Factors Influencing the Diversity and Abundance of Grassland Birds in the Waterton Foothills Parkland, Alberta, Canada

by

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Abstract

Grassland birds are among the most imperilled taxa in North America, with declines being primarily associated with the widespread conversion of grasslands for agriculture. However, alteration of existing vegetation communities and the landscape context in which habitats occur can be important factors affecting the use of remaining grassland habitats by birds. The Waterton Foothills Parkland region in southern Alberta, Canada is characterized by complex topography consisting of native grassland-forest-wetland mosaics. In this thesis, I used naturally occurring landscape heterogeneity and management-relevant habitat metrics to evaluate multi-scale ecological responses of grassland birds. I evaluated how the presence, abundance, and diversity of grassland birds responded to their habitat using Autonomous Recording Units, in-field vegetation surveys, and spatial landscape assessments. I found that the grassland bird community mostly responded to grassland fragmentation and topography within 400 to 800 m extents. Fragmentation increased the total diversity of grassland birds because spillover of facultative grassland birds at edges was greater than decreases in the diversity of a limited pool of obligate species in more fragmented landscapes. Sites with more rugged terrain was autocorrelated with native grasslands, suggesting that landscape-scale responses of grassland birds to terrain ruggedness were associated with the distribution of different grassland types. Local measures of grassland type represented by the percent composition of non-native species and rangeland health were key determinants of the grassland bird community. Healthy, native grasslands supported higher abundances of Vesper and Clay-coloured Sparrows and unhealthy, modified grasslands supported more

Savannah Sparrows and Western Meadowlarks. This research supports that sections and quarter-sections of land are informative units for examining the abundance and diversity of grassland birds in the Waterton Foothills Parkland based on responses of the grassland community to grassland fragmentation, topography, non-native vegetation invasion, and range health.

Contents

Acknowledgements **2**
Abstract **3**
Contents **5**
Thesis Summary **6**
1 Introduction **7**
1.1 Context 7
1.2 Scales of Effect 7
1.3 Grassland Type and Rangeland Management 13
1.4 Regional Context and Data Gap 15
1.5 Study Goals and Objectives 19
1.6 Literature Cited 21
1.7 Tables 37
1.8 Figures 39
2 Grassland Bird Abundance and Diversity in the Foothills Parkland **41**
2.1 Abstract 41
2.2 Introduction 44
2.3 Methods 50
2.3.1 Study Region & Site Selection 50
2.3.2 Bird Surveys 52
2.3.3 Vegetation Structure 53
2.3.4 Range Health 53
2.3.5 Scales of Effect and Landscape Structure 54
2.3.6 Statistical Analyses 57
2.4 Results 63
2.4.1 Mean Abundances and Diversity (Intercepts) 63
2.4.2 Survey Variables 64
2.4.3 Grassland Type 65
2.4.4 Range Health 67
2.4.5 Scales of Effect and Landscape Structure 68
2.5 Discussion 71
2.6 Conclusion 79
2.7 Literature Cited 79
2.8 Tables 100
2.9 Figures 106
3 Summary and Management Implications **116**
3.1 Summary 116
3.2 Management Implications 117
3.3 Notes on Future Research 119
3.3.1 Bobolink 119
3.3.2 Common Nighthawk 120
3.3.3 Underrepresented Bird Assemblages 120

3.3.4 Nest Productivity 121
3.3.5 Implications of Range Health versus Topography on Grassland Alteration.. 121
3.4 Literature Cited 122
Appendix 1: Comparing Land Cover Datasets 125
Introduction 125
Methods 125
Study Region & Validation Sites 125
Datasets Compared 126
Accuracy Assessment 128
Results 128
Conclusion 129
Literature Cited 130
Tables 134
Figures 140

1 Introduction

1.1 Context

Over the last 50 years, birds that live in grassland habitats have experienced greater population declines than the birds found in any other habitat in North America (Rosenberg et al., 2019). Declines include 74% of all native grassland bird species and are not restricted to rare or endangered species (Rosenberg et al., 2019). Grasslands throughout North America have been reduced to only a fraction of their former distribution, with estimates of > 70% of native grasslands being lost (Sampson et al. 2004). However, climate change, alterations to grassland communities, and other anthropogenic habitat alterations are significant factors affecting birds in the remaining grasslands (Bernath-Plaisted et al., 2023). Most remaining grassland is on private land, making conservation of these lands in conjunction with traditional public conservation efforts critical (Gauthier & Wiken, 2003). The habitats on which grassland birds evolved were historically disturbed and maintained by sporadic fire and grazing by American Bison (*Bison bison*; Knapp et al., 1999), but commercial production of cattle is now the dominant disturbance factor in maintaining these habitats (Allred et al., 2011; Bernath-Plaisted et al., 2023). Conserving remaining grassland habitat necessitates understanding different factors affecting avian habitat selection operating across multiple spatial scales.

1.2 Scales of Effect

Birds base their decision on where to live on the physical features of the environment at multiple spatial scales (Johnson, 1980). At a broad scale, regional variation in climate, topography, and geology filters the occurrence of species based on their physical tolerances (Pocheville, 2015). Where grasslands occur, they are distributed in different amounts and spatial configurations across landscapes (Davis et al., 2016; Fahrig, 2017), referred to as landscape structure (McGarigal & Marks, 1995). Within grassland habitats, local factors such as vegetation community composition and structure affect the availability of the resources that individuals need to survive and reproduce (Fisher & Davis, 2010). Because habitat preferences are at least partially based on factors occurring at these different regional, landscape, and local spatial scales, the importance of assessing biological responses at multiple scales has been repeatedly noted (Fletcher et al., 2023; Jackson & Fahrig, 2015; Johnson, 1980; Mayor et al., 2009; McGarigal et al., 2016).

Determining the spatial extent to which biotic communities most respond to landscape structure has been called the 'scale of effect' (Fletcher et al., 2023; Jackson & Fahrig, 2015). To determine the scale of an effect on a given focal group or species, researchers typically measure ecological responses (abundance, presence, diversity, etc.) in plots and pool responses across defined landscapes (landscape designs), within patches (focal-patch designs), or analyze responses independently (focal-plot designs; Fletcher et al., 2023). Researchers then determine the effects of landscape structure at varying extents (distances) from the focal plot, focal patch, or the pooled landscape (Fletcher et al., 2023), often referred to as the ecological neighbourhood (Addicott et al., 1987). The landscape extent that best predicts the response is usually defined as the extent with the steepest (largest) relationship to the response and is termed the scale of effect (Fletcher et al., 2023; Jackson & Fahrig, 2015). Scales of effect are important to determine because they have implications for understanding the relative impacts of the amount of habitat available versus its configuration (Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018, 2023), which contributes to discussions about the role of landscape heterogeneity in maintaining biological diversity (Duquette et al., 2022; Fuhlendorf et al., 2006; Hovick et al., 2015) and the benefits of conserving small habitat patches (Fahrig, 2020).

While local habitat features such as vegetation structure within patches remain a critical aspect of habitat selection (discussed in Section 1.3), grassland birds are highly influenced by habitat at the patch scale (Bernath-Plaisted et al., 2023). The size of grassland patches can limit 'area-sensitive' grassland bird species from occurring in patches below certain sizes (Davis, 2004), and was shown to increase densities of 13 out of 19 common grassland bird species examined in a review by Ribic et al. (2009). Generally, small habitat patches are associated with small population sizes which increase the risk of local extinctions through demographic stochasticity (Desharnais et al., 2006). Small patch sizes have also been linked to reductions in survival rates and breeding success (Kurki et al., 2000; Zitske et al., 2011). Mechanisms limiting the densities of area-sensitive bird species are often related to breeding behaviours and breeding success, particularly as these aspects of life history are affected by habitat edges (Ries et al., 2004). Increased risk of nest predation is one of the largest edge effects influencing breeding success and is especially prevalent in grassland to forest ecotones (Hannon & Cotterill, 1998; Kurki et al., 2000; Renfrew et al., 2005; Renfrew & Ribic, 2003). Other mechanisms at edges affecting breeding include increased Brown-headed Cowbird (*Molothrus ater*) brood parasitism (Bernath-Plaisted et al., 2017), altered vegetation structure (Archer et al., 2017), and active edge avoidance in establishing breeding territories (Fletcher & Koford, 2003). Through these effects on densities and reproduction, patch size and proximity to edges are key determinants of grassland bird densities within patches (Sliwinski & Koper, 2012).

Aside from mechanisms operating within habitat patches, grassland bird densities respond to the total amount of grassland habitat across landscapes. Some grassland bird species increase in density in landscapes with higher grassland cover (Renfrew & Ribic, 2008), generally corresponding with larger, contiguous grassland landscapes. As a corollary, many grassland birds have been classified as woodland-sensitive, meaning that their densities decrease as the amount of forest habitat in the landscape increases (Grant et al., 2004; Renfrew & Ribic, 2008). Patch-scale area sensitivity therefore interacts with the amount of habitat at landscape scales, whereby different habitat matrices (habitat types between the focal habitat type) can alter relationships between patch size and density (Renfrew & Ribic, 2008; McDonald & Koper, 2022). For example, Savannah Sparrow (*Passerculus sandwichensis*) density was shown to decrease with grassland core area in landscapes with low amounts of forest but increase with grassland core area in landscapes with high amounts of forest (Renfrew & Ribic, 2008).

Interactions between the amount of habitat and its configuration mean that even though there may be an appropriate amount of habitat for a given species at the landscape level, the fragmentation of the habitat may alter that species' usage. In some regions, grassland amount is more impactful than fragmentation (Renfrew & Ribic, 2008), and in others, fragmentation is more impactful than amount (Lockhart & Koper, 2018). These inconsistencies between regions highlight the necessity of studying factors involved in avian habitat selection in a regional context (Johnson & Igl, 2001).

Habitat fragmentation is generally thought to harm biodiversity through mechanisms associated with increased edge densities and decreased patch sizes (Fletcher et al., 2018), but the cumulative impacts of habitat configurations are complex (Fahrig, 2017; Fahrig et al., 2019). More patches can spread the risk that any one of the patches might go extinct due to a disturbance event, limit the ability of predators to access prey, or allow populations to access additional resources available in the land cover between the focal habitat patches (the habitat ‘matrix; Fletcher Jr. et al., 2023). Thus, when considering the impacts of higher fragmentation on populations and communities across landscapes, there are many possible outcomes when accounting for the effects of habitat amount. This idea has resulted in research suggesting that more fragmented landscapes can host higher levels of biological diversity when accounting for the amount of habitat present (Fahrig, 2003, 2020).

One mechanism by which complex landscape structure can increase biological diversity is landscape complementarity (Tscharntke et al., 2012). A greater diversity of habitat types within a landscape can increase species diversity within patches by increasing access to spatially distinct resources (Fletcher et al., 2023). Landscape complementarity is related to both local edge effects and the number of patches. Higher edge densities can cause a spillover of species from one habitat to another (e.g. from nesting to foraging areas; Barbaro et al., 2012). Higher numbers of patches can increase access to these resources across the landscape, affecting the community's diversity at a landscape scale (Tscharnke et al., 2012). In this way, landscape complementarity can result in more complex landscapes supporting higher levels of biological diversity, even if a focal habitat type is highly fragmented.

Increases in diversity with increasing fragmentation can be positive or negative from a conservation perspective. For example, increased diversity at edges might be a result of increased densities of invasive species (Jodoin et al., 2008), predators (Renfrew et al., 2005), or other natural enemies (Bernath-Plaisted et al., 2017) which could negatively impact species of conservation concern. However, increases in diversity from landscape complementarity can be positive in cases where the habitat matrix is not anthropogenically modified, corresponding to theories of the overall increase in diversity associated with spatial heterogeneity (Tews et al., 2004). For example, a useful dichotomy for understanding grassland bird communities is to separate the community into specialists that spend their entire life cycle in grasslands ('obligate' species) and species which primarily use other habitats but use grasslands for a portion of their life cycle ('facultative' species; Vickery et al., 1999), many of which are of conservation concern from declines over the last 50 years (Rosenberg et al., 2019). Because facultative grassland birds require both grasslands and another habitat type throughout their life cycle, increasing fragmentation of grasslands could have a net increase on the diversity of the grassland bird community if the benefits to facultative species are greater than the negative effects on obligate grassland species.

1.3 Grassland Type and Rangeland Management

Cattle grazing has a variety of impacts on grassland bird communities. Cattle grazing can directly impact birds through nest destruction, although this is generally a small impact compared to the benefits provided by maintaining grassland habitats (Bleho et al., 2014). Cattle indirectly impact birds through altering vegetation structure including plant height, litter amount and distribution, and levels of bare ground, all of which are critical attributes of avian habitat selection (Deutsch et al., 2010; Fisher & Davis, 2010; Harrison et al., 2011). Cattle-induced changes to vegetation structure can impact avian nesting success through increasing incidences of brood parasitism (Saab et al., 1995), altering invertebrate prey availability (Sutter & Ritchison, 2005), and increasing rates of predation by mammals or birds (Pipher et al., 2016; Renfrew & Ribic, 2003). Grazing can also result in significant changes to species composition (Herrero-Jáuregui & Oesterheld, 2018; Toledo et al., 2014). In some cases, too much or too little grazing disturbance can shift vegetation communities into non-native dominated states that have little possibility of recovery to native communities (Bestelmeyer et al., 2017). This process, often called grassland modification (Adams et al., 2016), can impact birds through changes in vegetation structure (Kennedy et al., 2009; Lipsey & Naugle, 2017) and ecosystem functioning (Toledo et al., 2014). The impacts of cattle within patches are thus critical aspects of the type, amount, configuration, and functioning of grassland habitats available for birds.

At the local scale, vegetation communities serve as a primary determinant of species densities for different bird species. The composition of plant species and the subsequent structure of the vegetation community impact avian breeding success, foraging preferences, and protection from predators (Fisher & Davis, 2010), with predation being one of the largest causes of nest failure (Bleho et al., 2014). It is well understood that vegetation structure is the main driver of bird habitat preferences (Fisher & Davis, 2010), but if vegetation structure is related to which species are present and impacts foraging or breeding, species may prefer different types of grasslands between native bunch-grass-dominated grasslands and grasslands invaded by or cultivated for agronomic grasses (Davis & Duncan, 1999; Gelbard & Harrison, 2003; Lloyd & Martin, 2005).

