common to groups of variables, and unique effects indicate how much variance is unique to a single variable (Reio et al. 2015). Refer to Table 3 for the effect combinations. PO_4-P = phosphate, TC = total carbon, TN = total nitrogen.
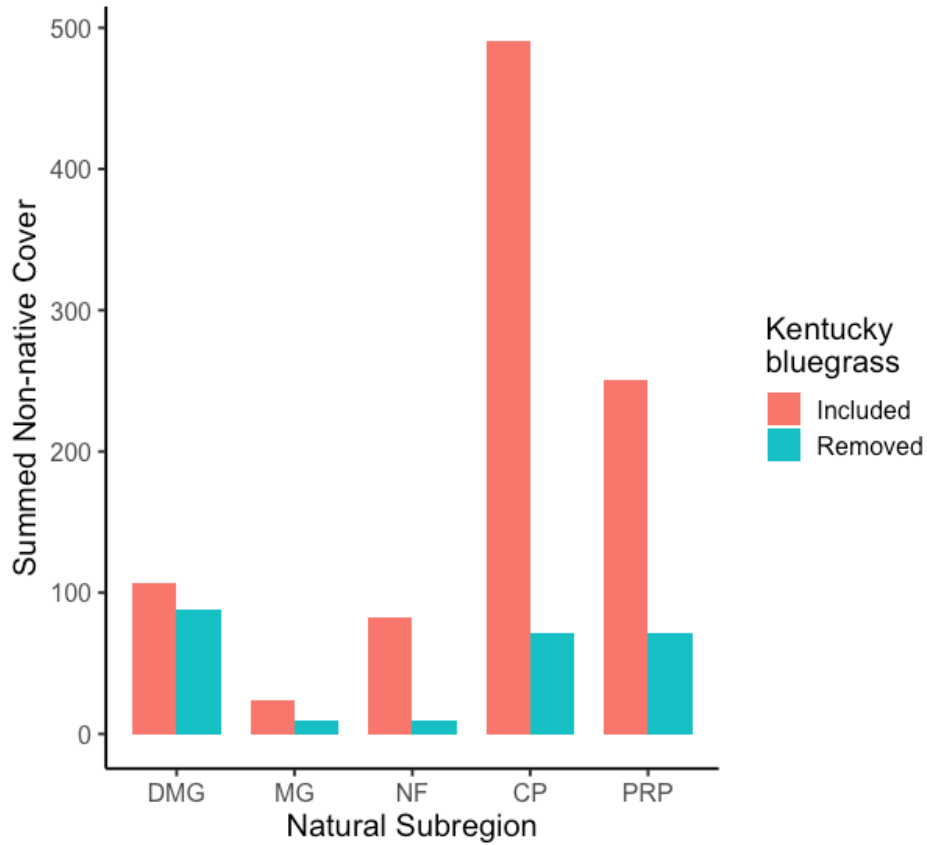
Figure 6. Summed percent cover of non-native plants for each sampled Natural Subregion. Red bars include Kentucky bluegrass and blue bars exclude Kentucky bluegrass. DMG = Dry Mixedgrass, MG = Mixedgrass, NF = Northern Fescue, CP = Central Parkland, PRP = Peace River Parkland.