Vegetation communities ideally serve as the primary determinants of rangeland management decisions including stocking rates, grazing duration, and seasonal timing (Adams et al., 2016; Dodd et al., 2016). These aspects of rangeland management feedback to alter key aspects of vegetation communities and landscape structure, creating a cycle impacting habitat for birds (Fuhlendorf et al., 2012). Often, avian responses to increases or decreases in cattle grazing are on the order of only a few years (Fischer et al., 2020), supporting the importance of rangeland management in determining avian habitat availability and usage.

An important management tool relating rangeland management to the ecology of grasslands in Alberta, Canada, is rangeland health assessment (‘range health’; Adams et al., 2016). Range health uses several metrics based on the composition and structure of the vegetation community to provide land managers with information regarding the ecological functioning of grasslands in response to the cumulative impacts of cattle grazing. These assessments are combined with spatial ecosystem mapping to determine Ecologically Sustainable Stocking Rates for cattle (ESSRs; Adams et al., 2005; DeMaere et al., 2012). Range health has been linked as a predictor of several grassland songbird species in the Mixedgrass and Dry Mixedgrass Natural Subregions of Alberta (Dodd et al., 2016). However, the links between range health and grassland bird communities in the Rocky Mountain Foothills of Alberta are unclear. If links between this commonly used management tool and the abundance of grassland birds can be elucidated in this region, it would facilitate communication of management recommendations for bird conservation specific to management in the study region.

1.4 Regional Context and Data Gap

The Rocky Mountain Foothills of southern Alberta, Canada, is a transition zone between the Canadian Prairies and the Rocky Mountains (Figure 1; Natural Regions Committee, 2006). This region is encompassed by a Natural Subregion called the Foothills Parkland, which differs from the other parkland subregion in Alberta, namely the large-spanning Central Parkland, in several important ways (Table 1). Although both contain similar mosaics of grassland and aspen forest, differences arise because the Foothills Parkland is a transition between grassland and montane cordillera driven by topography, while the Central Parkland is a transition between grassland and boreal forest driven by latitude (Natural Regions Committee, 2006). The Foothills Parkland is at higher elevations with more topographic variation, is warmer in the winter, cooler in the summer, receives more precipitation annually, has a shorter growing season, and is much smaller in area (Natural Regions Committee, 2006). The topographic complexity of this region has limited the historical conversion of native grasslands to agriculture (Simonson & Johnson, 2005), resulting in higher native ecosystem cover when compared to the Central Parkland (49% versus 18%; Dyson et al., 2019).

The Foothills Parkland Natural Subregion consists of two main patches: one extending from Bob Creek Wildland Provincial Park to Elkton along Highway 22 west of Calgary (the Black Diamond Upland), and one bordering the northeast boundary of Waterton Lakes National Park (the Waterton Foothills Parkland). These parklands differ from the surrounding grassland and montane ecosystems in that there are many open deciduous forests dominated by trembling aspen (*Populus tremuloides*) interspersed amongst a mosaic of bunchgrass grasslands, willow shrublands, and intermittent streams.

The Waterton Foothills Parkland is a highly conserved and managed area resulting from collaborations and partnerships between governments, private landowners, non-profit organizations, and other stakeholders and rightsholders. The area is recognized as a UNESCO World Biosphere Reserve, a Key Biodiversity Area, an Alberta Wilderness Association Area of Concern, and a Natural Area priority for the Nature Conservancy of Canada (NCC). Outside of public protected areas, the Nature Conservancy of Canada (NCC) manages over 70 conservation projects (owned lands or conservation easements) protecting ~130 km^2 (35%) of this distinct region (Table 2). This greatly exceeds the area of publicly protected land in the Waterton Foothills Parkland, which is ~44 km^2 (12%), mostly in Waterton Lakes National Park (Alberta, 2020). One of the primary focuses of the conservation initiatives in this region is the interaction between wide-ranging mammal species such as Grizzly Bear, Elk, and Moose with land use by people (McCue, 2016), but initiatives also include invasive plant species removal, bat monitoring, endangered fiveneedle pine conservation, and other projects (https://www.watertonbiosphere.com/wbr-projects/).

Despite the distinctiveness of the Waterton Foothills Parkland and its high level of active conservation, there is a lack of information about grassland bird communities (Figure 1). NCC documents incidental species observations on each of their projects, but these observations do not include standardized surveys outside of rangeland health assessments or baseline inventories conducted at the time of securing new projects (McCue, 2016; NCC, 2020b). The Breeding Bird Atlas (BBA) has multiple roadside transects near the Waterton Foothills Parkland, but none within the region itself (Birds Canada, 2019). No peer-reviewed academic studies on landscape ecology or avifauna were found to have been conducted in the Waterton Foothills Parkland, although some studies have been conducted on avian communities in the Central Parkland Natural Subregion of Alberta (Johns, 1993; Prescott & Murphy, 1995, 1996, 1999). As an additional example of the data gap in this region, the State of the Prairie Report from the ABMI quantifies aspects of the changes in native grassland cover from 1990 to 2010 for the Black Diamond Upland block of the Foothills Parkland but omits the Waterton Foothills Parkland block (Dyson et al., 2019). The lack of focus on grassland bird communities within this area likely stems from the fact that, despite being approximately ~45% grass cover (AAFC, 2020), this region is included in the Parkland Natural Region instead of the Grassland Natural Region in the provincial ecological framework (Natural Regions Committee, 2006), is included in the Montane Cordillera Ecozone directly adjacent to the Canadian Prairie Ecozone in the national ecological framework (ESWG, 1995), and falls just outside of Federal Birds

Conservation Region 11 (Prairie Potholes) where most prairie grasslands occur (ECCC 2024).

Although there are a lack of avian survey data within the region, there are two large-scale modelling initiatives examining grassland bird occurrences and distributions in Alberta. The first is by the Alberta Biodiversity Monitoring Institute (ABMI, www.abmi.ca). Since 2007, ABMI has compiled and created spatial distribution models that predict the relative abundance of many species, including birds, throughout Alberta in 800 m resolution raster layers (ABMI, 2016). These models are based on 1656 sampling locations spaced systematically across Alberta, one of which is located within the study region but has not been surveyed to date (ABMI, 2016, 2023). The second modelling initiative is the Central Grassland Avian Modelling Project (CGAMP), which also produces spatial abundance estimates in 800m raster layers (CWS et al., 2024). This North American initiative is being led by the Canadian Wildlife Service in Canada and data from this thesis will be used within this initiative (B. Robinson, 2020 pers. comm.). The predictive capacity of both initiatives is limited in this region due to its distinctive topographic characteristics.

The topography of this region presents an additional factor influencing the distribution of habitats throughout landscapes. Topography can impact birds directly if flatter areas are preferred for breeding territories (Jones & White, 2012; Pasinelli, 2016), and can indirectly impact birds by modulating the occurrences of vegetation communities associated with different aspects and elevations (Gennet et al., 2017; Reino et al., 2013), as topography is known to alter the distributions of native and non-native vegetation (Averett et al., 2016; Gelbard & Harrison, 2003). Grasslands in the Foothills Parkland

Natural Subregion present a gradient of open grasslands interspersed with aspen forests to closed coniferous forests at higher elevations. In this grassland-to-forest transition zone driven by increasing elevation moving from the Great Plains into the Rocky Mountains, there are very different types and distributions of grasslands than are present in areas further east (Natural Regions Committee, 2006), and require regional understanding of bird communities to effectively inform the many active conservation initiatives here (Johnson & Igl, 2001).

1.5 Study Goals and Objectives

The Waterton Foothills Parkland region of Alberta is a distinctive block of grassland-forest mosaic that is highly managed for both conservation and cattle production. In this region, there have been no peer-reviewed studies of the avian community and only incidental observations aside from monitoring initiatives within Waterton Lakes National Park. While modelling results have been extrapolated to the area, regionally specific habitat preferences of many grassland bird species hinder local relevance. Here, the grassland bird community is affected by multiple grassland community types interacting with cattle grazing in a complex landscape driven by topography. In addition to addressing a clear regional data gap for a taxon of significant conservation concern, this region also presents an opportunity to better understand the relative effects of mechanisms affecting grassland birds at different spatial scales.

In this thesis, I sought to achieve three broad goals related to examining the density and diversity of grassland bird communities. First, I wanted to evaluate bird community responses in a way that contributed to ongoing academic discussions surrounding the impacts of spatial scale on biological communities and, specifically, habitat fragmentation. Second, I wanted to frame discussions around the grassland bird community in a way that was helpful for conservation and rangeland management. Third, I wanted to address the data gap surrounding grassland bird communities in the complex context of this highly conserved transitional region.

To determine grassland bird habitat preferences in this region, I used Autonomous Recording Unit (ARU) surveys to measure the ecological responses (presence, abundance, and diversity) of grassland birds defined as obligate (full life cycle in grasslands) or facultative (portion of life cycle in grasslands) species. Few studies have attempted to examine these factors altogether, and no studies have examined them in the unique context of the Rocky Mountain Foothills. My specific objectives were to determine how the presence, abundance, and diversity of grassland birds were predicted by metrics representing [1] levels of grassland alteration by non-native species, [2] rangeland health, [3] landscape structure at varying spatial scales, and [4] the complex topography of the Rocky Mountain Foothills.

I accomplished my goals and objectives through one data chapter and one summary chapter in this thesis. In the data chapter (Chapter 2), I present my main findings on how habitat at different spatial scales affected the presence, abundance, and diversity of grassland birds. In the summary and management implications chapter (Chapter 3), I relate the conclusions of my research chapter in a management context, focusing specifically on regional applications. Together, this thesis is intended to support the ongoing conservation management of the Waterton Foothills Parkland by providing a regionally specific, science-based understanding of multiple factors affecting grassland bird communities.

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1.7 Tables

Table 1: Key differences between the Foothills Parkland and the Central Parkland Natural Subregions of Alberta. Foothills Parkland numbers summarize both the Waterton Foothills Parkland and the Black Diamond Upland blocks of the Foothills Parkland Natural Subregion. Data are from the Natural Regions Committee (2006) except for the estimated native cover (Dyson et al., 2019), which includes the Black Diamond Upland and excludes the Waterton Foothills Parkland, but still demonstrates the difference between these natural subregions.

Factor	*Central Parkland*	*Foothills Parkland*
Biogeoclimatic driver	Latitude	Elevation
Elevation	~750m	~1250m
Mean winter temp.	-14.7°C	-9.6°C
Mean summer temp.	23.0°C	22.1°C
Area	53,706km^2	3,921km^2
Wetlands	Less	More
Estimated native cover	18%	49%

Table 2: Areas of land under different management jurisdictions in the Waterton Foothills Parkland block of the Foothills Parkland Natural Subregion of Alberta (Natural Regions Committee, 2006). Publicly protected lands are calculated from the Alberta Protected Areas layer (Alberta, 2020) and NCC projects by data provided in 2020 (NCC, 2020a).

Region & Jurisdiction	***Area (km^2)***	***Percent Cover***
Waterton Foothills Parkland	**370**	**100%**
NCC Projects	129	35%
Publicly Protected Land	43	12%
Other	197	53%

1.8 Figures

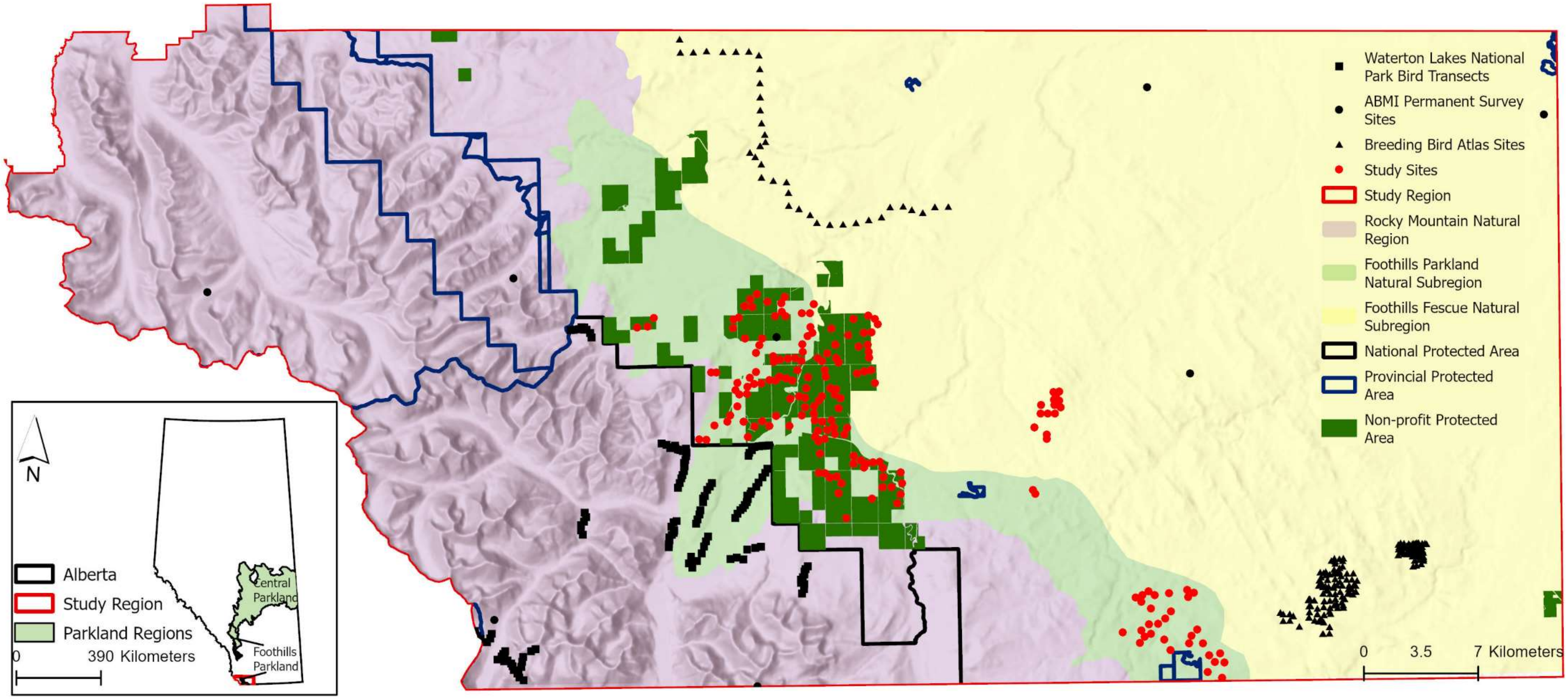
Waterton Lakes National Park Bird Transects
ABMI Permanent Survey Sites
Breeding Bird Atlas Sites
Study Sites
Study Region
Rocky Mountain Natural Region
Foothills Parkland Natural Subregion
Foothills Fescue Natural Subregion
National Protected Area
Provincial Protected Area
Non-profit Protected Area
0 3.5 7 Kilometers
N
Alberta
Study Region
Parkland Regions
0 390 Kilometers
Central Parkland
Foothills Parkland

Figure 1: Overview of study location showing Alberta Natural Region (NR) and Natural Subregion (NSR) designations (Natural Regions Committee, 2006), protected areas (Alberta, 2020; ECCC, 2023), sites for this study, and other known bird survey locations. The inset shows the study region within Alberta, Canada. All study sites were on private land, much of which was owned by non-profit land trusts. Waterton Lakes National Park monitors birds in the portion of the Waterton Foothills Parkland which stretches into the park (Parks Canada Agency, 2021). The Alberta Biodiversity Monitoring Institute (ABMI) has a single long-term surveying point identified within the Waterton Foothills Parkland, but it has not been surveyed to date (ABMI, 2023). There are many Breeding Bird Atlas (BBA) survey locations along roads within the Foothills Fescue Natural Subregion, but none within the Waterton Foothills Parkland (Birds Canada, 2019).

2 Grassland Bird Abundance and Diversity in the Foothills Parkland

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ZMM designed the study, conducted all field assays with field assistants, conducted all data analyses, and wrote the manuscript. BR, DH, RN, and NK provided advice on study design, data analysis, and writing. RN and NK supervised ZM throughout the project. NK provided funding throughout the project.

2.1 Abstract

Birds relying on grassland habitats have declined more in the past 50 years than the birds of any other habitat type across North America. Primarily, these declines have resulted from habitat loss, but the presence, abundance, and diversity of species in remaining grassland habitats are highly influenced by local vegetation structure, especially as it interacts with cattle grazing, landscape structure, and topography. I used Autonomous Recording Units to measure how the presence, abundance, and diversity of grassland birds in the Rocky Mountain Foothills were predicted by metrics representing [1] landscape structure, [2] levels of grassland alteration, [3] rangeland health, and [4] topographic complexity. Five of six grassland bird species assessed responded to landscape structure at 100 – 800 m landscape extents, whereas Western Meadowlark and obligate grassland species diversity both responded negatively to grassland amount and fragmentation within 1600 m extents. The overall diversity of obligate grassland birds was low (median 2 species

detected by auditory cues in surveys) and had limited negative responses to fragmentation and forest edges. Near forest edges and in more fragmented landscapes, the diversity of facultative species increased more than obligate diversity declined, resulting in higher total grassland bird diversity closer to forest edges and in more fragmented landscapes within 400 m extents. Presence, abundance, and diversity varied with grassland alteration as represented by levels of invasion by non-native vegetation. Native, invaded, and modified grasslands all supported similar levels of diversity, although haylands had lower total grassland bird diversity than other grassland types. Rangeland health score was an influential predictor of Savannah Sparrow (negative relationship) and Vesper Sparrow (positive relationship) abundances, reflecting the associations of each species with native and altered grasslands. Native grasslands sites were autocorrelated with higher positions on hills in more rugged terrain, and more altered grasslands were autocorrelated with lower positions on hills in less rugged terrain, suggesting that terrain ruggedness at landscape scales was an important proxy for the distribution of different grassland types across landscapes. Terrain ruggedness negatively affected total obligate species diversity, the abundances of Savannah Sparrows, and the occurrence of Brown-headed Blackbirds, but had positive effects on the abundances of Vesper and Clay-coloured Sparrows which were likely mediated by native grasslands and shrubby microhabitats. This research supports that grassland alteration and range health are good predictors of grassland birds in this region based on differences in vegetation structure, and that landscape heterogeneity plays a key role in mediating the abundance and diversity of grassland birds through mircohabitats associated with terrain ruggedness and cross-habitat edge spillover of species.

2.2 Introduction

While the precipitous declines of birds in North American grasslands over recent history are largely the result of anthropogenic conversion of >70% of the Great Plains (Bernath-Plaisted et al., 2023; Rosenberg et al., 2019; Samson et al., 2004), birds in the remaining grasslands choose their habitat based on environmental characteristics at multiple spatial scales (Johnson, 1980; Mayor et al., 2009). As remaining grasslands are mostly distributed in small patches on private lands (Gauthier & Wiken, 2003; Koper et al., 2010), their management (Fuhlendorf et al., 2006), landscape (Tscharnke et al., 2012), and regional (Johnson & Igl, 2001) contexts are all critical determinants of their ability to provide habitat for birds.

Cattle grazing is the dominant disturbance factor in managing grassland habitats in North America (Allred et al., 2011; Bernath-Plaisted et al., 2023). Disturbance by large herbivores is critical in grasslands as it affects soil chemistry (Naeth et al., 1991), promotes vegetation recruitment by removing plant litter (Fuhlendorf et al., 2010), promotes plant diversity by altering plant interspaces (Derner & Whitman, 2009), prevents woody plant encroachment (Archer et al., 2017), and contributes to an overall 'shifting mosaic' of heterogeneity in conditions benefiting biodiversity (Knapp et al., 1999; Lwiwski et al., 2015). Cattle grazing can directly impact birds through nest destruction (Bleho et al., 2014), although this is generally a small impact compared to indirect impacts on birds through altering vegetation structure such as plant height, litter amount and distribution, and amounts of bare ground (Deutsch et al., 2010; Fisher & Davis, 2010; Harrison et al., 2011). These cattle-driven changes to vegetation structure can affect rates of predation

(Pipher et al., 2016; Renfrew & Ribic, 2003), rates of brood parasitism (Bernath-Plaisted et al., 2017; Saab et al., 1995), or invertebrate prey availability (Sutter & Ritchison, 2005; Kennedy et al., 2009). Vegetation structure is considered one of the most influential aspects of grassland bird habitat (Fischer & Davis, 2010), and has complex relationships with the composition of vegetation communities, especially as it pertains to invasions by non-native plant species and cattle grazing (DeMaere et al., 2012). In some cases, too much or too little grazing can shift vegetation communities into states dominated by disturbance-tolerant non-native species (DeMaere et al., 2012; Herrero-Jáuregui & Oesterheld, 2018; Toledo et al., 2014). This shift is generally referred to as grassland 'modification' and, like cultivation of native grasslands for perennial forage crops (haylands), is generally considered an irreversible ecosystem shift (Bestelmeyer et al., 2017) that affects habitat for birds through vegetation structure (Davis et al., 2013; Davis & Duncan, 1999; Kennedy et al., 2009). Because these grassland 'alterations' significantly and permanently alter the composition, structure, and functioning of native grasslands, preventing both modification and cultivation can often be a priority for both rangeland management and biological conservation (Adams et al., 2016; Samson et al., 2004).

Rangeland health assessment ('range health') is a common tool used to understand the cumulative impacts of livestock grazing on the ecology of grasslands, including bird communities (Adams et al., 2016). Range health produces a final score out of 100 composed of five assessment parameters related to ecosystem function including net primary productivity, stabilizing soil, cycling nutrients, holding water, and maintaining diversity (Adams et al., 2016; Dodd et al., 2016). Assessment parameters include vertical vegetation structure (10% of score), litter cover as a proxy for moisture retention (25%), evidence of increased bare ground or erosion (15%), and invasion by noxious weeds (10%). The ecological integrity parameter is largest, composing 40% of the final score, and is related to how grazing has altered the grassland in comparison to established reference plant communities (Adams et al., 2005, 2016; DeMaere et al., 2012). In mixedgrass regions in Canada, range health and similar monitoring protocols have been found to predict the abundance of bird species depending on species' associations with different vegetation structures (Davis et al., 2014; Dodd et al., 2016). These relationships between grazing monitoring tools and the ecology of grassland birds can help to establish common language between managers and conservationists (Henderson & Davis, 2014), but are important to understand in their regional contexts (Adams et al., 2016; Ahlering & Merkord, 2016; Harrison et al., 2011; Lipsey & Naugle, 2017).

Like grazing, topography affects grassland birds through its integral role in grassland distribution and alteration, especially in foothills regions. Foothills regions with higher terrain ruggedness have been shown to have a lower risk of conversion to agriculture (Simonson & Johnson, 2005), resulting in higher covers of native grasslands than flatter prairie regions (Dyson et al., 2019). Grasslands in foothills regions are typically distributed in smaller patches interspersed between forests, wetlands, and shrublands (Natural Regions Committee, 2006). Differences in vegetation structure and patch size associated with these kinds of heterogeneous landscapes have been shown to affect the densities of many grassland birds (Brambilla et al., 2020; Duquette et al., 2022; Gennet et al., 2017; Renfrew & Ribic, 2002). Topography can impact birds directly if flatter areas are preferred for breeding territories (e.g. Western Meadowlark, Gennet et al. 2017), or indirectly by affecting the distribution of vegetation communities based on slope and aspect (Gennet et al., 2017; Pasinelli, 2016; Reino et al., 2013) or cattle access and grazing preferences (Collins & Calabrese, 2012; Fuhlendorf et al., 2006; Hartnett et al., 1996). Topography thus affects the alteration of grasslands; invasions by non-native vegetation can be more common in areas with low canopy cover and high disturbance (Averett et al., 2016), especially in more productive soils (Gelbard & Harrison, 2003) such as in moist valley bottoms (Adams et al., 2005; DeMaere et al., 2012), and is a critical aspect of landscape heterogeneity (Fuhlendorf et al., 2006; Hovick et al., 2015; Lipsey & Naugle, 2017).

Grassland birds are affected by both the amount of habitat available to them (Davis et al., 2013) and the configuration of these habitats (Reino et al., 2013), often described as 'landscape structure' (McGarigal & Marks, 1995). Habitat edges are particularly important features (Ries et al., 2004; Tscharntke et al., 2012), and their effects vary depending on the types of habitats surrounding grassland patches (the habitat 'matrix'; McDonald & Koper, 2022; Sliwinski & Koper, 2012). Close to forest edges, for example, increased risk of nest predation is one of the largest edge effects influencing breeding success (Hannon & Cotterill, 1998; Kurki et al., 2000; Renfrew et al., 2005; Renfrew & Ribic, 2003). Other mechanisms at edges affecting breeding include increased Brown-headed Cowbird (*Molothrus ater*) brood parasitism (Bernath-Plaisted et al., 2017), altered vegetation structure (Archer et al., 2017), and active edge avoidance in establishing breeding territories (Fletcher & Koford, 2003). Cumulatively, these edge effects can result in patch-size 'area-sensitivity', meaning many species which spend their full life cycle in grasslands ('obligate' grassland birds) tend to avoid patches below threshold sizes (Davis, 2004; Ribic et al., 2009). However, although edge effects for obligate grassland birds often have negative impacts on breeding success and abundance (e.g. Sliwinski & Koper, 2012), edges can positively affect the abundance and diversity of birds that use grasslands for only part of their life cycle ('facultative' grassland birds; Vickery et al., 1999; Barbaro et al., 2012). Closer to forest edges, bird diversity can be higher as species spillover from a separate habitat type to accumulate complementary resources that are not available in their primary habitat (Barbaro et al., 2012; Ries et al., 2004; Tscharntke et al., 2012). This relationship between diversity and complementary habitats can operate at 'local' spatial scales if diversity increases are primarily related to proximity to edges (habitat spillover), or 'landscape' scales if the distribution of habitat types affects the abundance and diversity of edge specialist species at the landscape scale (Fletcher et al., 2023; Tscharntke et al., 2012). Determining the spatial extents to which bird communities are affected by their habitat is important because these 'scales of effect' have implications for understanding the relative impacts of the amount of grassland available versus its configuration (Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018, 2023), which contributes to discussions about the role of landscape heterogeneity in maintaining biological diversity (Duquette et al., 2022; Fuhlendorf et al., 2006; Hovick et al., 2015) and the benefits of conserving small habitat patches (Fahrig, 2020).

In the complex landscapes of the Rocky Mountain foothills in Alberta, I assessed how the presence, abundance, and diversity of grassland birds responded to habitat at multiple spatial scales. First, I determined how and at what scale habitat fragmentation affected the diversity of grassland birds. If more complex landscapes provided complementary habitat for facultative grassland birds, then I hypothesized facultative species diversity would respond positively to higher levels of grassland fragmentation at landscape scales. Alternatively, if facultative species simply spilled-over into grasslands at habitat edges, then I hypothesized that the diversity of facultative species would simply be higher closer to forest edges. Second, I determined how grassland birds responded to different levels of non-native vegetation invasion as represented by types of grassland (native, invaded, modified, or hayland). If different types of grassland represented different vegetation structures, I hypothesized that the presence, abundance, and diversity of grassland birds would respond to different grassland types. Third, I determined how grassland birds responded to different levels of range health. If species were associated with aspects of grassland habitats captured by range health (such as ecological integrity), I hypothesized that range health assessments would be a reliable predictor of the abundance and diversity of grassland birds. Finally, I determined how the complex foothills topography of the study region interacted with these aspects of local habitat and landscape structure. I hypothesized that topography may mediate the abundance and diversity of birds by altering the distribution of different grassland types throughout landscapes. If grassland types were autocorrelated with topography at the site scale, then I predicted that species with strong associations with grassland types would also respond to measures of terrain ruggedness at the landscape scale. Together, these hypotheses provide a multi-scaled perspective of the grassland bird community in the heterogeneous landscapes of the Rocky Mountain Foothills.