Figure 7. Relationship between relative non-native richness (RNR) in a 10 x 10 m plot and total carbon (TC) in the Dry Mixedgrass ($P<0.05$). The line was fitted using a generalized additive model (GAM; n = 27 plots).
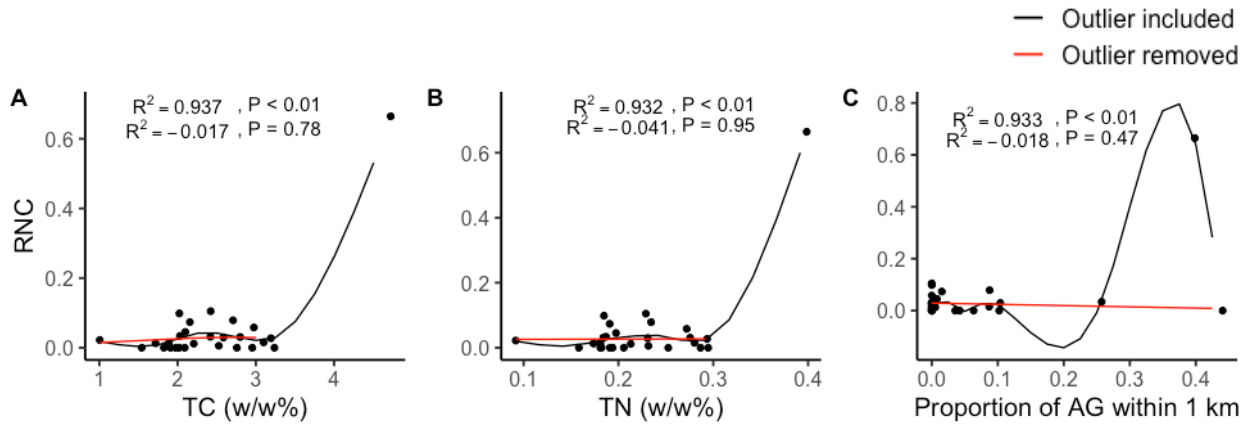
Figure 8. Relationship between relative non-native cover (RNC) within a 10 x 10 m plot and the significant (P<0.05) predictors A) total carbon (TC), B) total nitrogen (TN), and C) proportion of agriculture (AG) within 1 km of plot in the Dry Mixedgrass. Lines were fitted using generalized additive models (GAMs; n = 27 plots) and were plotted using the full dataset (black line) and with an outlier removed (red line) to illustrate the influence of an outlier that altered model significance. This also shows that the outlier had both exeptionally high RNC and soil fertility.
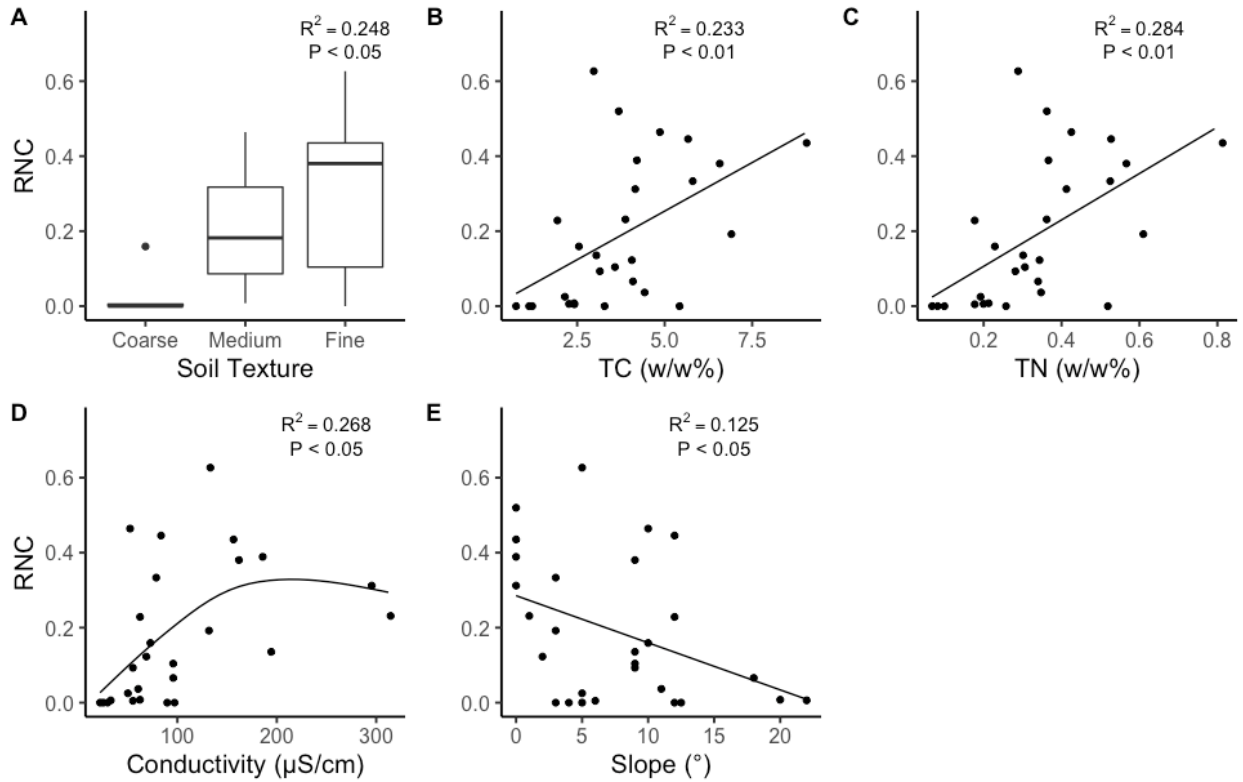
Figure 9. Relationship between relative non-native cover (RNC) within a 10 x 10 m plot and the significant (P<0.05) predictors A) soil texture, B) total carbon (TC), C) total nitrogen (TN), D) conductivity, and (E) slope in the Central Parkland. Lines were fitted using generalized additive models (GAMs; n = 28 plots). Model significance for conductivity was unaffected by an outlier value, so the outlier-removed model (n = 27) is shown here for better visual effect.
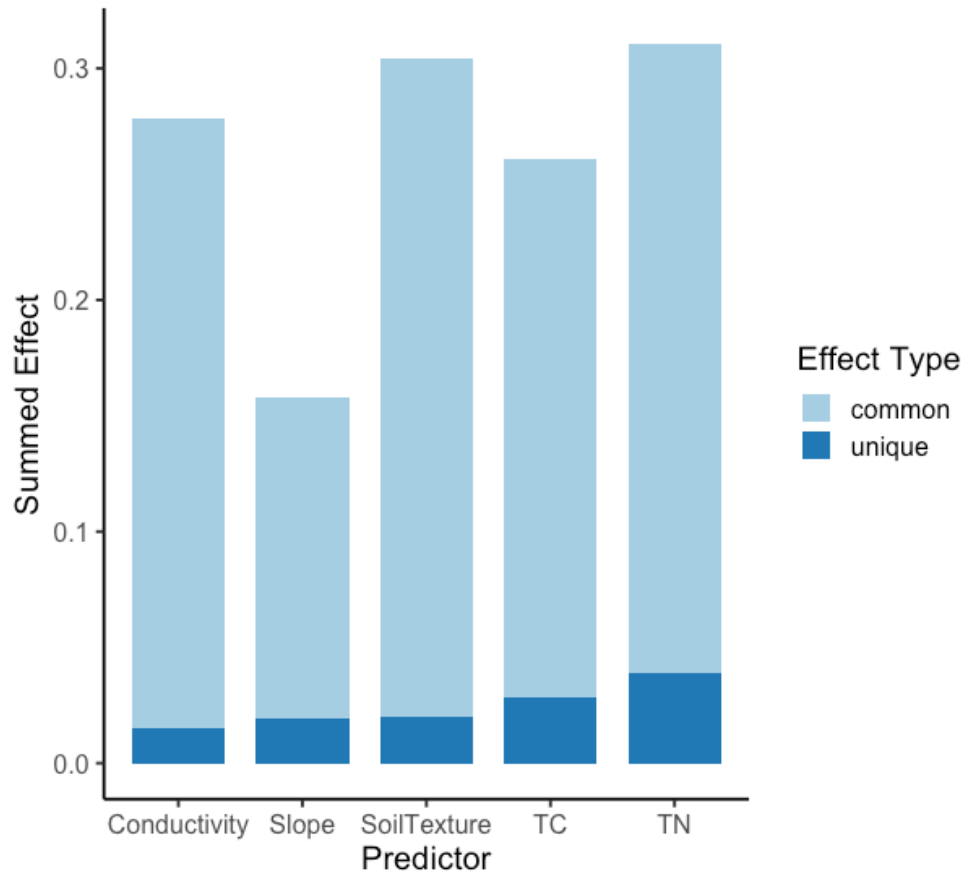
Figure 10. Summed effects from the commonality coefficient analysis for relative non-native cover in the Central Parkland. Common effects indicate how much variance (R^2) is common to groups of variables, and unique effects indicate how much variance is unique to a single variable (Reio et al. 2015). Refer to Table 4 for the effect combinations. TC = total carbon, TN = total nitrogen.
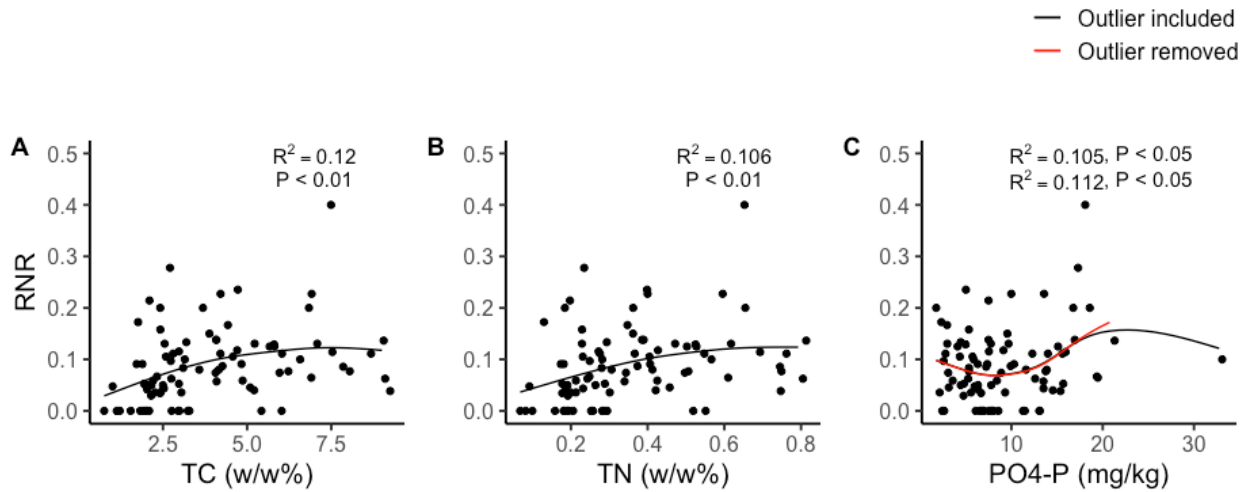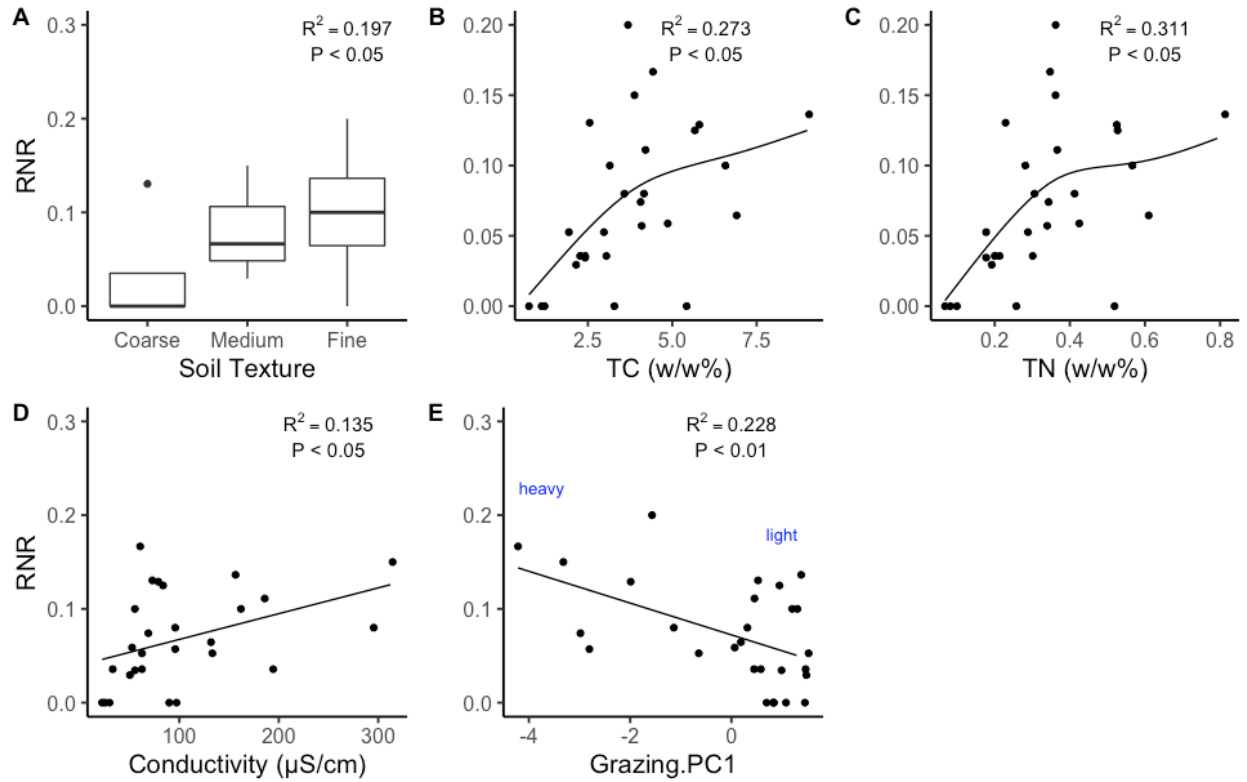