2.3 Methods

2.3.1 Study Region & Site Selection

The Waterton Foothills Parkland is a distinct block of the Rocky Mountain Foothills in southern Alberta, Canada (Figure 1). This region has a high (~49%) native ecosystem cover (Dyson et al., 2019; McCue, 2016; Natural Regions Committee, 2006) and contains active cattle grazing operations on private conservation projects, many of which are associated with the Nature Conservancy of Canada (NCC; McCue, 2016). Habitats in this region show an east-to-west gradient of open grassland in the east through to grassland-forest-wetland mosaics and closed forest habitats in the west that is driven by rising elevation moving from the Prairies into the Rocky Mountains (Natural Regions Committee, 2006). Native grasslands are dominated by bunchgrasses including *Festuca campestris*, *Festuca idahoensis*, and *Danthonia parryi*, rhizomatous species such as *Elymus lanceolatus*, and high forb diversity. Common shrubs include *Dasiophora fruticosa, Symphoricarpos occidentalis*, *Amelanchier alnifolia*, and *Salix* species. Most agricultural land conversion in this region has historically been to haylands cultivated for agronomic grasses including *Phleum pratense*, *Poa pratensis*, *Dactylis glomera*, and *Bromus inermis* or for forage species including *Medicago sativa*. There are few annually cultivated croplands (AAFC, 2020), likely because the regional complexity in topography has limited rates of cultivation (Simonson & Johnson, 2005). Agronomic species have invaded native grasslands (e.g. Otfinowski et al., 2008) creating different ‘grassland types’ represented by varying levels of non-native plant composition and subsequent differences in vegetation structure (Adams et al., 2016).

I studied grassland bird communities by examining focal sites with varying types of grassland and management conditions. I defined focal study ‘sites’ as the 100 m buffer around a centre point in grassland habitat. I categorized the grassland type of 187 unique sites as ‘native’ (<30% non-native vegetation; n = 40), ‘invaded’ (30-70% non-native vegetation; n = 59), ‘modified’ (>70% non-native vegetation and grazed by livestock; n = 65), or ‘haylands’ (previously cultivated for tame grasses and annually cut and baled; n = 23; modified from range health protocols in Adams et al. 2016 to account for ‘invaded’ grasslands). Sites were > 75% of a single grassland type, < 10% cover of trees or shrubs taller than 2 m, and > 250 m from other sites (average ± standard deviation [SD] distance between sites: 505 ± 196 m). I started site selection from existing NCC range health assessment locations to provide overlap with consistently monitored sites relevant to management and expanded site selection to include other grassland sites. I selected sites based on aerial imagery, the Grassland Vegetation Inventory (AEP, 2019), and ecosystem mapping polygons provided by NCC (2020). All properties accessed were within the Foothills Parkland Natural Subregion of Alberta except for two small areas of private land up to 6 km northeast into the Foothills Fescue Natural Subregion (Natural Regions Committee, 2006), which were included to represent a greater gradient of landscape structures. Sites did not contain fences, oil and gas infrastructure, or water features, but ~10 contained low-use single-track truck trails, rock piles, or cattle watering/salting/hay feeding sites. All non-hayland sites were active or resting cattle pasture grazed within 3 years, but data associated with rangeland management (stocking rates, timing, or duration) or historical cultivation were not consistently available across all sites because sites were spread across multiple management units. Due to these data gaps, four sites that might have been considered ‘tame pasture’ (grasslands previously cultivated for agronomic grass species but contemporarily grazed by cattle; Adams et al., 2016) were included as ‘modified’ grasslands due to their similar plant species composition.

2.3.2 Bird Surveys

I conducted bird point count surveys in 2021 and 2022 between May 24th and July 5th using Autonomous Recording Units (ARUs) at the centre point of each focal site. I surveyed 168 sites in 2021 and 145 in 2022 (126 surveyed in both years). ARUs were deployed at sites for 2-14 days and programmed to record for five minutes at one-hour intervals in the mornings and overnight. Four recordings were transcribed from each ARU deployment (sunrise, sunset, midnight, and 2 am recordings) by staff at Birds Canada (www.birdscanada.org) using Wildtrax (www.wildtrax.ca). For each transcription, I selected the recording from the earliest date in the deployment with suitable weather conditions (low wind and no rain). In 11 instances, wildlife rendered one of the two recording channels inoperable. These recordings were included in analyses as they were the only suitable recordings at the time intended. In addition to these ‘deployed’ ARU surveys, I manually collected 106 five-minute recordings within three hours of sunrise to increase sample size and transcribed them as the deployed recordings. Manual recordings differed from the deployed recordings because manual recordings were only conducted in 2021, had humans present, and did not occur at sunrise. In analyses, recording type, Julian day, year, and survey coordinates were included as covariates and are referred to as ‘survey variables’.

2.3.3 Vegetation Structure

To determine the differences in vegetation structure associated with grassland alteration, I conducted structural vegetation assessments concurrently with bird surveys using 100 m transects in the direction of travel between sites. During transects, I recorded the dominant vegetation cover type (grasses, shrubs 0.1-2m in height, or 'other') within 50 cm of either side of the transect line to 10 cm precision. The length covered by each dominant vegetation type in the 100 m transect was used as percent cover for grasses and shrubs. At 0m, 50m, and 100m in the transect, I assessed the overlapping percent canopy cover of forbs, litter, and bare ground in 20 x 50 cm plots using nine percent cover classes (0-0.1%, 0.1-1%, 1-3%, 3-10%, 10-25%, 25-50%, 50-75%, 75-95%, and 95-100%; Table S1; Modified from Daubenmire, 1959). At each of the three plots, I took a single visual obstruction reading of a Robel Pole in 5 cm increments observed from 4 m away at a height of 1 m (Robel et al., 1970). I also measured vegetation height at each of the four plot corners as the highest contact point of live vegetation. For all plot variables, I averaged measurements to produce a single value for each transect in each year. I assessed the same transect bearing between years to limit structural variation within the 100 m site from confounding structural differences between years.

2.3.4 Range Health

I conducted rangeland health assessments ('range health') at each site once between July and August in 2021 or 2022. These assessments followed standard range health protocols (Adams et al., 2016), with the caveat of assessing the defined 100 m site scale instead of the extent of a given grassland community or pasture. During assessments, I traversed the site, determined the reference plant community (using Adams et al., 2005; DeMaere et al., 2012), estimated the percent of the community composed of non-native vegetation to classify grassland types, and determined each of the five range health assessment parameters (Adams et al., 2016). Per the range health protocol, I estimated litter amount in lbs/acre by comparing the amount of hand-raked litter in three 50 x 50 cm plots placed randomly throughout the site to reference photographs in Adams et al. (2016). I did not assess range health in the 23 haylands where no grazing occurred, and I assessed the four sites that might have been considered 'tame pasture' using the 'grassland' form for consistency (Adams et al., 2016).

2.3.5 Scales of Effect and Landscape Structure

I assessed landscape structure using a focal plot design with ecological neighbourhoods calculated at seven different spatial extents (Fletcher et al., 2023; Jackson & Fahrig, 2015). When assessing the scales at which biological communities respond to landscape structure, it has been recommended to evaluate many extents ranging from individual territory sizes to at least nine times the dispersal distance of species because simulations predicted scales of effect often occurred between four and nine times dispersal distances (Jackson & Fahrig, 2015). The average breeding dispersal (individuals banded as adults and recaptured in the following year) distance of the most common focal species in this study, Savannah Sparrow (*Passerculus sandwichensis*), has been documented as 113 m (Fajardo et al., 2009). Because Savannah Sparrow was not the only focal species modelled in this study and other species may have larger dispersal distances between breeding seasons (e.g. Fajardo et al., 2009), I chose to calculate landscape structure at 100, 200, 400, 800, 1200, 1600, and 2000 m extents as these represented a range from individual territories (100 m) to nearly 20 times the average breeding dispersal distance of Savannah Sparrows (2000 m). Other extents included two approximations of common management units (‘quarter sections’ with 400 m landscapes and ‘sections’ with 800 m landscapes), and other extents at intermediate intervals to increase precision in estimating scales of effect (200, 1200, and 1600 m). I chose not to model extents greater than 2000 m because sites were distributed ~500 m apart on average across a relatively small (~370 km^2) region with limited site access. Although landscapes measured as ecological neighbourhoods in this way had overlap between sites, overlapping landscape extents do not in and of themselves lead to violations of independence amongst observations (Zuckerberg et al., 2012), and likely represented biologically meaningful interpretations of landscape structure for each site within the landscape extents included.

For each site, I calculated grassland percent cover and the Landscape Shape Index (LSI, a measure of habitat fragmentation) at each landscape extent using the *landscapemetrics* package in R (Hesselbarth et al., 2019; R Core Team, 2024). I used a reclassification of the 2020 Annual Crop Inventory 30 m raster layer (AAFC, 2020) where each ‘cover class’, or raster cell value, was reclassified as one of grassland, shrubland, forest, agriculture, wetland, water, or ‘other’ (Table S2). This raster layer provided the highest accuracy (~91% for grasslands) of several available datasets assessing grassland cover in this region but did not accurately differentiate between native, invaded, or modified grasslands or consistently identify haylands as ‘agriculture’ (Appendix 1). This limitation of land cover dataset was part of the rationale for including terrain ruggedness (see below) as a proxy for the distribution of grassland types within the generalized 'grassland' cover class.

I calculated three metrics using the Alberta 25 m resolution Digital Elevation Model (DEM; AEP, 2017) to assess how topography was autocorrelated with site conditions and influenced birds at landscape scales. At each landscape extent, I calculated the standard deviation in elevation as a metric of 'terrain ruggedness' (as in Hawkshaw et al., 2021). At the site extent, I calculated elevation and the Topographic Position Index (TPI; Wilson et al., 2007). The TPI is calculated based on the value of each raster cell relative to its eight neighbour cells and is < 0 when a cell is at a lower elevation than those surrounding it (depressions), 0 when the site is at the same elevation as those surrounding it (flat), and > 0 when the cell is above those surrounding it (hills; Wilson et al., 2007). I used TPI in lieu of other metrics because it provided a metric describing the relative position of sites along slopes (crests, hillsides, depressions) instead the degree of slope of the site itself, and because many measures of topography were highly correlated in initial data exploration. Elevation and TPI represented an interpretable understanding of topography at the site scale that did not logically provide greater interpretations at greater extents.

Finally, I calculated the distance to forests as a proxy for the local effects of proximity to forest edges. I included this metric to discern between effects occurring primarily at habitat edges and effects occurring at landscape scales. I first converted forest cover from the reclassified Annual Crop Inventory (AAFC, 2020) to points using the Raster to Point tool in ArcGIS Pro. I used cluster analysis and calculated the distance from each site to the nearest cluster of three or more forest raster cells because there were instances where single cells were visibly misclassified as forest. This variable had a low correlation with grassland fragmentation measured by LSI across landscape extents (Pearson correlation between -0.14 and 0.01; Figure S2), supporting the distinction between interpretations of these variables at local and landscape scales.

2.3.6 Statistical Analyses

I used Generalized Linear Models (GLMs) to examine how the presence, abundance, or diversity (‘ecological responses’) of individual species or assemblages of the grassland bird community responded to local, landscape, and survey variables. I ran a suite of models to determine ‘scales of effect’ and created separate GLMs to assess the effect of ‘range health’. I separated these analyses because range health was not assessed at the 23 hayland sites that were not grazed and because controlling for other variables would not explain the usefulness of this management tool in predicting grassland bird responses alone.

During model selection, I examined model fit diagnostics and adherence to assumptions. I examined pairwise plot matrices and used Variance Inflation Factor (VIF) values greater than 5 units as an indication to remove variables. This process resulted in removing several topography metrics, vegetation structure metrics, non-grassland landscape cover classes, and prospective interactions which produced high VIF values even after being centred and standardized (Iacobucci et al., 2016). To examine model adherence to assumptions, I examined diagnostic plots using the DHARMa package

(Hartig, 2022), and visually assessed the linearity of relationships with simple regression plots for each explanatory variable against the response variable.

I used Simpson's Reciprocal Index (1/D; also called the Hill-Simpson Index) to test how the diversity of different grassland bird assemblages responded to habitat at local and landscape scales. Simpson's Reciprocal Index is more sensitive to common species than rare species and logically corresponds to the number of hypothetical species given equal abundances (Hill, 1973; Roswell et al., 2021; Simpson, 1949). Diversity was calculated according to Equation [1],

$$Diversity = \frac{1}{\sum_{i=1}^{S} p_i^2} \quad [1]$$

where *p* is the proportion of species *i* summed across a total species richness of *S*. I classified each species as an 'obligate' or 'facultative' grassland species based on edits and additions to the list in Vickery et al. (1999; Table S3) and created three separate model suites: 'obligate' diversity, 'facultative' diversity, and 'total' diversity (all obligate and facultative grassland bird species combined). I excluded bird species from analysis if they were likely to be inconsistently detected or counted by auditory cues alone (e.g. waterfowl, raptors, and gregarious species like blackbirds; B. Robinson, pers. comm.). In total, 15 obligate and 36 facultative grassland bird species were detected (Table S3), of which 10 and 17, respectively, were assumed to be reliably detected and counted in morning ARU surveys and were subsequently included in diversity models (n = 27 total species; Table 1). Diversity was analyzed using GLMs with Gaussian distributions and log-transformation of this response variable improved model fit based on examining AIC differences.