Figure 11. Relationship between relative non-native richness (RNR) within a 10 x 10 m plot and the significant (P<0.05) predictors A) soil texture, B) total carbon (TC), C) total nitrogen (TN), D) conductivity, and E) grazing intensity in the Central Parkland. Lines were fitted using generalized additive models (GAMs; n = 28 plots). Model significance for conductivity was unaffected by an outlier value, so the outlier-removed model (n = 27) is shown here for better visual effect.
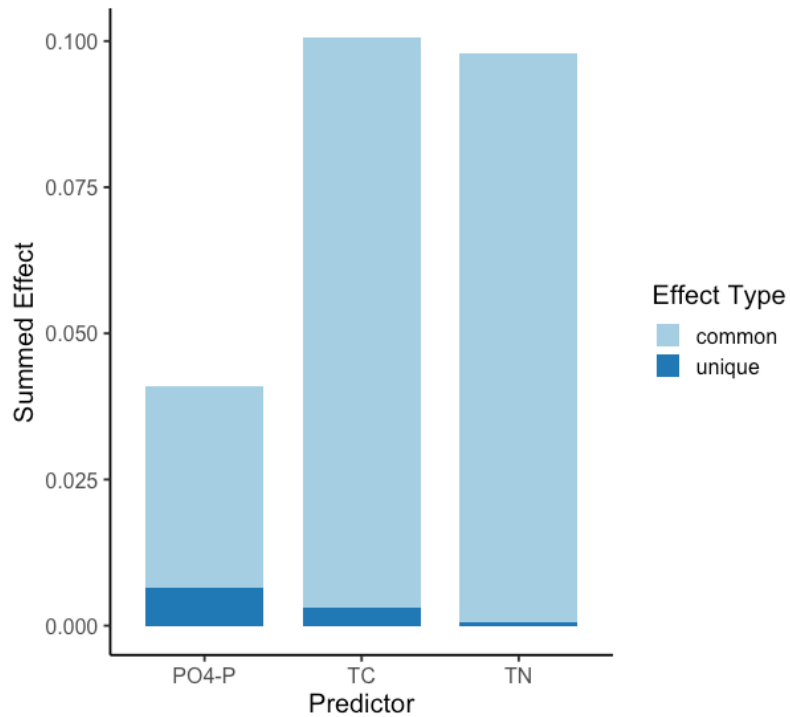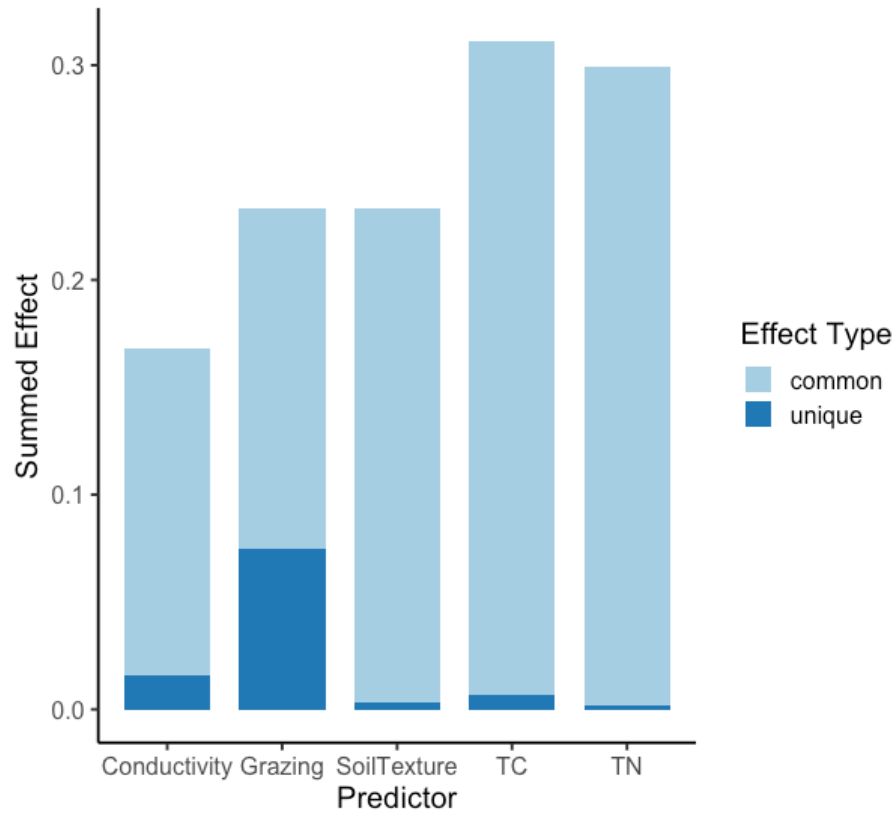
Figure 12. Summed effects from the commonality coefficient analysis for relative non-native richness in the Central Parkland. Common effects indicate how much variance (R^2) is common to groups of variables, and unique effects indicate how much variance is unique to a single variable (Reio et al. 2015). Refer to Table 5 for the effect combinations. TC = total carbon, TN = total nitrogen.
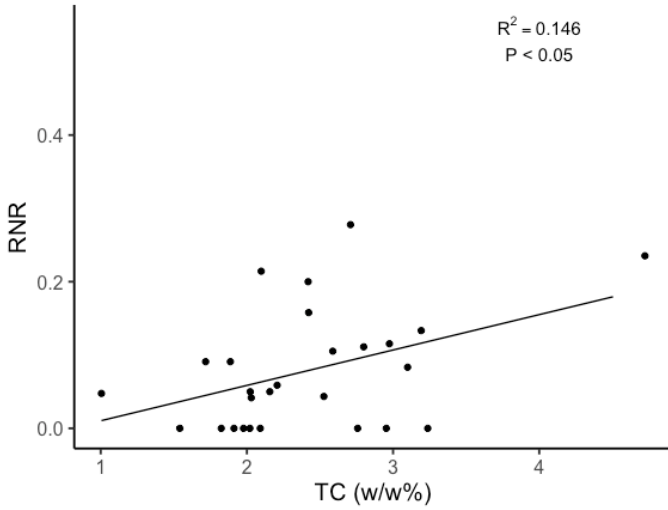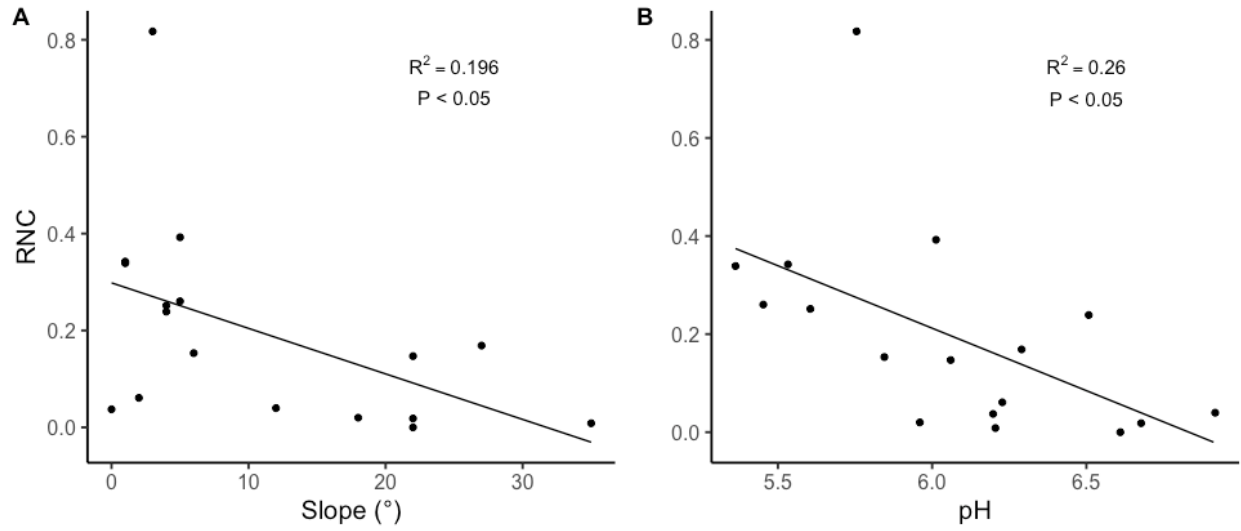
Figure 13. Relationship between relative non-native cover (RNC) in a 10 x 10 m plot and the significant ($P<0.05$) predictors A) slope and B) pH in the Peace River Parkland. Lines were fitted using generalized additive models (GAMs; n = 17 plots).
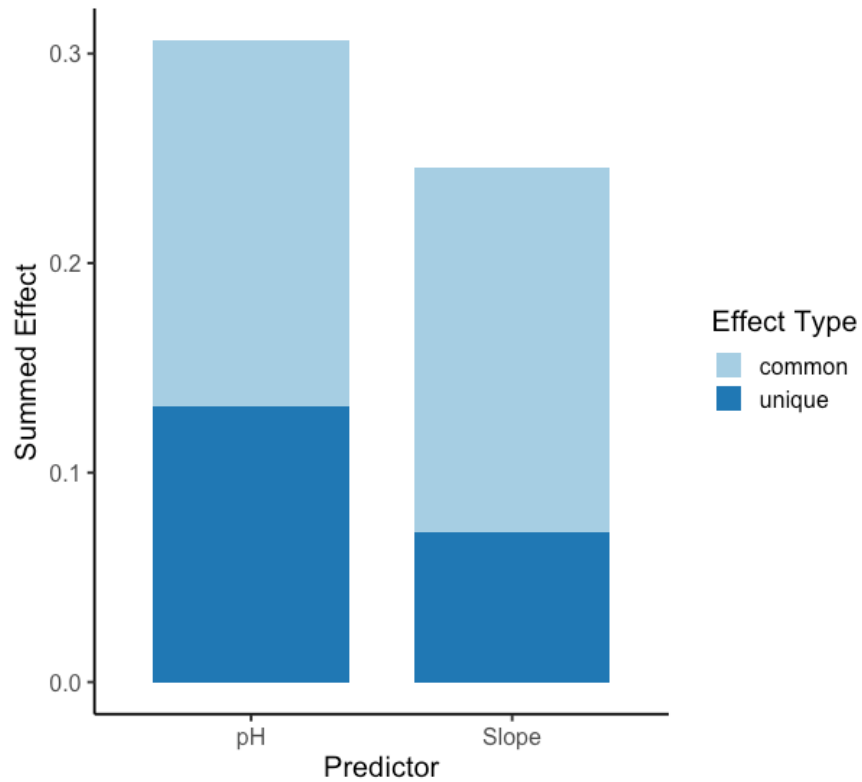
Figure 14. Visual summary of the commonality coefficient analysis (R^2) for relative non-native cover in the Peace River Parkland. Common effects indicate how much variance is common to groups of variables, and unique effects indicate how much variance is unique to a single variable (Reio et al. 2015). Refer to Table 6 for the effect combination details.
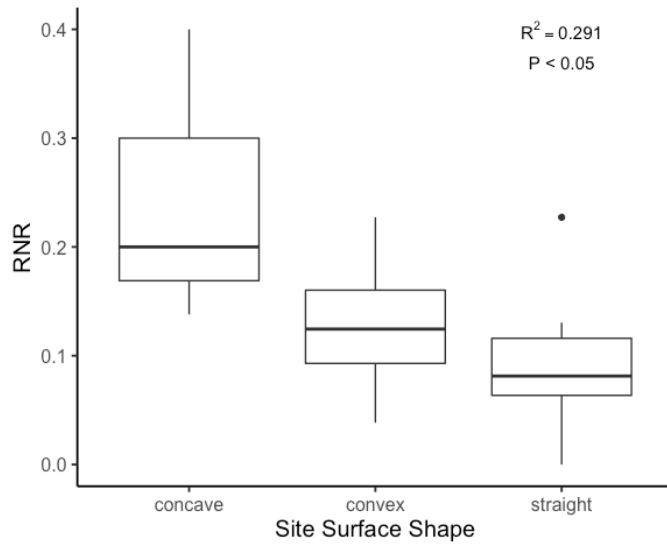
Figure 15. Relationship between relative non-native richness (RNR) within a 10 x 10 m plot and site surface shape in the Peace River Parkland (P<0.05). The model was fitted using a generalized additive model (GAM; n = 17 plots).