In addition to the diversity of grassland bird assemblages, I modelled the presence or abundance of individual grassland bird species (Table 2). I only modelled species if they were observed in more than 50 surveys and reliably detected and counted by auditory cues alone (B. Robinson, pers. comm.). Obligate species modelled included Savannah Sparrow (*Passerculus sandwichensis*), Vesper Sparrow (*Pooecetes gramineus*), and Western Meadowlark (*Sturnella neglecta*). Facultative species modelled included Brown-headed Cowbird (*Molothrus ater*), Clay-coloured Sparrow (*Spizella pallida*), and House Wren (*Troglodytes aedon*). Wilson's Snipe (*Gallinago delicata*) was included in diversity models but was not modelled individually because this species was often detected at high distances outside of sites (up to 200-300 m away; pers. obs.). No primarily night-vocalizing species had enough observations to model individually. For each species, I first attempted to model abundance using GLMs with Poisson distributions, followed by negative binomial distributions if models were over-dispersed, and finally, in cases where fit was still poor, binomial distributions for presence and absence. Models for Savannah Sparrow, Vesper Sparrow, Clay-coloured Sparrow, and House Wren abundances fit well with either Poisson or negative binomial distributions (Table 2). However, models of abundance for Western Meadowlark and Brown-headed Cowbird fit poorly, so I modelled the presence or absence of these species using binomial distributions.

I used an information theoretic approach to select the best-fitting landscape extent for each ecological response modelled ('scale of effect' models; Jackson & Fahrig, 2015; McDonald & Koper, 2022). For each of the 9 grassland bird ecological responses measured, I created a suite of 7 models, each with 11 variables (14 coefficients including factor levels) according to Equation [2],

$$y = year_f + recordingType_f + eastingCoordinate + JulianDay + grasslandType_f + distanceToForest + elevation + TPI + terrainRuggedness_{ex} + \%coverGrassland_{ex} + fragmentationGrassland_{ex} \quad [2]$$

where *y* is the ecological response (presence, abundance, or diversity) subscript *f* denotes factors (*year* = 2021 or 2022; *recordingType* = sunrise or manual; and *grasslandType* = native, invaded, modified, or cultivated), and subscript *ex* denotes variables calculated at each of the 7 landscape extents (100, 200, 400, 800, 1200, 1600, and 2000 m). Grassland fragmentation was not included in the 100 and 200 m extent model because grassland amount and fragmentation were highly correlated at these extents (Pearson correlation at 100 m = -0.81 and 200 m = -0.76) and produced VIF > 5. Grassland fragmentation and amount were moderately correlated at 400-2000 m extents (Pearson correlation between -0.32 and -0.54; Figure S1), but generally presented a reasonable gradient of combinations for analyses (e.g. Figure 2). I accepted and interpreted the lowest AIC landscape extent as the best-fitting model unless 100 m or 200 m extent models, which contained one less variable, had ΔAIC < 2 (Arnold, 2010). When interpreting models at the best-fitting extents, I did not interpret the 'significance' of individual model estimates based on p-values but instead interpreted 'influential' predictors as estimates where 85% confidence intervals did not overlap with zero (Arnold, 2010).

To determine the effect of range health, I created separate GLMs for the ecological responses of the three grassland bird assemblages and the six individually modelled species (Table 2). In these models, I only included the final range health score as an explanatory variable because this most explicitly allowed for testing the relationship of this management-relevant variable with the abundance and diversity of the grassland bird community. I modelled log-transformed diversity using a Gaussian distribution and abundance using a negative binomial distribution because these distributions matched those of the scale of effect models and because they fit better than alternatives based on examination of AIC values (Arnold, 2010). For Western Meadowlark and Brown-headed Cowbird, I modelled presence using a binomial distribution as in the scale of effect models. To maintain consistency with interpretations of the scaled models, I evaluated range health as an 'influential' predictor of presence, abundance, or diversity if the 85% confidence interval for the estimate did not overlap zero.

In GLMs, I used raw count data from ARU surveys to calculate my response variables without adjusting relative abundances to densities using coefficients derived from distance or removal sampling (Buckland et al., 2004; Sólymos et al., 2013). These methods are often employed to improve the comparability of datasets from multiple protocols (ie. separate studies) or different methods (ie. human versus ARU point counts; Sólymos et al., 2013), although they are not used universally (Pérez-Granados & Traba, 2021). As recording units and methods were consistent within this research, these corrections would not meaningfully affect interpretations of individual species models (as they would only scale response values by a coefficient) but could have affected estimates of community diversity if detectability varied substantially across species included. However, this is not likely to be true considering only species readily detected and counted by auditory cues alone were included in diversity metrics. Using unadjusted count data for grassland birds has been completed in several other studies (e.g. Nenninger & Koper, 2017; McDonald & Koper, 2022) for various rationale related to demonstrations that unadjusted counts can be appropriate for estimating relative abundances of grassland birds (Henderson & Davis, 2014) and high overall detectability of grassland birds (albeit demonstrated with double-observer human point counts instead of ARUs; Leston et al., 2015).

Interpretations of model estimates benefited from centring and standardizing all continuous explanatory variables (Iacobucci et al., 2016). This process allowed variable estimates to be directly compared with each other and between landscape extents. Response variables in models were represented by different metrics (back-transformed log diversity with Gaussian distributions, incidence rate ratios of abundance with Poisson and negative binomial distributions, or odds ratios for species presence with binomial distributions), but all coefficient estimates corresponded to the proportional change in the response variable given a 1 standard deviation increase in a continuous explanatory variable from its mean or the effect of a factor relative to its first level. Model intercepts thus corresponded to the value of the ecological response at the means of all continuous explanatory variables and the first level of factors (sunrise ARU recordings, 2021 surveys, and native grassland).

For all GLMs produced, I conducted sensitivity power analyses using G*Power 3.1.9.7 (Faul et al., 2007) based on model sample sizes and the number of predictors with α error = 0.15 and β error = 0.85. Sample sizes were the same within each model type (scale of effect and range health) except between diversity models because Simpson's Reciprocal Index was undefined when a species group was undetected (Table 2). All models were sensitive enough to detect small effect sizes (f^2 between 0.02 and 0.06). All other assessments were performed in R version 4.2.3 (R Core Team, 2024) and ArcGIS Pro version 3.2.0.

I used Analysis of Variance (ANOVA) to examine differences in topographic variables and vegetation structure between grassland types (native, invaded, modified, and haylands) at the site (100 m) scale. I used separate ANOVAs for terrain ruggedness, TPI, vegetation height, Robel obstruction, and the percent cover of grasses, shrubs, forbs, bare ground, and litter. I used Tukey's Honestly Significant Difference (HSD) test to determine significant differences between grassland types at the 85% confidence level.

2.4 Results

2.4.1 Mean Abundances and Diversity (Intercepts)

Model intercepts represented the point of comparison for the relative effects of explanatory variables in the scale of effect models based on the scaling and centring of independent variables (Table 3). From model intercepts, estimated total grassland bird species diversity was 3.56 (85% confidence interval [CI] = 3.25 – 3.91) in units of 'species' (Roswell et al., 2021). Facultative species diversity was higher (β = 2.15, 85% CI = 1.89 – 2.45) than obligate species diversity (β = 1.60, 85% CI 1.47 – 1.75), and these diversity intercepts were close to median species richness. To put these metrics of diversity in context, 15 obligate grassland birds and 30 facultative grassland birds were detected in total, but only 10 obligate and 17 facultative grassland birds were included in models based on their ability to be detected and counted by auditory cues alone, and all results presented herein must be interpreted in this context. Of species included in models, median species richness in point counts was 2 obligate species (range 0 – 4), 3 facultative species (range 0 – 7), and 4 total grassland birds (range 1 – 10). In native grasslands at mean values of the centered and standardized independent variables (model intercepts), the probability of Western Meadowlark occurrence was very low (β = 0.06, 85% CI = 0.03 – 0.14) and the probability of Brown-headed Cowbird occurrence was 0.41 (85% CI = 0.26 – 0.56). Vesper Sparrow (β = 2.05, 85% CI = 1.60 – 2.62 individuals), Savannah Sparrow (β = 1.66, 85% CI = 1.38 – 1.99), and Clay-coloured Sparrow (β = 1.98, 85% CI = 1.60 – 2.44 individuals) had similar abundances, but House Wren abundance was lower than the other species (β = 0.89, 85% CI = 0.68 – 1.16).

2.4.2 Survey Variables

The four survey variables included in models impacted ecological responses (Table 3). The probability of Western Meadowlark presence was 2.52 times higher in 2022 relative to 2021, (Relative Effect [RE] = 2.52, 85% CI = 1.55– 4.11), and was the only response which differed between years. Manual recordings detected fewer Savannah Sparrows (RE = 0.75, 85% CI = 0.67 – 0.85) and fewer Clay-coloured Sparrows (β = 0.78, 85% CI = 0.62 – 0.97), but had a higher probability of detecting Western Meadowlark (RE = 2.21, 85% CI = 1.33 – 3.67) than the sunrise recordings from ARU deployments. Later in the breeding season, the probability of Western Meadowlark (RE = 0.67, 85% CI = 0.52 – 0.87 per 12-day standard deviation [SD] from the mean date, June 15th) and Brown-headed Cowbird (RE = 0.62, 85% CI = 0.47 – 0.83) occurrences were lower, but abundances of Savannah Sparrow (RE = 1.27, 85% CI = 1.22 – 1.32) and House Wren (RE = 1.21, 85% CI = 1.14 – 1.28) were higher, reflecting seasonal variation in calling rates (e.g. Moran et al., 2019). Sites further east had fewer Savannah Sparrows (RE = 0.91, 85% CI = 0.87 – 0.95 per 9 km SD from the mean ~593 km coordinate in the Alberta 10 TM Forest projection), higher abundance of Clay-coloured Sparrow (RE = 1.09, 85% CI = 1.03 – 1.16), higher probability of Brown-headed Cowbird presence (RE = 1.55, 85% CI = 1.33 – 1.82), higher diversity of facultative species (RE = 1.13, 85% CI = 1.10 – 1.17), and higher total diversity of grassland birds (RE = 1.16, 85% CI = 1.13 – 1.18).

2.4.3 Grassland Type

Grassland type, categorized by the percent composition of non-native vegetation, was autocorrelated with topography (Figure 3). Sites classified as native grassland were more common in higher on slopes in hillier areas, while invaded grasslands, modified grasslands, and haylands were more common lower on slopes in flatter areas. This finding suggests terrain ruggedness represented a measure of landscape heterogeneity that was autocorrelated with microhabitats for different grassland types (ie. higher terrain ruggedness was autocorrelated with more native grassland microhabitats across landscapes).

Vegetation structure also varied between grassland types (Figure 3). Relative to all other grassland types, haylands had taller, denser vegetation; higher covers of grasses and forbs; and lower covers of litter and shrubs. Forb cover did not vary significantly between native, invaded, and modified grasslands, but vegetation height and Robel obstruction (vegetation density) increased with levels of non-native vegetation invasion. Interestingly, the intermediate categorization of invaded grasslands had higher shrub cover, higher litter cover, and lower bare ground cover than both native and modified grasslands. This demonstrates that vegetation structure between these grassland types does not always vary linearly with the percent composition by non-native vegetation and suggests these categorizations represent distinct habitat conditions for birds.

Grassland type was an influential predictor of grassland bird responses in the scale of effect models, particularly for obligate species (Table 3; Figure 4). The abundance of Savannah Sparrow was successively higher in invaded, modified, and haylands relative to native grasslands, with 2.44 (85% CI = 1.92 – 3.12) times higher abundances in haylands. Western Meadowlark was not detected in any haylands, although occurrence was 4.74 (85% CI = 2.39 – 9.41) times more likely in invaded grasslands and 6.43 (85% CI = 3.02 – 13.67) times more likely in modified grasslands than in native grasslands. Conversely, Vesper Sparrow abundance was lower in invaded, modified, and hayland sites than in native grasslands, with 73% lower abundances (RE = 0.37, 85% CI = 0.25 – 0.54) in haylands.

The presence, abundance, and diversity of facultative grassland bird species also varied with grassland type (Table 3; Figure 4). In haylands, there was a 79% lower probability of Brown-headed Cowbird occurrence (RE = 0.21, 85% CI = 0.08 – 0.54) and a 71% lower abundance of Clay-coloured Sparrow (RE = 0.29, 85% CI = 0.20 – 0.42) than in native grasslands. Clay-coloured Sparrow abundance was also 27% lower in modified grasslands than in native grasslands (RE 0.73, 85% CI = 0.59 – 0.90). Conversely, House Wren abundance was 1.60 (85% CI = 1.09 – 2.35) times higher in haylands than in native grasslands. Overall, facultative species diversity was 18% lower (RE = 0.82, 85% CI = 0.69 – 0.99) and total grassland bird diversity was 29% lower (RE = 0.71, 85% CI = 0.63 – 0.81) in haylands than in native grasslands. Obligate bird diversity did not vary between grassland types.

2.4.4 Range Health

Range health scores at the 155 unique sites assessed ranged from 3 to 100 (Mean = 52.5 ± 20.5 standard deviation) and was an influential predictor of four ecological responses (Figure 4). Vesper Sparrow abundance (RE = 1.008, 85% CI = 1.003 – 1.013) and obligate species diversity (RE = 1.001, 85% CI = 1.000 – 1.003) increased with range health. Savannah Sparrow abundance (RE = 0.990, 85% CI = 0.987 – 0.993) and probability of Brown-headed Cowbird occurrence (RE = 0.987, 85% CI = 0.978 – 0.996) decreased with range health. Relationships between range health and the abundances of both Vesper Sparrow and Savannah Sparrow were likely related to the ‘ecological integrity’ component of range health (40% of the final score; Adams et al., 2016) because these species were highly associated with different grassland types corresponding to high (native grasslands) or low (modified grasslands) ecological integrity scores. In contrast, neither Brown-headed Cowbird occurrence nor obligate bird diversity were associated with grassland types, and thus these declines with higher range health scores must be related to one of the other four range health assessment parameters (vertical vegetation structure, litter amount, bare ground, or invasive species), although these relationships were not specifically investigated in this research.

2.4.5 Scales of Effect and Landscape Structure

Obligate grassland bird responses to forest edges were negative and facultative grassland bird responses to forest edges were positive (Table 3; Figure 4). Savannah Sparrow abundance (RE = 1.09, 85% CI = 1.03 – 1.15 per 275 m SD from the 410 m mean distance from centre points to forest edges), and probability of Western Meadowlark occurrence (RE = 1.93, 85% CI = 1.4 – 2.66) were higher further from forest edges. Clay-coloured Sparrow abundance (RE = 0.89, 85% CI = 0.80 – 0.98) and House Wren abundance (RE = 0.36, 85% CI = 0.30 – 0.43) were higher closer to forest edges. Overall, the positive effect of proximity to forests on facultative species diversity (RE = 0.87, 85% CI = 0.84 – 0.91) was greater than the negative effect on obligate species diversity (RE = 1.05, 85% CI = 1.01 – 1.08), culminating in higher total grassland bird diversity closer to forest edges (RE = 0.95, 85% CI = 0.91 – 0.98).

Obligate species responded to landscape structure at varying extents (Table 4; Figure 5). Only two obligate ecological responses were best explained at the 1600 m extent, where higher grassland fragmentation negatively affected both obligate species diversity (RE = 0.93, 85% CI = 0.9 – 0.97 per 1.4 LSI unit SD from the mean 9.3 LSI; Figure 6) and Western Meadowlark occurrence (RE = 0.55, 85% CI = 0.39 – 0.77). Western Meadowlark occurrence also increased with the amount of grassland habitat at 1600 m extents (RE = 1.83, 85% CI = 1.29 – 2.61 per 16.2% SD from the mean 61.9% grassland cover). Vesper Sparrow abundance responded negatively to both increasing grassland amount (RE = 0.89, 85% CI = 0.79 – 1.00 per 17% SD from the mean 64.7% grassland cover) and degree of fragmentation (RE = 0.78, 85% CI = 0.70 – 0.87 per 1.0 LSI unit SD from the mean 5.0 LSI level) at the 800 m extent, suggesting higher abundances in smaller, more isolated grassland patches. Savannah Sparrow abundance was best explained at the 200 m landscape extent, but three other extents (100, 400, and 800 m) were within 2 AIC units. Despite the similar weights of models at different extents for Savannah Sparrow abundance, including landscape variables at larger extents did not improve model fit, suggesting these more complex models included uninformative parameters (Arnold, 2010) and that grassland type and distance to forest edges were more influential than landscape structure at larger spatial extents.

The ecological responses of facultative grassland birds were primarily explained by smaller (100 to 400 m) landscape extents (Table 4; Figure 5). Occurrence of Brown-headed Cowbird decreased when there was more grassland habitat in the 400 m landscape (RE = 0.57, 85% CI = 0.43 – 0.77 per 16.3% SD from the mean 71.7% grassland cover; Figure 6) and was not influenced by the degree of grassland fragmentation. Clay-coloured Sparrow abundance increased with the degree of grassland fragmentation in the 400 m landscape (RE = 1.31, 85% CI = 1.20 – 1.44 per 0.8 LSI unit SD from the mean 2.7 LSI level) and was not influenced by grassland amount. House Wren abundance was best explained at the 100 m extent, where it responded positively to grassland amount (RE = 1.28, 85% CI = 1.14 – 1.42 per 13.3% SD from the mean 92.9% grassland cover; Figure 6). Similarly to Savannah Sparrows, facultative species diversity was best explained at the 100 m extent but had three other extents (200, 400, and 800 m) perform similarly well. Including landscape variables at larger extents did not improve model fit, suggesting these more complex models included uninformative parameters (Arnold, 2010) and that grassland type and distance to forest edges were more influential than landscape structure at larger spatial extents.

Pooling across all grassland bird species, total diversity increased with the degree of grassland fragmentation in the 400 m landscape (RE = 1.09, 85% CI = 1.04 – 1.13 per 0.8 LSI unit SD from the mean 2.7 LSI level) and was not influenced by grassland amount. These results suggest that some of the increase in diversity in more fragmented landscapes may be explained by complementarity operating at 400 m extents. However, the primarily localized effect of distance to forest edges on the diversity of facultative species suggests much of this effect resulted from habitat spillover of facultative species at forest edges.

Terrain ruggedness at the best-fitting landscape extent was influential in six of nine scale of effect models (Table 3; Figure 6). Hillier landscapes, as represented by higher terrain ruggedness, were associated with lower obligate species diversity (RE = 0.97, 85% CI = 0.93 – 1.00 per 11.3 m SD from the mean 27.1 m SD in elevation at 1600 m extents), lower probability of Western Meadowlark occurrence (RE = 0.52 85% CI = 0.38 – 0.71 at 1600 m extents), lower probability of Brown-headed Cowbird occurrence (RE = 0.69, 85% CI = 0.53 – 0.89 per 6.2 m SD from the mean 10.4 m SD in elevation at 400 m extents), and fewer Savannah Sparrows (RE = 0.94, 85% CI = 0.88 – 1.00 per 8.7 m SD from the mean 16.8 m SD in elevation at 200 m extents). Conversely, the abundances of Vesper Sparrow (RE = 1.16, 85% CI = 1.07 – 1.27 per 8.7 m SD from the mean 16.8 m SD in elevation at 800 m extents) and Clay-coloured Sparrow (RE = 1.09, 85% CI = 1.01 – 1.17 per 6.2 m SD from the mean 10.4 m SD in elevation at 400 m extents) were higher in more rugged landscapes.

Site elevation and TPI were only influential in three of the nine best-fitting models (Table 3). At higher elevations, House Wren abundance was higher (RE = 1.10, 85% CI = 1.00 – 1.20 per 53 m SD from the mean 1350 m elevation), and facultative species diversity was lower (RE = 0.91, 85% CI = 0.87 – 0.95). The TPI was only influential for Clay-coloured Sparrow abundance, and the negative relationship (RE = 0.89, 85% CI = 0.82 – 0.97 per 0.13 SD from the mean 0.09 TPI value) indicated higher abundances in depressional areas (sites with negative TPI values).

2.5 Discussion

The results of this study support four main conclusions. First, total grassland bird diversity increased with the degree of grassland fragmentation because the increase in diversity from habitat spillover of facultative species at forest edges was greater than the reductions in obligate species diversity associated with area-sensitive species. Second, in this region of the Rocky Mountain foothills, topography plays a significant role in landscape heterogeneity. Because all grassland types were autocorrelated with distinct topographies and vegetation structures, terrain ruggedness likely mediated the abundance and diversity of grassland birds across landscapes through the distribution of vegetation communities. Third, species abundances varied in different grassland types as categorized by levels of grassland alteration through non-native vegetation invasion. Native, invaded, and modified grasslands supported similar total grassland bird diversity. Haylands were ~1 species unit lower diversity than other grassland types but supported the highest abundances of

Savannah Sparrow. Finally, sites with higher range health had higher obligate grassland bird diversity, more Vesper Sparrows, fewer Savannah Sparrows, and a lower probability of Brown-headed Cowbird occurrence. This trend echoed the grassland types associated with higher abundances of Vesper Sparrows (native grasslands) and Savannah Sparrows (modified grasslands), suggesting the association was explained by the 'ecological integrity' range health assessment parameter. Together, these results support a multi-scaled perspective of factors affecting the abundance of diversity of grassland birds in foothills regions.

This research contributes to the understanding of the importance of landscape heterogeneity in moderating biodiversity (Tews et al., 2004). Total grassland bird diversity was higher closer to forest edges and in more fragmented landscapes within 400 m extents. These interdependent measures of landscape structure are difficult to separate from one another (Fahrig, 2017; Fletcher et al., 2023), but the minimal correlation of distance to forest and fragmentation at the 400 m extent (Pearson's correlation = -0.12) suggests that both local (spillover) and landscape scale effects (complementarity) were indeed influential. However, given that facultative species diversity itself responded mostly to habitat edges, localized increases in diversity resulting from habitat spillover were likely greater than effects of landscape complementarity (Tscharntke et al., 2012). Higher diversity of species which use both open and forest habitats at edges has been documented for a variety of mechanisms relating to individual dispersal, food availability, and microhabitat preferences (Barbaro et al., 2012).

The overall positive response of total diversity to fragmentation in this region was likely related to a small obligate species pool (Tscharntke et al., 2012; Zobel, 2016). Other studies have documented that habitat fragmentation can affect the regional distribution of grassland birds (Reino et al., 2013). In this research, grassland birds commonly observed elsewhere in the Canadian Prairies were not present (e.g. Chestnut-collared Longspur [*Calcarius ornatus*], Sprague's Pipit [*Anthus spragueii*]), or were only observed on the eastern periphery of the study region (e.g. Baird's Sparrow [*Centronyx bairdii*], Brewer's Sparrow [*Spizella breweri*]). Many of these species have been previously documented as having some level of area sensitivity (Ribic et al., 2009) and Western Meadowlark was the only individually modelled species with large-extent (1600 m) responses to grassland amount and fragmentation. Landscape openness (ie. non-forested habitat including croplands and wetlands) is as a critical factor mitigating patch area-sensitivity in grassland birds (McDonald & Koper, 2022), and the amount of forest in the landscape affects birds through complex interactions with patch size (Grant et al., 2004; Renfrew & Ribic, 2008). Therefore, within the limited bounds of the study region, it is possible that levels of grassland fragmentation by a primarily forest matrix prevented occurrence of many obligate species and limited the negative response of observed obligate species community to grassland fragmentation.

The relative importance of the amount versus the configuration of habitats has been a subject of intense debate in recent literature related to habitat fragmentation (Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018). Some argue that when accounting for the known negative effects of lower amounts or loss of habitat, habitat fragmentation itself often results in neutral or positive biodiversity responses across landscapes (Fahrig, 2003) and is closely associated to concepts of landscape heterogeneity (Tews et al., 2004). In this way, the idea that collections of smaller patches are always inferior to larger patches is often erroneous and has negative policy implications for the protection of small habitat patches (Riva et al., 2024; Riva & Fahrig, 2022). Others argue that issues of scale, interdependence, and sampling bias limit the ability to interpret the mechanisms acting on any perceived benefits of higher fragmentation, and that the idea that fragmentation positively impacts biodiversity is dangerous from a conservation perspective (Fletcher et al., 2023). While increasing fragmentation associated with habitat loss as a process is indeed one of the greatest threats to biodiversity globally (Davison et al., 2021), this research presents an example whereby the pattern of increasingly complex configurations of a focal habitat type by a non-anthropogenically altered matrix increased overall levels of alpha diversity based on available species pools, habitat spillover, and landscape complementarity. An important aspect of this result is that it is limited to the fragmentation of a generalized 'grassland' cover by a forest-wetland matrix, and that different types of grassland were unable to be differentiated by the land cover raster used to assess habitat types (Appendix A).

Terrain ruggedness represented a measure of landscape heterogeneity that likely influenced grassland bird communities through the distribution of different grassland types. At the site scale, topography was significantly autocorrelated with levels of grassland alteration; native grasslands sites were autocorrelated with higher positions on hills in rugged terrain, and more altered grasslands were autocorrelated with lower positions on hills in less rugged terrain. It is well understood that topography affects the distribution of vegetation communities (Adams et al., 2005; DeMaere et al., 2012) and particularly occurrences of non-native vegetation (Averett et al., 2016; Foster et al., 2004; Gelbard & Harrison, 2003; Gennet et al., 2017; Simonson & Johnson, 2005). At this site scale, terrain ruggedness was a less influential predictor of grassland bird abundance and diversity than the actual composition and structure of the vegetation community (grassland type), which is echoed in the results of other research (Duquette et al., 2022). At the landscape scale, the type and amount of different grassland types can influence the abundance of obligate grassland birds (Davis et al., 2013), and the direction of species' responses to terrain ruggedness echoed associations with different grassland types. For example, higher Vesper Sparrow abundances were associated with smaller, isolated patches of native grassland in this research and elsewhere (Davis et al., 2016; Harrison et al., 2011; Johns, 1993), and responded positively to terrain ruggedness at 800 m extents, suggesting higher terrain ruggedness was likely associated with higher amounts of native grassland throughout landscapes. In addition, Clay-coloured sparrow responded positively to increasing terrain ruggedness at 400 m extents. Clay-coloured Sparrows were also associated with native grassland sites in this study, but because shrubs are critical for Clay-coloured Sparrow nesting, foraging, and territory displays (Dechant et al., 2002), higher terrain ruggedness may have also been autocorrelated with more depressional sites with higher shrub cover (DeMaere et al., 2012). Combined, these results suggest that terrain ruggedness represented a meaningful proxy of the distribution of different types of vegetation communities across landscapes not represented in metrics of grassland fragmentation. Although spatial heterogeneity created by fire, grazing, and grassland productivity across landscapes has been shown to contribute to higher grassland bird species diversity (Fuhlendorf et al., 2006; Hovick et al., 2015; Lipsey & Naugle, 2017; Lwiwski et al., 2015), it is worth noting that the overall effect of increasing terrain ruggedness on obligate species diversity was slightly negative.

Aside from the effects of landscape heterogeneity on species abundances and diversity, local habitat characteristics were critical determinants of individual obligate bird species in this region. Native grasslands hosted similar abundances of Vesper, Clay-coloured, and Savannah Sparrows, and communities were gradually more dominated by Savannah Sparrow and Western Meadowlark at higher levels of alteration. Despite estimated population declines of 45% over the last 50 years (Rosenberg et al., 2019), Savannah Sparrow is known to occur in nearly any kind of open habitat (ABMI, 2023; Davis & Duncan, 1999; Swanson, 2002). The taller, denser structures present in modified grasslands and haylands are known to provide substantial habitat for Bobolink (*Dolichonyx oryzivorus*), which is modelled to be at its highest abundance in this part of the province (ABMI, 2023), but was only observed in 8 of 299 morning recordings despite representation of these site types in this study. Modified grasslands and haylands thus represent important habitat for the grassland bird community in this region with similar overall diversity, but native grasslands should still be prioritized in conservation and management for birds as well as for their multitude of other conservation benefits (D’Antonio & Vitousek, 1992; Reed et al., 2005; Toledo et al., 2014).