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Appendix A. Map showing the locations of 86 sample plots. Black lines delineate boundaries for the Alberta Natural Subregions (Downing and Pettapiece 2006). DMG = Dry Mixedgrass, MG = Mixedgrass, NF = Northern Fescue, CP = Central Parkland, PRP = Peace River Parkland.

PRP

CP (28 plots)

NF (10 plots)

DMG (27 plots)

MG (4 plots)
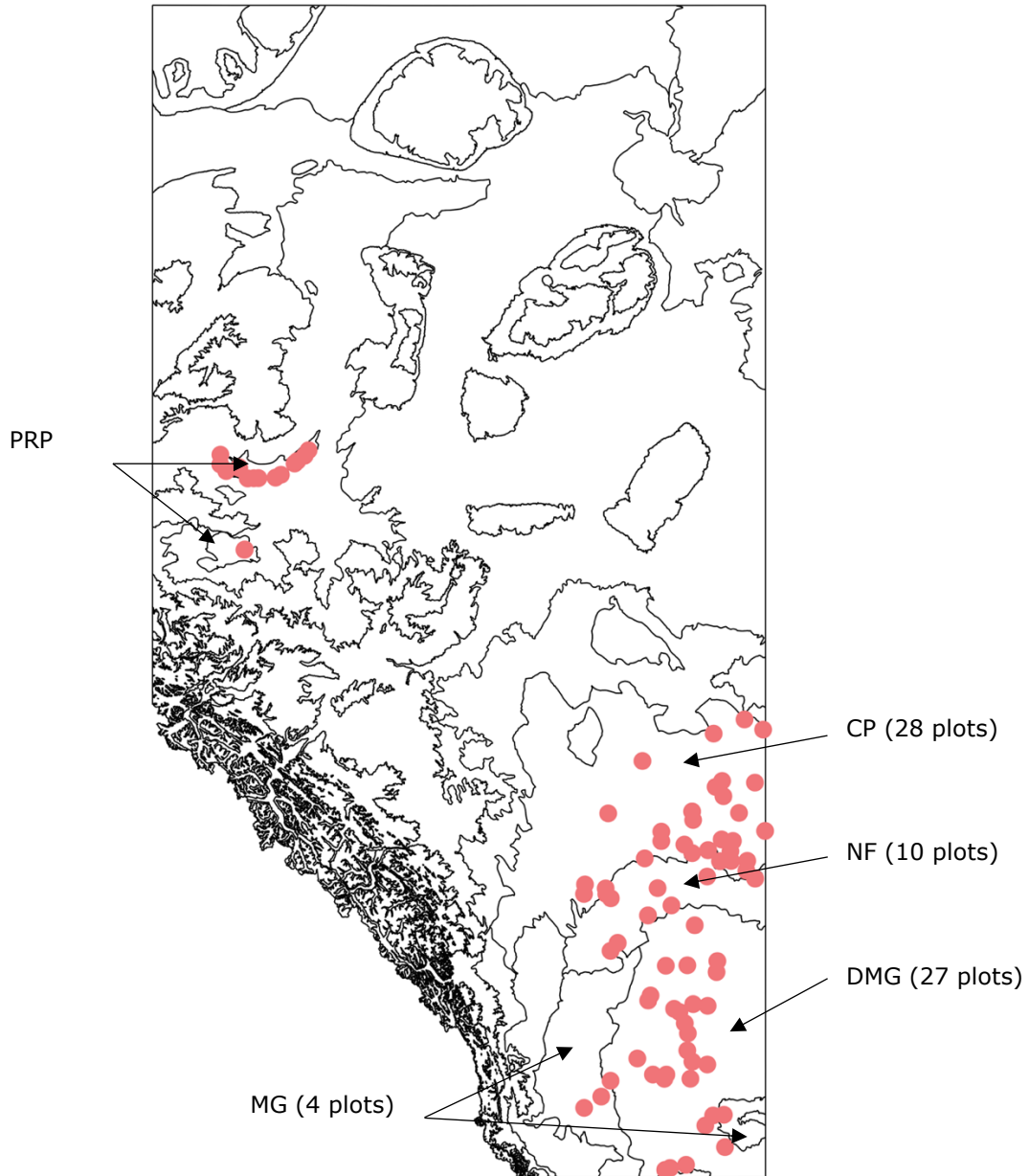
Appendix B. Vascular plant species observed among 86 native grassland plots

Scientific Name	Vernacular Name	Habit	Origin
Achillea millefolium	common yarrow	Herb	Native
Agoseris glauca	pale agoseris	Herb	Native
Agoseris glauca var. *glauca*	pale agoseris	Herb	Native
Agropyron cristatum	crested wheatgrass	Herb	Introduced
Agrostis scabra	rough bentgrass	Herb	Native
Allium cernuum	nodding onion	Herb	Native
Allium textile	prairie onion	Herb	Native
Amelanchier alnifolia	saskatoon	Shrub	Native
Androsace septentrionalis	northern fairy-candelabra	Herb	Native
Anemone sp.	anemone	Herb	Native
Anemone cylindrica	long-headed anemone	Herb	Native
Anemone multifida	cut-leaved anemone	Herb	Native
Antennaria neglecta	field pussytoes	Herb	Native
Antennaria parvifolia	small-leaved pussytoes	Herb	Native
Arctostaphylos uva-ursi	common bearberry	Shrub	Native
Arnica sp.		Herb	Native
Arnica fulgens	hillside arnica	Herb	Native
Arnica sororia	twin arnica	Herb	Native
Artemisia cana	silver wormwood	Herb	Native
Artemisia dracunculus	dragon wormwood	Herb	Native
Artemisia frigida	prairie sagebrush	Herb	Native
Artemisia ludoviciana	silver wormwood	Herb	Native
Artemisia ludoviciana subsp. *ludoviciana*	silver wormwood	Herb	Native
Asclepias speciosa	showy milkweed	Herb	Native
Astragalus sp.		Herb	Native
Astragalus agrestis	field milk-vetch	Herb	Native
Astragalus americanus	American milk-vetch	Herb	Native
Astragalus bisulcatus	two-grooved milk-vetch	Herb	Native
Astragalus canadensis	Canada milk-vetch	Herb	Native
Astragalus flexuosus	flexible milk-vetch	Herb	Native
Astragalus laxmannii var. *robustior*	ascending purple milk-vetch	Herb	Native
Astragalus missouriensis	Missouri milk-vetch	Herb	Native
Astragalus pectinatus	narrow-leaved milk-vetch	Herb	Native
Astragalus tenellus	loose-flowered milk-vetch	Herb	Native
Atriplex gardneri	Gardner's saltbush	Herb	Native
Axyris amaranthoides	Russian pigweed	Herb	Introduced
Boechera sp.	rockcress	Herb	Native
Boechera retrofracta	reflexed rockcress	Herb	Native
Bouteloua gracilis	blue grama	Herb	Native
Bromus ciliatus	fringed brome	Herb	Native
Bromus inermis	smooth brome	Herb	Introduced
Bromus japonicus	Japanese brome	Herb	Introduced
Bromus porteri	Porter's brome	Herb	Native
Bromus riparius	Asian meadow brome	Herb	Introduced
Calamagrostis montanensis	plains reedgrass	Herb	Native
Camelina microcarpa	small-seed false-flax	Herb	Introduced
Campanula rotundifolia	bluebell of Scotland	Herb	Native
Carex sp.	sedge	Herb	Native
Carex duriuscula	needle-leaved sedge	Herb	Native
Castilleja lutescens	stiff yellow paintbrush	Herb	Native
Cerastium arvense	field chickweed	Herb	Native
Chenopodium album	common lamb's-quarters	Herb	Introduced
Chenopodium leptophyllum	slim-leaved goosefoot	Herb	Native
Cirsium arvense	Canada thistle	Herb	Introduced

Scientific Name	Vernacular Name	Habit	Origin
Cirsium flodmanii	Flodman's thistle	Herb	Native
Comandra umbellata	bastard toadflax	Herb	Native
Crepis occidentalis	western hawksbeard	Herb	Native
Crepis runcinata	dandelion hawksbeard	Herb	Native
Crepis tectorum	narrow-leaved hawksbeard	Herb	Introduced
Dalea candida	white prairie-clover	Herb	Native
Dalea purpurea var. *purpurea*	purple prairie-clover	Herb	Native
Danthonia intermedia	timber oatgrass	Herb	Native
Deschampsia cespitosa	tufted hairgrass	Herb	Native
Descurainia pinnata	green tansy mustard	Herb	Native
Descurainia sophia	flixweed	Herb	Introduced
Dichanthelium wilcoxianum	Wilcox's panicgrass	Herb	Native
Draba nemorosa	woodland draba	Herb	Native
Drymocallis arguta	tall wood beauty	Herb	Native
Elaeagnus commutata	wolf-willow	Tree Shrub	Native
Elymus sp.	wildrye	Herb	Native
Elymus albicans	Montana wildrye	Herb	Native
Elymus elymoides	long-bristled wildrye	Herb	Native
Elymus lanceolatus	thick-spike wildrye	Herb	Native
Elymus lanceolatus subsp. *lanceolatus*	thick-spike wildrye	Herb	Native
Elymus trachycaulus	slender wildrye	Herb	Native
Elymus trachycaulus subsp. *subsecundus*	one-sided wildrye	Herb	Native
Equisetum hyemale	common scouring-rush	Herb	Native
Eremogone congesta	ballhead sandwort	Herb	Native
Ericameria nauseosa var. *nauseosa*	rubber rabbitbrush	Shrub	Native
Erigeron caespitosus	tufted fleabane	Herb	Native
Erigeron glabellus	streamside fleabane	Herb	Native
Erigeron glabellus var. *pubescens*	streamside fleabane	Herb	Native
Erigeron pumilus	shaggy fleabane	Herb	Native
Eriogonum flavum var. *flavum*	alpine golden wild buckwheat	Herb	Native
Erysimum asperum	prairie rocket	Herb	Native
Erysimum inconspicuum	small-flowered wallflower	Herb	Native
Escobaria vivipara	pincushion cactus	Herb	Native
Euphorbia glyptosperma	ridge-seeded spurge	Herb	Native
Festuca hallii	plains rough fescue	Herb	Native
Festuca idahoensis	Idaho fescue	Herb	Native
Festuca saximontana	Rocky Mountain fescue	Herb	Native
Fragaria virginiana	wild strawberry	Herb	Native
Gaillardia aristata	great blanketflower	Herb	Native
Galium boreale	northern bedstraw	Herb	Native
Geranium richardsonii	white geranium	Herb	Native
Geum macrophyllum	large-leaved avens	Herb	Native
Geum triflorum	three-flowered avens	Herb	Native
Glycyrrhiza lepidota	wild licorice	Herb	Native
Grindelia squarrosa	curly-cup gumweed	Herb	Native
Gutierrezia sarothrae	broom snakeweed	Herb	Native
Hedysarum americanum	alpine hedysarum	Herb	Native
Helianthus pauciflorus subsp. *subrhomboideus*	rhombic-leaved sunflower	Herb	Native
Helictochloa hookeri	Hooker's oatgrass	Herb	Native
Hesperostipa sp.	needle grass	Herb	Native
Hesperostipa comata	needle-and-thread grass	Herb	Native
Hesperostipa curtiseta	northern porcupine grass	Herb	Native
Hesperostipa spartea	plains porcupine grass	Herb	Native
Heterotheca villosa	hairy goldenaster	Herb	Native
Heuchera parvifolia	little-leaved alumroot	Herb	Native
Heuchera richardsonii	Richardson's alumroot	Herb	Native

Scientific Name	Vernacular Name	Habit	Origin
Hieracium umbellatum	umbellate hawkweed	Herb	Native
Hordeum jubatum	foxtail barley	Herb	Native
Hymenoxys richardsonii	Richardson's bitterweed	Herb	Native
Juncus balticus	Baltic rush	Herb	Native
Juniperus communis	common juniper	Shrub	Native
Juniperus horizontalis	creeping juniper	Shrub	Native
Koeleria macrantha	prairie junegrass	Herb	Native
Krascheninnikovia lanata	winterfat	Herb	Native
Lappula occidentalis	western stickseed	Herb	Native
Lepidium densiflorum	common peppergrass	Herb	Native
Liatris punctata	dotted blazing-star	Herb	Native
Lilium philadelphicum	wood lily	Herb	Native
Linaria vulgaris	butter-and-eggs	Herb	Introduced
Linum lewisii	Lewis' wild blue flax	Herb	Native
Lithospermum incisum	narrow-leaved puccoon	Herb	Native
Lomatium macrocarpum	large-fruited desert-parsley	Herb	Native
Lupinus pusillus	low lupine	Herb	Native
Lygodesmia juncea	rush skeletonplant	Herb	Native
Medicago sativa	alfalfa	Herb	Introduced
Mirabilis albida	hairy four-o'clock	Herb	Native
Nassella viridula	green needlegrass	Herb	Native
Oenothera biennis	common evening-primrose	Herb	Native
Oenothera suffrutescens	scarlet gaura	Herb	Native
Opuntia fragilis	brittle prickly-pear cactus	Herb	Native
Opuntia polyacantha	plains prickly-pear cactus	Herb	Native
Oxytropis campestris var. *spicata*	early yellow locoweed	Herb	Native
Oxytropis sericea	silky locoweed	Herb	Native
Oxytropis splendens	showy locoweed	Herb	Native
Packera cana	woolly groundsel	Herb	Native
Pascopyrum smithii	western wheatgrass	Herb	Native
Pediomelum argophyllum	silver-leaved Indian breadroot	Herb	Native
Penstemon albidus	white beardtongue	Herb	Native
Penstemon gracilis	slender beardtongue	Herb	Native
Penstemon procerus	small-flowered beardtongue	Herb	Native
Phleum pratense	common timothy	Herb	Introduced
Phlox hoodii	Hood's phlox	Herb	Native
Plantago eriopoda	saline plantain	Herb	Native
Plantago patagonica	woolly plantain	Herb	Native
Poa arida	plains bluegrass	Herb	Native
Poa interior	inland bluegrass	Herb	Native
Poa pratensis subsp. *agassizensis*	Agassiz's bluegrass	Herb	Native
Poa pratensis subsp. *angustifolia*	Kentucky bluegrass	Herb	Introduced
Poa pratensis subsp. *pratensis*	Kentucky bluegrass	Herb	Introduced
Poa secunda	Sandberg's bluegrass	Herb	Native
Polygonum aviculare subsp. *aviculare*	prostrate knotweed	Herb	Introduced
Populus tremuloides	trembling aspen	Tree	Native
Potentilla gracilis	slender cinquefoil	Herb	Native
Potentilla hippiana	Hipp's cinquefoil	Herb	Native
Potentilla pensylvanica	Pennsylvania cinquefoil	Herb	Native
Prunus virginiana	chokecherry	Tree Shrub	Native
Puccinellia nuttalliana	Nuttall's alkaligrass	Herb	Native
Pulsatilla nuttalliana	prairie pasqueflower	Herb	Native
Ranunculus sp.	buttercup	Herb	Native
Ranunculus cardiophyllus	heart-leaved buttercup	Herb	Native
Ranunculus rhomboideus	prairie buttercup	Herb	Native
Ratibida columnifera	upright prairie coneflower	Herb	Native

Scientific Name	Vernacular Name	Habit	Origin
Ribes hirtellum	swamp gooseberry	Shrub	Native
Rosa acicularis	prickly rose	Shrub	Native
Rosa arkansana	prairie rose	Shrub	Native
Rosa woodsii	Woods' rose	Shrub	Native
Rubus idaeus	red raspberry	Shrub	Native
Rumex crispus	curled dock	Herb	Introduced
Salsola sp.		Herb	Introduced
Selaginella densa	prairie spikemoss	Herb	Native
Silene drummondii	Drummond's catchfly	Herb	Native
Sisymbrium loeselii	Loesel's tumble mustard	Herb	Introduced
Sisyrinchium montanum	strict blue-eyed-grass	Herb	Native
Solidago sp.	goldenrod	Herb	Native
Solidago missouriensis	Missouri goldenrod	Herb	Native
Sphaeralcea coccinea	scarlet globe-mallow	Herb	Native
Spiraea alba	white meadowsweet	Shrub	Native
Sporobolus cryptandrus	sand dropseed	Herb	Native
Sporobolus rigidus var. *rigidus*	prairie sandreed	Herb	Native
Stellaria sp.		Herb	Native
Stellaria longifolia	long-leaved starwort	Herb	Native
Symphoricarpos occidentalis	western snowberry	Shrub	Native
Symphyotrichum ericoides var. *pansum*	tufted white prairie aster	Herb	Native
Symphyotrichum falcatum	white prairie aster	Herb	Native
Symphyotrichum falcatum var. *commutatum*	white prairie aster	Herb	Native
Symphyotrichum falcatum var. *falcatum*	white prairie aster	Herb	Native
Symphyotrichum laeve	smooth aster	Herb	Native
Taraxacum erythrospermum	red-seeded dandelion	Herb	Introduced
Taraxacum officinale	common dandelion	Herb	Introduced
Tetraneuris acaulis var. *acaulis*	stemless four-nerved daisy	Herb	Native
Thermopsis rhombifolia	prairie golden bean	Herb	Native
Tragopogon dubius	yellow goatsbeard	Herb	Introduced
Trifolium sp.	clover	Herb	Introduced
Trifolium repens	white clover	Herb	Introduced
Vicia americana	American vetch	Herb	Native
Viola adunca	hooked violet	Herb	Native
Viola canadensis var. *rugulosa*	rugose violet	Herb	Native
Viola nuttallii	Nuttall's violet	Herb	Native
Vulpia octoflora	eight-flowered fescue	Herb	Native
Xanthisma spinulosum var. *spinulosum*	lacy tansy-aster	Herb	Native

Appendix C. Generalized additive model (GAM) summaries for the effects of single predictor variables on A) total vegetation cover and B) total vegetation richness across all plots. Significant effects are bolded. AHM = annual heat:moisture index, TC = total carbon, TN = total nitrogen, PO_4-P = phosphate.

Parameter[1]	df	n	F	P	adj-R^2
A) Total Vegetation Cover					
AHM	1	86	1.71	0.195	0.008
Topo Pos	3	86	0.913	0.439	-0.003
Site Shape	2	86	0.757	0.472	-0.006
Slope	1	86	5.856	**<0.05**	0.054
Soil Texture	2	86	2.6	0.08	0.036
pH	2.76	86	2.348	0.064	0.084
Conductivity[1]	2.498	86	1.58	0.188	0.047
TC	1	86	2.137	0.146	0.014
TN	1	86	1.833	0.179	0.01
PO_4-P	1.292	86	0.126	0.829	-0.007
B) Total Vegetation Richness					
AHM	1	86	19.89	**<0.01**	0.182
Topo Pos	3	86	2.375	0.076	0.046
Site Shape	2	86	1.053	0.354	0.001
Slope	1.62	86	0.651	0.508	0.007
Soil Texture	2	86	1.271	0.286	0.006
pH	2.532	86	2.713	**<0.05**	0.085
Conductivity[1]	2.604	86	1.876	0.125	0.059
TC	1	86	0.893	**<0.01**	0.095
TN	1	86	8.929	**<0.01**	0.085
PO_4-P	1	86	0.329	0.568	-0.008

[1] Visual inspection revealed an outlier which influenced the prediction line for conductivity. All models were run with and without the outlier, but the model significance did not change the results for any of the predictors.

Appendix D. Summary statistics for relative non-native cover (RNC) and relative non-native richness (RNR) for all plots, and within the Dry Mixedgrass (DMG), Central Parkland (CP), and Peace River Parkland (PRP) plots. The summary table is followed by histograms showing the distributions of plots for the RNC and RNR values for all plots (A, B), DMG (C, D), CP (E, F), and PRP (G, H).