Invaded grasslands represented an important subclass of grasslands relevant for management and understanding grassland bird communities in this region. The understanding that bird communities vary across continuums of vegetation composition is echoed in other studies (Lipsey & Naugle, 2017). In this study, responses of Savannah Sparrow, Vesper Sparrow, and Western Meadowlark in invaded grasslands were intermediate between native and modified grasslands. Rangeland health assessment typically includes the categorization of all grasslands with < 70% non-native vegetation composition as native and all grasslands with > 70% non-native vegetation composition as modified (Adams et al., 2016). Similar proportional distinctions are commonly used elsewhere (e.g. Davis et al., 2013), but this categorization likely fails to account for meaningful structural changes associated with increasing invasions by non-native species. Previous research has shown that grasslands with up to ~50% composition of non-native species did not have significant effects on grassland bird reproduction but shifted bird diet from Coleoptera to Orthoptera with lower covers of bare ground associated with non-native vegetation invasion (Kennedy et al., 2009). Although the effects of high grazing intensity on vegetation structure have been shown to reverse within a few years of resting (Fischer et al., 2020), the substantial changes in vegetation composition in modified grasslands are generally considered irreversible transitions (Bestelmeyer et al., 2017; DeMaere et al., 2012). Rangeland community guides for this region indicate that many of the reference communities for these invaded classifications are ‘successional’, which suggests that they could perhaps recover to the native or transition to the modified states depending on ongoing disturbance levels (Adams et al., 2005; DeMaere et al., 2012).

Overall, it is clear these invaded communities represent a meaningful habitat distinction for birds but it is unclear whether invaded communities represent an irreversible state change (Bestelmeyer et al., 2017) or a reversible perturbation (Fischer et al., 2020).

The results of this study support the value of rangeland integrity as a predictor for the abundance of certain grassland species. In this study, sites with higher range health had higher obligate grassland bird diversity, more Vesper Sparrows, fewer Savannah Sparrows, and a lower probability of Brown-headed Cowbird occurrence. Davis et al. (2014) found that range condition, an earlier rangeland integrity monitoring protocol, outperformed vegetation structure data when predicting abundances of several grassland bird species but did not outperform null models for Clay-coloured Sparrow, Western Meadowlark, Savannah Sparrow, or Vesper Sparrow. My results concur that Clay-coloured Sparrow and Western Meadowlark did not respond specifically to measures of rangeland integrity, but contrast Davis et al. (2014) in the strong negative responses of Savannah Sparrow and positive responses of Vesper Sparrow. That these species responded to range health in the Foothills Parkland Natural Subregion and not in the Dry Mixedgrass Natural Subregion could be related to differences in vegetation communities between regions (i.e. differences in composition and structure in comparing DeMaere et al., 2012 and Adams et al., 2013). Both Vesper Sparrow and Savannah Sparrow showed strong relationships with levels of grassland alteration associated with the ecological integrity assessment parameter in range health (Adams et al., 2016). Henderson & Davis (2014) found that measures of vegetation structure underlying range health assessment parameters were often better predictors than the range health score itself, suggesting that this parameter is critical in understanding this difference in responses between regions.

2.6 Conclusion

This study presents a comprehensive examination of grassland bird responses to habitat at different scales across heterogeneous landscapes in the Rocky Mountain Foothills. Landscape heterogeneity influenced the abundance and diversity of birds through the configuration of grasslands within a forest-wetland matrix and likely through terrain ruggedness influencing the distribution and alteration of grassland types. More fragmented grasslands in complex landscapes resulted in higher grassland bird diversity and higher terrain ruggedness was likely autocorrelated with higher amounts of native grasslands. Levels of grassland alteration were key determinants of the grassland bird community and likely explained relationships between range health and grassland bird abundances. These links may communicate common goals between managers and conservationists for high range health, native grassland communities moving forward.

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2.8 Tables

Table 1: Number of Autonomous Recording Unit (ARU) surveys with observations of each avian species and their categorization used in analysis. This table contains all species included in models for total grassland bird diversity. 21 other obligate and facultative grassland species were discounted because they were not likely to be consistently detected or accurately counted based on sound alone (Table S3). Bolded species were included in individual species analyses. This table includes only ‘morning’ recording types (sunrise or manual, n = 299) used in models and discounts observations from recordings that were not included in assessments (ie. bad weather or unit malfunction). Statuses were matched from the most recent versions of the datasets available from COSEWIC (Canada, 2024) and the Alberta Government (AEP, 2020). Species trends from Rosenberg et al. (2019) are matched from supplementary data and indicate long-term population changes between 1970 and 2017. Blanks indicate no status is available from that entity for that species.

Categorization	Common Name	Scientific Name	Morning ARU Surveys Detected	Morning Individuals Detected	COSEWIC Status	Alberta Wild Species Status 2020	Rosenberg et al. (2019) Long-term Population Trend
Obligate	**Savannah Sparrow**	***Passerculus sandwichensis***	**263**	**767**		Secure	Declining
Facultative	**Clay-coloured Sparrow**	***Spizella pallida***	**211**	**468**		Secure	Declining
Obligate	**Vesper Sparrow**	***Pooecetes gramineus***	**181**	**379**		Secure	Declining
Facultative	**House Wren**	***Troglodytes aedon***	**178**	**340**		Secure	Increasing
Obligate	**Western Meadowlark**	***Sturnella neglecta***	**109**	**208**		Secure	Declining
Facultative	Wilson's Snipe	*Gallinago delicata*	129	179		Secure	Increasing
Facultative	**Brown-headed Cowbird**	***Molothrus ater***	**100**	**122**		Secure	Declining
Facultative	Black Tern	*Chlidonias niger*	23	49	Not at Risk	Sensitive	Declining
Facultative	Common Yellowthroat	*Geothlypis trichas*	33	41		Sensitive	Declining
Facultative	Eastern Kingbird	*Tyrannus tyrannus*	33	34		Sensitive	Declining
Facultative	Gray Catbird	*Dumetella carolinensis*	19	21		Secure	No significant change
Facultative	Lincoln's Sparrow	*Melospiza lincolnii*	15	20		Secure	No significant change
Facultative	Killdeer	*Charadrius vociferus*	16	16		Secure	Declining
Facultative	American Bittern	*Botarus lentiginosus*	11	13		Sensitive	Declining
Obligate	Brewer's Sparrow	*Spizella breweri*	7	10		Sensitive	Declining
Obligate	Bobolink	*Dolichonyx oryzivorus*	8	8	Special Concern	Sensitive	Declining
Facultative	Common Nighthawk	*Chordeiles minor*	7	7	Special Concern	Sensitive	Declining
Facultative	Willet	*Tringa semipalmata*	7	7		Secure	Declining
Facultative	Mountain Bluebird	*Sialia currucoides*	4	5		Secure	Declining
Obligate	LeConte's Sparrow	*Ammodramus leconteii*	1	4		Secure	Declining
Obligate	Horned Lark	*Eremophila alpestris*	2	3		Secure	Declining
Obligate	Baird's Sparrow	*Ammodramus bairdii*	2	3	Special Concern	Sensitive	Declining
Obligate	Nelson's Sparrow	*Ammospiza nelsoni*	1	2		Secure	Increasing
Obligate	Grasshopper Sparrow	*Ammodramus savannarum*	1	2		Sensitive	Declining
Facultative	Song Sparrow	*Melospiza melodia*	2	2		Secure	Declining
Facultative	Western Kingbird	*Tyrannus verticalis*	2	2		Secure	
Facultative	Lark Sparrow	*Chondestes grammacus*	1	1		Secure	Declining
Total Species Observations and Individuals Detected			**1366**	**2713**			

Table 2: Number of recordings analyzed (sample sizes) by response variable. Sample sizes differ between diversity models because Simpson's Reciprocal Index (1/D), used to measure diversity, was undefined when a species group (obligate or facultative) was not detected. Sample sizes differ between scaled and range health models because range health was not assessed in 23 haylands. Detectable effect sizes correspond to sensitivity power analyses.

Model Type	Species Info	Dependent Variable	Scaled Models			Range Health Models		
			Sample Size	Detectable Effect Size (f^2)	Distribution	Sample Size	Detectable Effect Size (f^2)	Distribution
Diversity								
Facultative Diversity	17 included species	Simpson's Reciprocal Index	280	0.06	Gaussian	243	0.03	Gaussian
Obligate Diversity	10 included species	Simpson's Reciprocal Index	289	0.05	Gaussian	250	0.02	Gaussian
Total Diversity	27 obligate and facultative species	Simpson's Reciprocal Index	299	0.05	Gaussian	259	0.02	Gaussian
Obligate Species								
Savannah Sparrow	*Passerculus sandwichensis*	Relative Abundance	299	0.05	Poisson	259	0.02	Negative Binomial
Vesper Sparrow	*Pooecetes gramineus*	Relative Abundance	299	0.05	Negative Binomial	259	0.02	Negative Binomial
Western Meadowlark	*Sturnella neglecta*	Presence/ Absence	299	0.05	Binomial	259	0.02	Binomial
Facultative Species								
Brown-headed Cowbird	*Molothrus ater*	Presence/ Absence	299	0.05	Binomial	259	0.02	Binomial
Clay-coloured Sparrow	*Spizella pallida*	Relative Abundance	299	0.05	Poisson	259	0.02	Negative Binomial
House Wren	*Troglodytes aedon*	Relative Abundance	299	0.05	Poisson	259	0.02	Negative Binomial

Table 3: Model results for the best-fitting extent of the six individual species models and three grouped community diversity models. Model intercepts indicate species abundance, diversity (in units of species), or the probability of presence (depending on model type) at the first level of factors and variable means. Except for including all model intercepts, only estimates with 85% confidence intervals not overlapping zero are shown. Presence model estimates are odds ratios, abundance model estimates are incidence rate ratios, and diversity model estimates are back-transformed model estimates from log (diversity) models. Estimates are shown as decimals indicating the proportional effect of the factor level relative to the first level of factors or one standard deviation (SD) increase in continuous variables from their means (ie. the effect relative to the intercept). Blue values indicate positive effects (relative effects greater than 1), and red values indicate negative effects (relative effects less than 1). Extents are the distance from the site centres at which variables were calculated with dashes indicating no value is applicable. Estimates for landscape variables are only shown at the best-fitting landscape extent.

Category	Variable	Extent (m)	Mean	SD	Savannah Sparrow Abundance	Vesper Sparrow Abundance	Western Meadowlark Presence	Obligate Species Diversity	Brown-headed Cowbird Presence	Clay-coloured Sparrow Abundance	House Wren Abundance	Facultative Species Diversity	Total Grassland Bird Diversity
Model	**Intercept**	-	Means, Native Grassland, 2021, and Sunrise Rec.		1.66 (1.38, 1.99)	2.05 (1.60, 2.62)	0.06 (0.03, 0.14)	1.60 (1.47, 1.75)	0.41 (0.26, 0.56)	1.98 (1.60, 2.44)	0.89 (0.68, 1.16)	2.15 (1.89, 2.45)	3.56 (3.25, 3.91)
Survey	Easting Coord. (km)	-	593	9	0.91 (0.85, 0.97)				1.55 (1.24, 1.95)	1.09 (1.01, 1.19)		1.13 (1.08, 1.19)	1.16 (1.12, 1.20)
	Julian Date	-	166	12	1.27 (1.20, 1.34)		0.66 (0.53, 0.83)		0.69 (0.56, 0.85)		1.21 (1.11, 1.32)		
	Year (2022)	-	Relative to Intercept				2.52 (1.25, 5.09)						
	Manual Rec.	-			0.75 (0.64, 0.89)		2.21 (1.06, 4.59)			0.75 (0.61, 0.92)			
Local	Topo. Position Index (TPI)	100	0.09	0.13						0.89 (0.82, 0.97)			
	Elevation (m)	100	1360	53							1.10 (1.00, 1.20)	0.91 (0.87, 0.95)	
	Invaded Grassland	100	Relative to Intercept		1.52 (1.28, 1.81)	0.63 (0.51, 0.78)	4.74 (2.39, 9.41)						
	Modified Grassland	100			1.90 (1.59, 2.27)	0.44 (0.34, 0.56)	6.43 (3.02,13.67)			0.73 (0.59, 0.90)			
	Cultivated Grassland	100			2.44 (1.92, 3.12)	0.37 (0.25, 0.54)			0.21 (0.08, 0.54)	0.29 (0.20, 0.42)	1.60 (1.09, 2.35)	0.82 (0.69, 0.99)	0.71 (0.63, 0.81)
Patch	Distance to Forest (m)	-	410	275	1.09 (1.03, 1.15)		1.93 (1.40, 2.66)	1.05 (1.01, 1.08)		0.89 (0.80, 0.98)	0.36 (0.30, 0.43)	0.87 (0.84, 0.91)	0.95 (0.91, 0.98)
Landscape	**Best Fitting Extent (m)**	**-**	**AIC model selection**		**200**	**800**	**1600**	**1600**	**400**	**400**	**100**	**100**	**400**
	Terrain Ruggedness - Standard Deviation in Elevation (m)	100	2.8	2.3									
		200	5.6	3.8	0.94 (0.88, 1.00)								
		400	10.4	6.2					0.69 (0.53, 0.89)	1.09 (1.01, 1.17)			
		800	16.8	8.7		1.16 (1.07, 1.27)							
		1200	22.3	10.2									
		1600	27.1	11.3			0.52 (0.38, 0.71)	0.97 (0.93, 1.00)					
		2000	31.3	12.2									
	Grassland Cover (%)	100	92.9	13.3							1.28 (1.14, 1.43)		
		200	84.5	14.0									
		400	71.7	16.3					0.57 (0.43, 0.77)				
		800	64.7	17.0		0.89 (0.79, 1.00)							
		1200	63.0	16.4									
		1600	61.9	16.2			1.83 (1.29, 2.61)						
		2000	61.1	15.7									
	Grassland Fragmentation (LSI)	400	2.7	0.8						1.31 (1.20, 1.44)			1.09 (1.04, 1.13)
		800	5.0	1.0		0.78 (0.70, 0.87)							
		1200	7.2	1.2									
		1600	9.3	1.4			0.55 (0.39, 0.77)	0.93 (0.90, 0.97)					
		2000	11.5	1.7									

Table 4: Rankings of top and competing models based on extent. k is the number of variables in each model, AIC is Akaike's Information Criterion, Relative Log(L) is the log-likelihood scaled for the best model to equal 1, and ω_i is the Akaike weight. Models with weights < 0.1 are not shown.