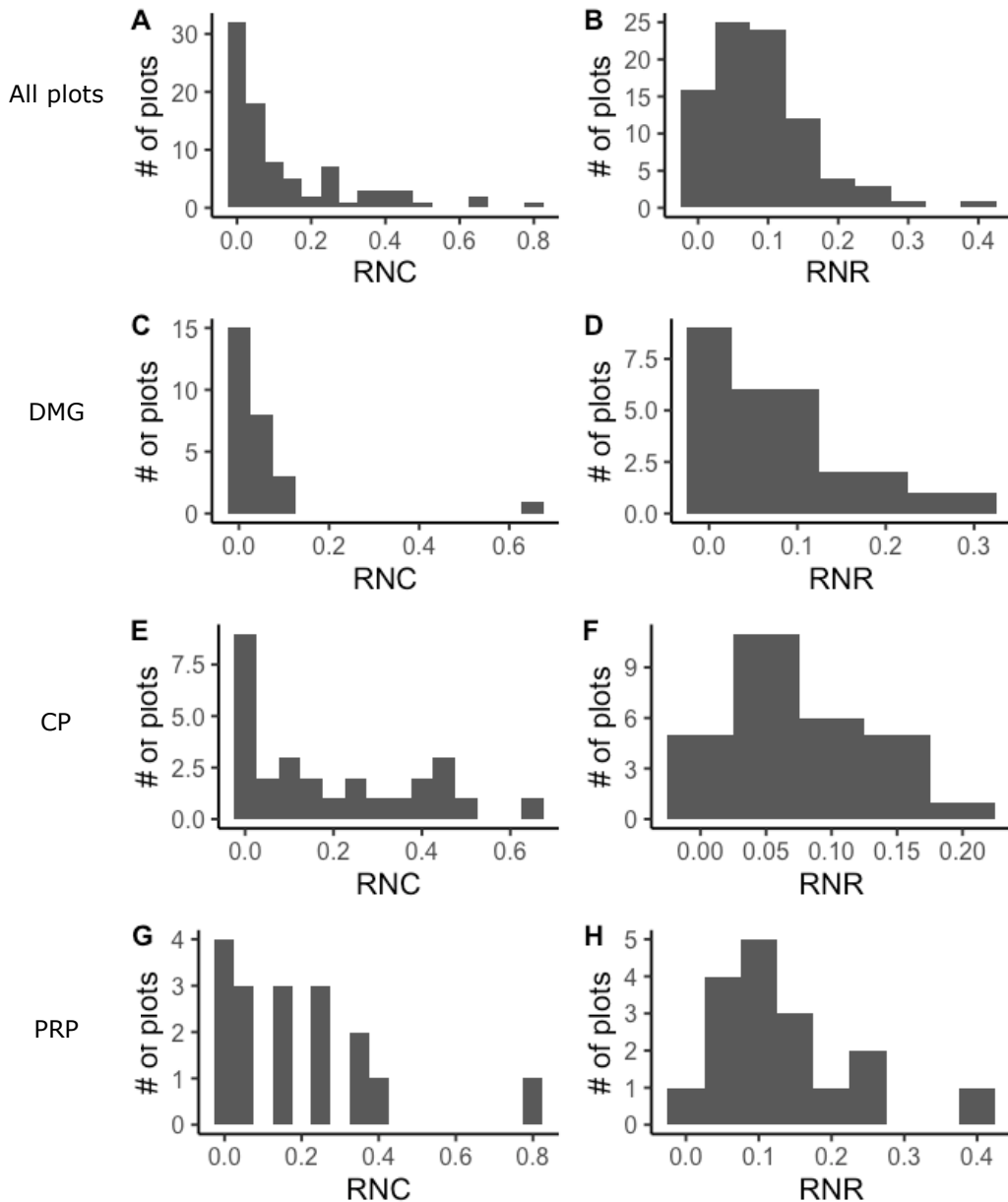|	Relative Non-native Cover					Relative Non-native Richness				
	Min	*Med*	*Mean*	*Max*	*SD*	*Min*	*Med*	*Mean*	*Max*	*SD*
All plots	0	0.048	0.13	0.82	0.17	0	0.078	0.088	0.4	0.073
DMG	0	0.015	0.05	0.66	0.13	0	0.05	0.078	0.28	0.082
CP	0	0.13	0.19	0.63	0.19	0	0.062	0.073	0.2	0.055
PRP	0	0.15	0.19	0.82	0.21	0	0.11	0.13	0.4	0.094

Appendix E. Generalized additive model (GAM) summaries for the effects of single predictor variables on A) relative non-native cover (RNC) and B) relative non-native richness (RNR) across all plots. Additional GAMs for the significant RNC models were also run with Kentucky bluegrass (KB) excluded from the dataset. Significant effects are bolded. AHM = annual heat:moisture index, TC = total carbon, TN = total nitrogen, PO_4-P = phosphate, OR = outlier removed.

A) Relative Non-native Cover – All Plots

Parameter	df	n	F	P	adj-R^2	AICc	delta	df	n	F	P	adj-R^2
			KB included							*KB excluded*		
AHM	1.493	86	6.586	**<0.01**	0.132	-63.4	13.8	1	86	0.087	0.796	-0.011
Topo Pos	3	86	2.882	**<0.05**	0.062	-55.8	21.5	3	86	1.993	0.121	0.004
Site Shape	2	86	0.375	0.688	-0.015	-	-	-	-	-	-	-
Slope	1	86	4.622	**<0.05**	0.041	-56.2	21	1	-	1.157	0.285	0.002
Soil Texture	2	86	1.564	0.215	0.013	-	-	-	-	-	-	-
Grazing	2.089	86	1.358	0.353	0.027	-	-	-	-	-	-	-
pH[1]	1.81	86	2.492	0.074	0.056	-	-	-	-	-	-	-
pH (OR) [1]	1	85	8.165	**<0.01**	0.079	-	-	-	-	-	-	-
Conductivity[1]	1	86	10	**<0.01**	0.096	-	-	-	-	-	-	-
Conductivity (OR)[1]	1.812	85	2.881	0.056	0.062	-	-	-	-	-	-	-
TC	1.261	86	16.95	**<0.01**	0.236	-75	2.3	2.088	86	1.914	0.155	0.0465
TN	1.006	86	28.79	**<0.01**	0.249	-77.3	0	2.21	86	1.751	0.174	0.0485
PO_4-P	1	86	8.699	**<0.01**	0.083	-60.1	17.2	1	86	0.127	0.722	-0.0104
Human Footprint	1	86	2.003	0.161	0.012	-	-	-	-	-	-	-
Agriculture	1.992	86	6.275	**<0.01**	0.145	-63.9	13.4	2.15	86	1.851	0.118	0.054
Oil and Gas	1	86	0.073	0.788	-0.011	-	-	-	-	-	-	-
Roads	2.141	86	1.382	0.329	0.03	-	-	-	-	-	-	-

[1] Visual inspection revealed an outlier that changed model outcomes for pH, which became significant when the outlier was removed, and conductivity, which became insignificant when the outlier was removed (see Figures 2e and 2f).

B) Relative Non-native Richness – All Plots

Parameter	df	n	F	P	adj-R^2	AICc	delta
AHM	2.359	86	0.705	0.497	0.019	-	-
Topo Pos	3	86	0.91	0.44	-0.003	-	-
Site Shape	2	86	0.422	0.657	-0.014	-	-
Slope	1	86	0.03	0.863	-0.012	-	-
Soil Texture	2	86	2.687	0.074	0.038	-	-
Grazing	2.321	86	1.867	0.127	0.055	-	-
pH	1	86	0.118	0.732	-0.011	-	-
Conductivity[1]	1	86	2.247	0.138	0.015	-	-
TC	2.082	86	4.713	**<0.01**	0.12	-209.5	0
TN	1.812	86	4.78	**<0.01**	0.106	-208.6	0.9
PO_4-P[1]	3.279	86	2.638	**<0.05**	0.105	-204.3	5.1
Human Footprint	1	86	0.74	0.392	-0.003	-	-
Agriculture	1.699	86	0.81	0.454	0.009	-	-
Oil and Gas	1	86	0.001	0.97	-0.012	-	-
Roads	2.548	86	2.025	0.108	0.065	-	-

[1] Visual inspection revealed potential influential points for conductivity (plot 45), and PO_4-P (plot 46), but their respective inclusion or exclusion did not influence the significant results.

Appendix F. Generalized additive model (GAM) summaries for the effects of single predictor variables on A) relative non-native cover (RNC) and B) relative non-native richness in the Dry Mixedgrass. Significant effects are bolded. AHM = annual heat:moisture index, TC = total carbon, TN = total nitrogen, PO_4-P = phosphate, OR = outlier removed.

A) Relative Non-native Cover – Dry Mixedgrass

Parameter	df	n	F	P	adj-R^2
Topo Pos	3	27	1.418	0.263	0.046
Site Shape	2	27	0.753	0.482	-0.019
Slope	1	27	0.622	0.438	-0.015
Soil Texture	1	27	2.295	0.142	0.047
Grazing	1	27	0	0.966	-0.04
pH	1	27	1.098	0.305	0.004
Conductivity	1	27	0.466	0.501	-0.021
TC [1]	5.045	27	64.82	**<0.01**	0.937
TC (OR)[1]	1.304	26	0.337	0.748	-0.017
TN [1]	5.256	27	57.67	**<0.01**	0.932
TN (OR)[1]	1	26	0.004	0.951	-0.042
PO_4-P	1	27	0.227	0.638	-0.031
Human Footprint	1	27	0.844	0.367	-0.006
Agriculture [1]	6.911	26	747.18	**<0.01**	-0.019
Agriculture (OR)[1]	1	26	0.546	0.467	-0.019
Oil and Gas	1.485	27	0.606	0.466	0.029
Roads	3.266	27	1.614	0.167	0.198

[1] Visual inspection revealed a RNC outlier (plot 18) that influenced the prediction lines for the TN, TC, and agriculture models (see Figure 8) but not for other predictors. Models for TN, TC, and agriculture were no longer significant once the outlier was removed. Both scenarios are reported here.

B) Relative Non-native Richness – Dry Mixedgrass

Parameter	df	n	F	P	adj-R^2
Topo Pos	3	27	1.07	0.381	0.008
Site Shape	2	27	0.928	0.409	-0.006
Slope	1	27	0.02	0.89	-0.039
Soil Texture	1	27	1.579	0.221	0.022
Grazing	2.426	27	2.271	0.106	0.184
pH	1	27	0.012	0.913	-0.04
Conductivity	1	27	0.171	0.683	-0.033
TC	1	27	5.445	**<0.05**	0.146
TN	1	27	2.977	0.097	0.071
PO_4-P [1]	2.917	27	3.207	**<0.05**	0.291
PO_4-P (OR)[1]	1	26	4.161	0.052	0.112
Human Footprint	1	27	3.368	0.787	0.087
Agriculture	1	27	0.185	0.671	-0.032
Oil and Gas	2.038	27	0.524	0.511	0.052
Roads	2.054	27	1.566	0.235	0.106

[1] Visual inspection revealed one PO_4-P observation (plot 15) which influenced the prediction line for PO_4-P. The model was no longer significant after the influential point was removed. Both scenarios are reported here, but phosphate will not be reported as a significant predictor due to the change in model outcome. The inclusion or exclusion of the influential point did not impact any other RNR models in the DMG.

Appendix G. Generalized additive model (GAM) summaries for the effects of single predictor variables on A) relative non-native cover (RNC) and B) relative non-native richness (RNR) in the Central Parkland. Additional GAMs for the significant RNC models were run with Kentucky bluegrass (KB) excluded from the dataset. Significant effects are bolded. AHM = annual heat:moisture index, TC = total carbon, TN = total nitrogen, PO_4-P = phosphate, OR = outlier removed.

A) Relative Non-native Cover – Central Parkland

Parameter	df	n	F	P	adj-R2	AICc	delta	df	n	F	P	adj-R2
				KB included							*KB excluded*	
Topo Pos	3	28	2.533	0.081	0.146	-	-	-	28	-	-	-
Site Shape	2	28	1.324	0.284	0.023	-	-	-	28	-	-	-
Slope	1	28	4.872	**<0.05**	0.125	-12	5.6	1	28	0.964	0.335	-0.001
Soil Texture	2	28	5.462	**<0.05**	0.248	-14.6	3	2	28	1.003	0.381	0
Grazing	1.595	28	0.267	0.763	-0.005	-	-	-	28	-	-	-
pH	1	28	2.144	0.155	0.041	-	-	-	28	-	-	-
Conductivity [1]	1.821	28	5.462	**<0.05**	0.292	-	-	1.578	28	2.753	0.116	0.123
Conductivity (OR)[1]	2.039	27	4.141	**<0.05**	0.268	-15.3	2.3	1	27	0	0.987	-0.04
TC	1	28	9.187	**<0.01**	0.233	-15.7	1.9	1.541	28	0.914	0.337	0.047
TN	1	28	11.7	**<0.01**	0.284	-17.6	0	1.742	28	1.18	0.315	0.064
PO_4-P	1	28	3.359	0.078	0.08	-	-	-	28	-	-	-
Human Footprint	1	28	0.693	0.413	-0.012	-	-	-	28	-	-	-
Agriculture	1.721	28	1.896	0.169	0.102	-	-	-	28	-	-	-
Oil and Gas	1.566	28	0.757	0.539	0.017	-	-	-	28	-	-	-
Roads	1	28	1.582	0.22	0.021	-	-	-	28	-	-	-

[1] Visual inspection revealed an outlier which influenced the prediction line for conductivity. All models were run with and without the outlier, but model significance did not change the results for any of the predictors.

B) Relative Non-native Richness – Central Parkland

Parameter	df	n	F	P	adj-R2	AICc	delta
Topo Pos	3	28	2.323	0.1	0.128	-	-
Site Shape	2	28	1.696	0.204	0.049	-	-
Slope	3.556	28	2.611	0.062	0.279	-	-
Soil Texture	2	28	4.31	**<0.05**	0.197	-82.2	2.73
Grazing	1	28	8.954	**<0.01**	0.228	-85	0
pH	3.987	28	2.561	0.054	0.3	-	-
Conductivity [1]	1	28	13.2	**<0.05**	0.135	-	-
Conductivity (OR)[1]	1	27	5.043	**<0.05**	0.135	-83.8	1.21
TC	1.954	28	4.649	**<0.05**	0.273	-83.6	1.34
TN	2.253	28	4.819	**<0.05**	0.311	-84.4	0.57
PO_4-P	1	28	1.445	0.24	0.016	-	-
Human Footprint	1.54	28	1.066	0.291	0.061	-	-
Agriculture	2.287	28	1.716	0.148	0.155	-	-
Oil and Gas	2.339	28	1.418	0.198	0.134	-	-
Roads	1	28	0.428	0.519	-0.022	-	-

[1] Visual inspection revealed an outlier which influenced the prediction line for conductivity. All models were run with and without the outlier, but model significance did not change the results for any of the predictors.

Appendix H. Generalized additive model (GAM) summaries for the effects of single predictor variables on A) relative non-native cover (RNC) and B) relative non-native richness (RNR) in the Peace River Parkland. Additional GAMs for the significant RNC models were run with Kentucky bluegrass (KB) excluded from the dataset. Significant effects are bolded. AHM = annual heat:moisture index, TC = total carbon, TN = total nitrogen, PO_4-P = phosphate, OR = outlier removed.

A) Relative Non-native Cover – Peace River Parkland

Parameter	df	n	F	P	adj-R2	df	n	F	P	adj-R2
			KB included					*KB excluded*		
Topo Pos	2	17	3.397	0.063	0.231	-	17	-	-	-
Site Shape [1]	2	17	6.2	**<0.05**	0.394	2	17	5.612	**<0.05**	0.366
Site shape (OR)[1]	2	16	2.537	0.117	0.17	-	16	-	-	-
Slope	1	17	4.891	**<0.05**	0.196	1	17	0.77	0.394	-0.015
Soil Texture	1	17	0.845	0.372	-0.895	-	17	-	-	-
Grazing	1	17	0.001	0.979	-0.067	-	17	-	-	-
pH	1	17	6.622	**<0.05**	0.26	1	17	0.554	0.468	-0.029
Conductivity	1	17	0.464	0.506	-0.035	-	17	-	-	-
TC	1	17	2.386	0.143	0.08	-	17	-	-	-
TN	1	17	2.705	0.121	0.096	-	17	-	-	-
PO4-P	1	17	0.133	0.72	-0.057	-	17	-	-	-
Human Footprint	1	17	0.377	0.548	-0.041	-	17	-	-	-
Agriculture	1	17	0.538	0.474	-0.03	-	17	-	-	-
Oil and Gas	1	17	0.474	0.502	-0.034	-	17	-	-	-
Roads[1]	3.285	17	5.084	**<0.05**	0.553	2.207	17	2.01	0.158	0.222
Roads (OR)[1]	1.585	16	0.755	0.43	0.052	-	16	-	-	-

[1] Visual inspection revealed a RNC outlier (plot 70) that strongly influenced the prediction lines for site shape and roads, which were no longer significant once the influential point was removed. The model outcomes of other predictors were unaffected by the inclusion or exclusion of the influential point. Both scenarios are reported here, but site shape and roads were not considered significant predictors in the analysis nor discussion.

B) Relative Non-native Richness – Peace River Parkland

| Parameter	df	n	F	P	adj-R^2
Topo Pos	2	17	1.636	0.23	0.074
Site Shape	2	17	4.278	**<0.05**	0.291
Slope	1	17	0.126	0.728	-0.058
Soil Texture	1	17	0.126	0.728	-0.058
Grazing	1	17	0.437	0.519	-0.063
pH	1	17	0.25	0.624	-0.049
Conductivity	1	17	0.366	0.554	-0.041
TC	1.841	17	0.783	0.533	0.048
TN	1.963	17	0.924	0.478	0.075
PO4-P	1	17	1.972	0.18	0.057
Human Footprint	1	17	1.755	0.205	0.045
Agriculture	1	17	1.794	0.2	0.047
Oil and Gas	1	17	0.025	0.876	-0.065
Roads	2.678	17	3.237	0.054	0.378

Appendix I. Summary of relationships among environmental variables. A) shows analysis of variance (ANOVA) results for continuous soil variables and the categorical variables of topographic position, site shape, and soil texture. Significant relationships are bolded. B) shows boxplots of the variables in A that significantly differed among categorical predictors. C) shows correlation matrix heat maps for continuous predictors. Blue circles indicate positive correlation while red circles indicate negative correlation. Large circles indicate strong correlation while small circles indicate weak correlation. AHM = annual heat:moisture index, TC = total carbon, TN = total nitrogen, PO_4-P = phosphate, DMG = Dry Mixedgrass, CP = Central Parkland, PRP = Peace River Parkland.

## A) Continuous Soil Variables vs. Categorical Topography and Texture Variables

Response	n		Topo position				Site shape				Soil texture	
		df	F	P	df	F	P	df	F	P		
All plots												
TC	86	3	0.578	0.631	2	2.462	0.0915	2	9.117	**<0.01**		
TN	86	3	0.525	0.666	2	2.533	0.0855	2	10.8	**<0.01**		
PO_4	86	3	1.503	0.22	2	0.303	0.739	2	2.206	0.117		
pH	86	3	0.22	0.882	2	2.421	0.0951	2	0.83	0.44		
Conductivity	86	3	1.832	0.148	2	0.205	0.815	2	2.792	0.0671		
DMG												
TC	27	3	0.656	0.588	2	1.027	0.373	2	0.003	0.96		
TN	27	3	0.397	0.757	2	0.593	0.561	2	0.007	0.93		
PO_4	27	3	0.277	0.841	2	0.091	0.914	2	0.676	0.419		
pH	27	3	1.262	0.311	2	4.449	**<0.05**	2	0.665	0.422		
Conductivity	27	3	0.926	0.444	2	1.091	0.352	2	1.294	0.266		
CP												
TC	28	3	0.996	0.412	2	2.803	0.0798	2	9.623	**<0.01**		
TN	28	3	1.053	0.387	2	2.577	0.096	2	10.64	**<0.01**		
PO_4	28	3	4.511	**<0.05**	2	0.596	0.559	2	2.559	0.0975		
pH	28	3	0.698	0.563	2	0.087	0.917	2	0.135	0.875		
Conductivity	28	3	4.809	**<0.01**	2	0.987	0.387	2	2.795	0.0803		
PRP												
TC	17	3	0.293	0.751	2	0.071	0.932	2	3.879	0.0677		
TN	17	3	0.359	0.705	2	0.007	0.993	2	3.794	0.0704		
PO_4	17	3	1.534	0.25	2	1.402	0.279	2	3.051	0.101		
pH	17	3	0.02	0.98	2	1.77	0.206	2	0.088	0.77		
Conductivity	17	3	1.002	0.392	2	5.368	**<0.05**	2	1.331	0.267		

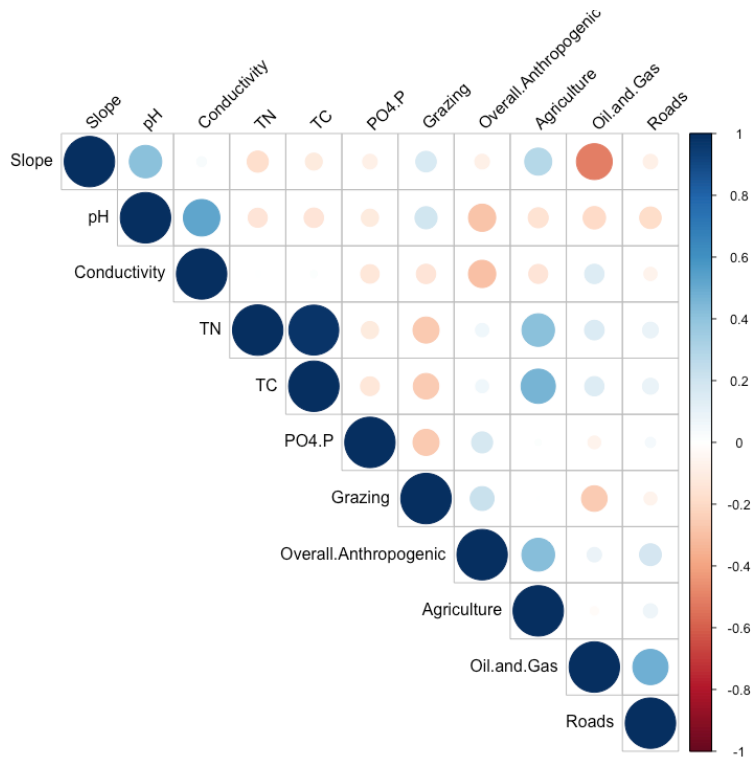**B) Significant Soil Differences Among Categorical Variables**
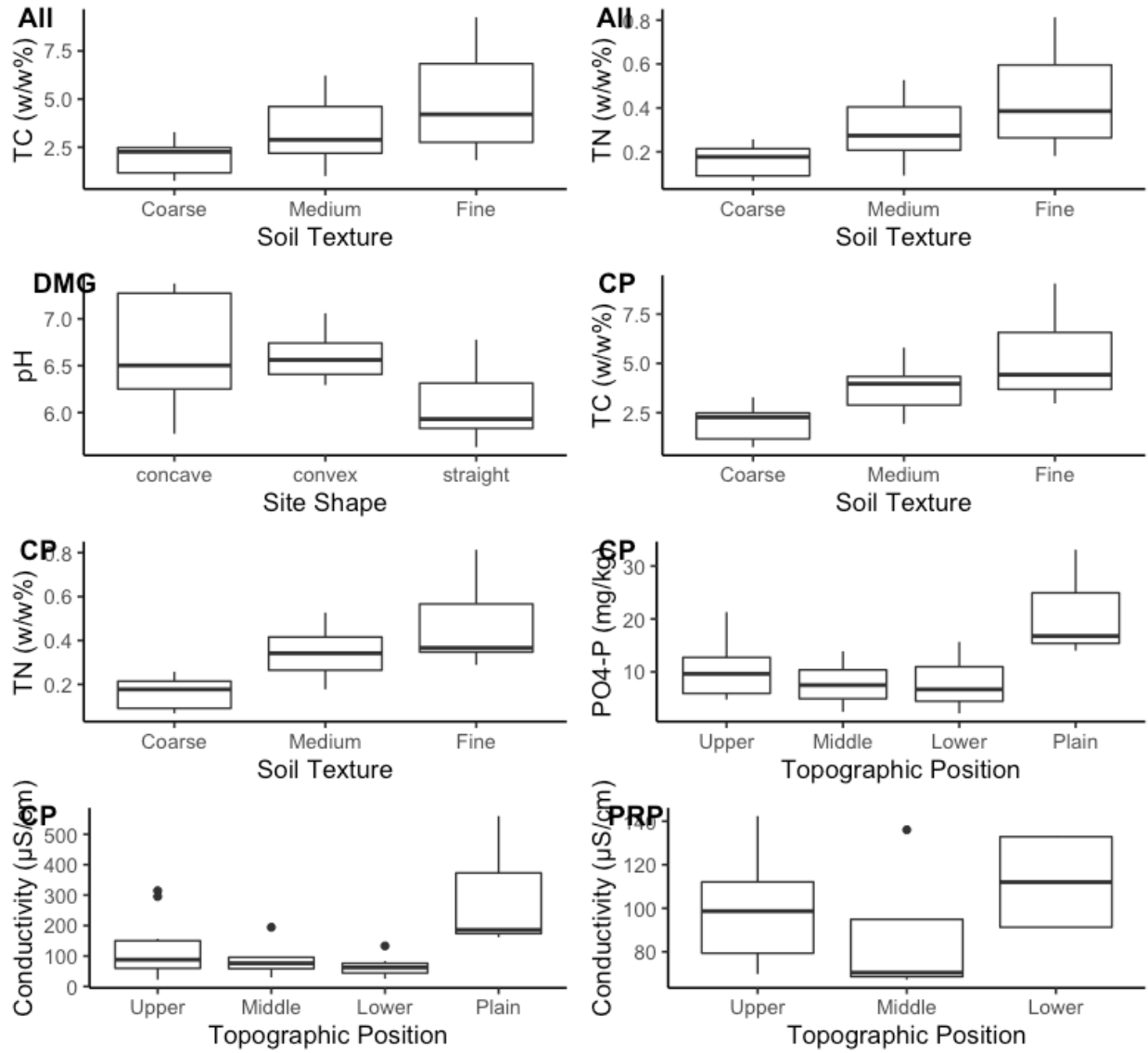
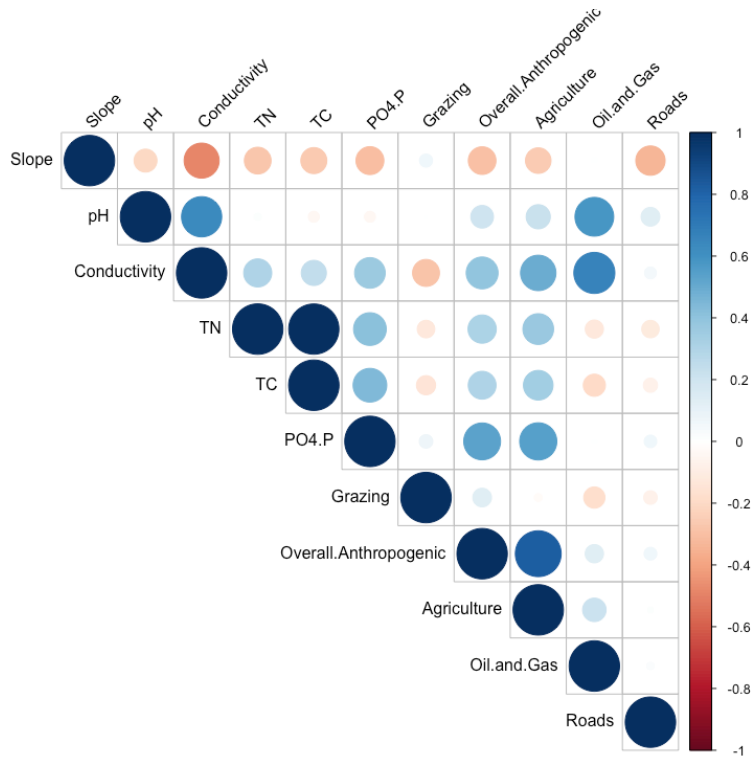## C) Correlation Matrix Heat Maps for All Continuous Variables

All plots
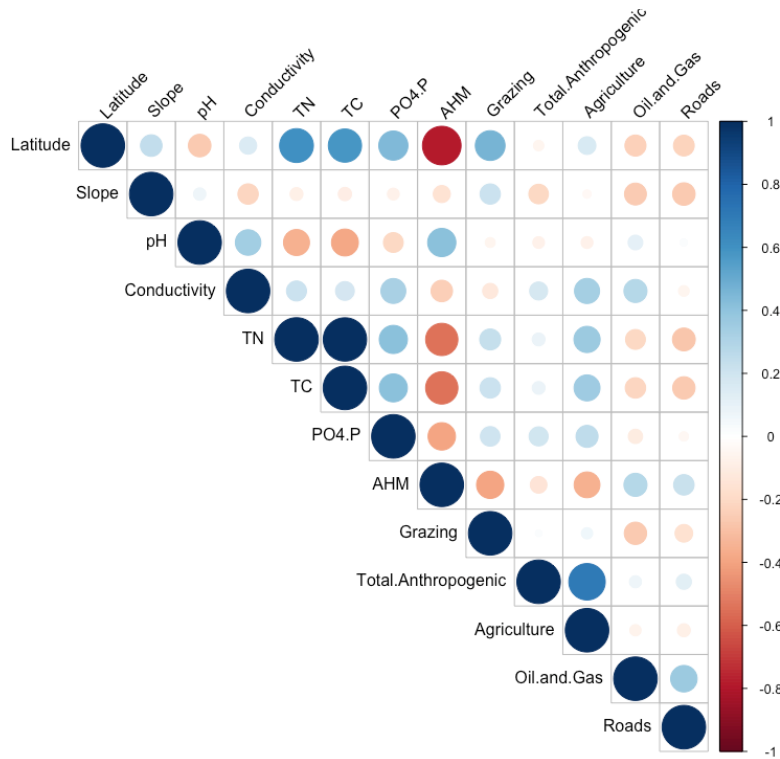
Dry Mixedgrass

Central Parkland

Peace River Parkland