Model Type	Model	Extent (m)	k	AIC	ΔAIC	Relative Log(L)	ω_i
Diversity	Facultative Diversity	100	13	363.20	0.00	1.00	0.25
		800	14	363.46	0.26	0.88	0.22
		400	14	363.98	0.77	0.68	0.17
		200	13	364.24	1.03	0.60	0.15
	Obligate Diversity	1600	14	185.05	0.00	1.00	0.50
		2000	14	185.45	0.39	0.82	0.41
	Total Diversity	400	14	217.57	0.00	1.00	0.77
		200	13	221.23	3.65	0.16	0.12
Facultative Species	Brown-headed Cowbird	400	14	353.70	0.00	1.00	0.97
	Clay-coloured Sparrow	400	14	936.06	0.00	1.00	0.83
		200	13	939.24	3.18	0.20	0.17
	House Wren	100	13	766.38	0.00	1.00	0.87
Obligate Species	Savannah Sparrow	200	13	1047.44	0.00	1.00	0.27
		400	14	1047.89	0.45	0.80	0.21
		800	14	1048.06	0.63	0.73	0.20
		100	13	1048.37	0.93	0.63	0.17
	Vesper Sparrow	800	14	889.24	0.00	1.00	0.86
		400	14	893.47	4.23	0.12	0.10
	Western Meadowlark	1600	14	305.96	0.00	1.00	0.75
		2000	14	309.39	3.43	0.18	0.14
		1200	14	309.86	3.90	0.14	0.11

2.9 Figures

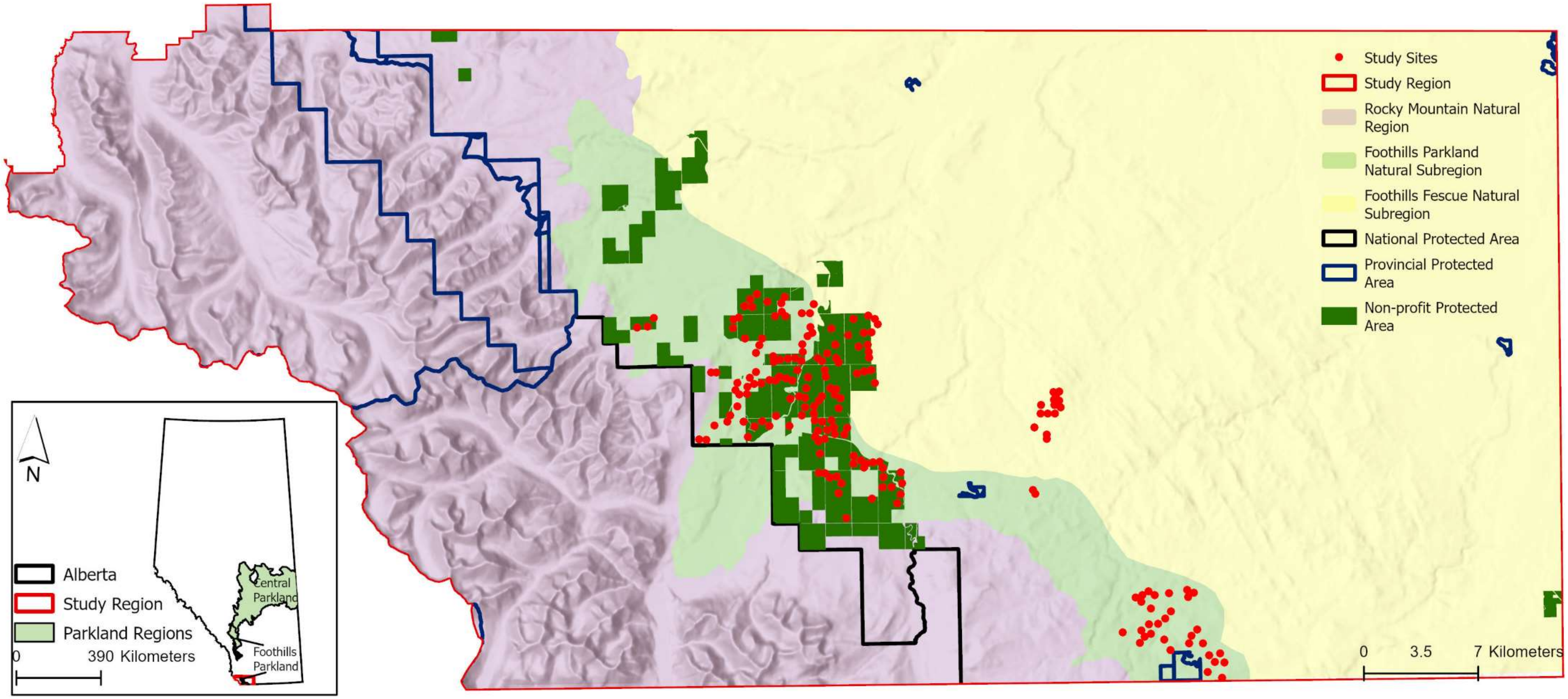


Figure 1: Overview of study location showing Alberta Natural Region (NR) and Natural Subregion (NSR) designations (Natural Regions Committee, 2006), protected areas (Alberta, 2020; ECCC, 2023), and sites for this study. The inset shows the study region within Alberta, Canada. All 187 study sites were on private land, much of which was owned by non-profit land trusts.

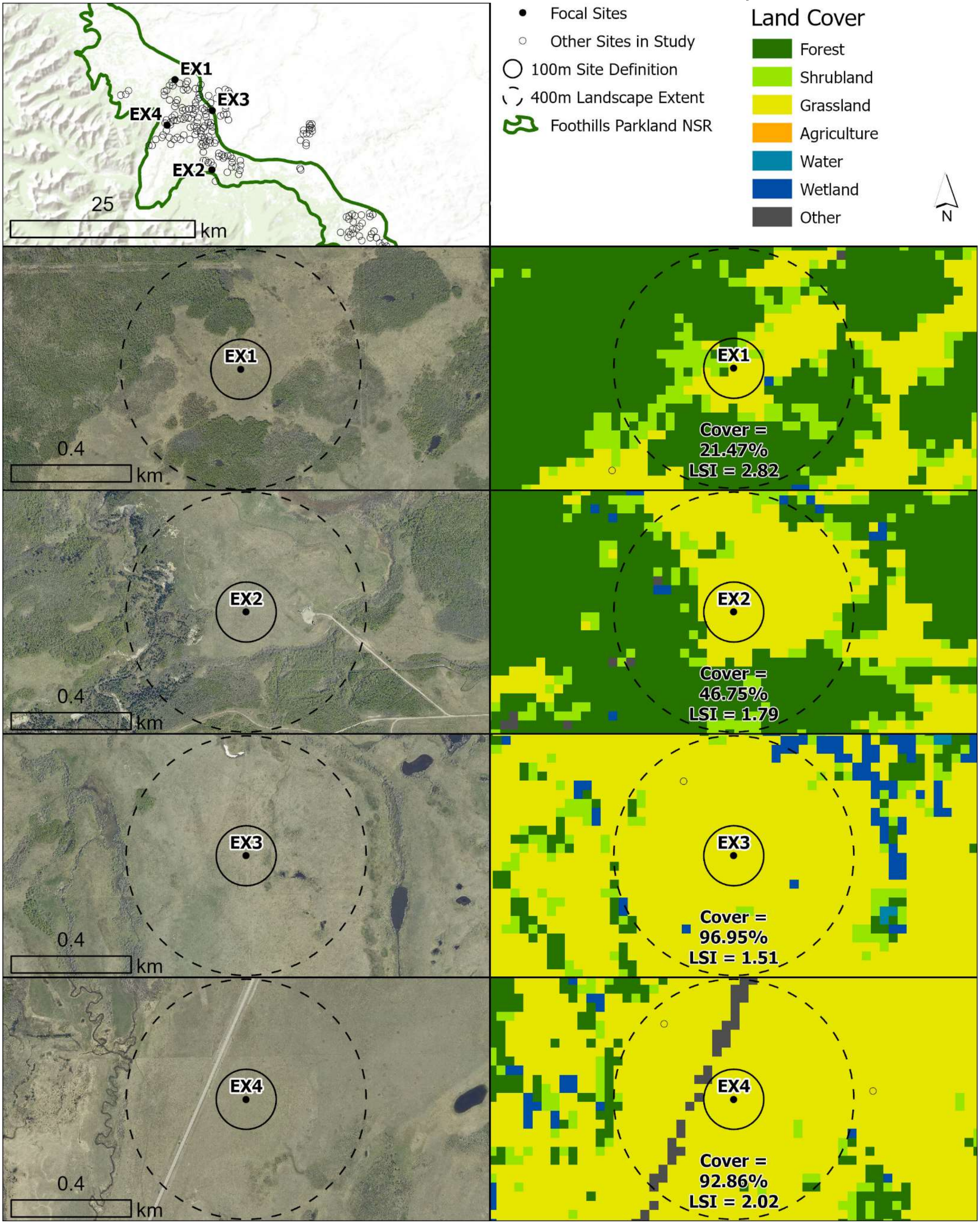
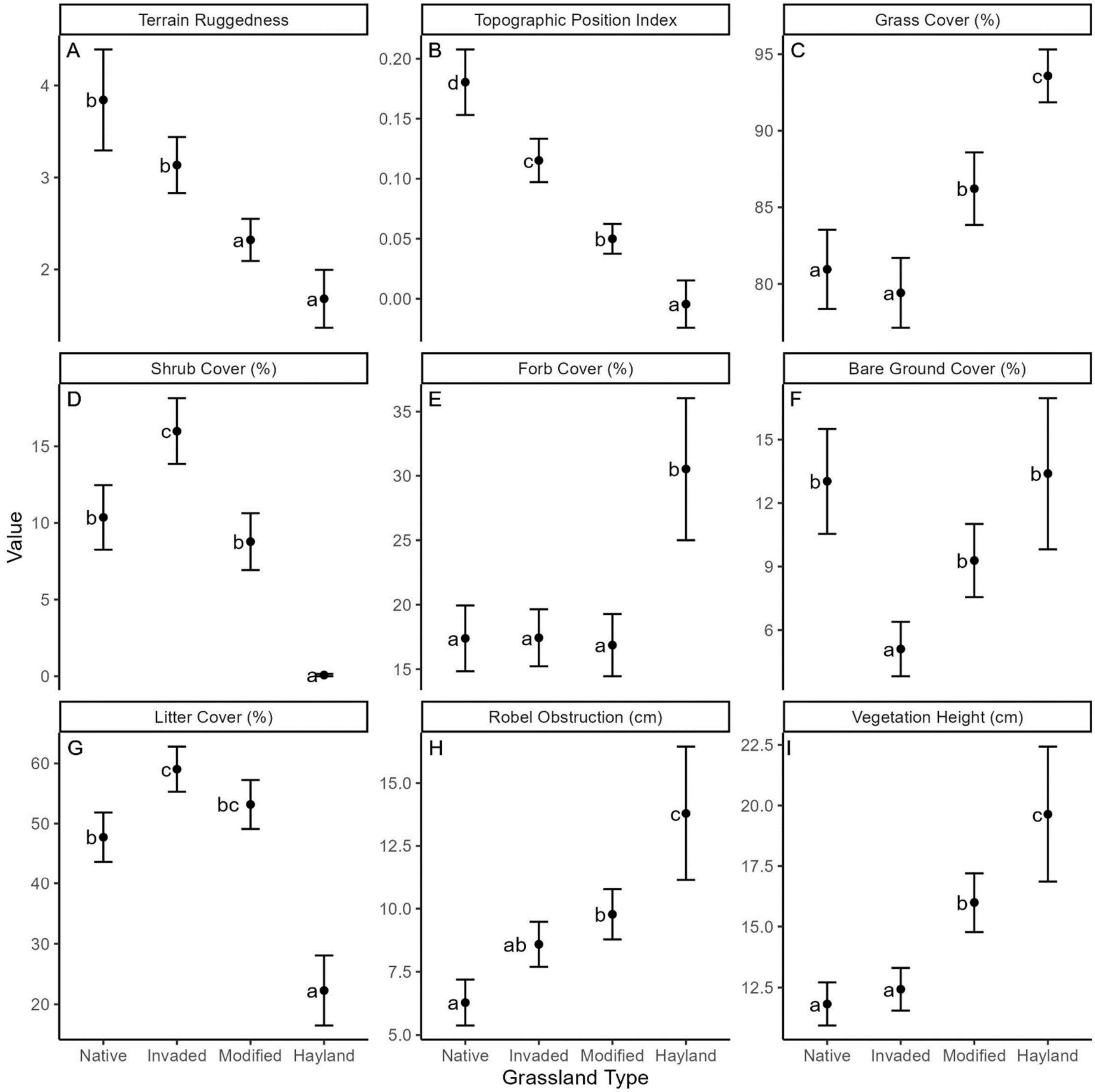

EX1
EX3
EX4
EX2
25
km
Focal Sites
Other Sites in Study
100m Site Definition
400m Landscape Extent
Foothills Parkland NSR
Land Cover
Forest
Shrubland
Grassland
Agriculture
Water
Wetland
Other
N
EX1
0.4
km
EX1
Cover =
21.47%
LSI = 2.82
EX2
0.4
km
EX2
Cover =
46.75%
LSI = 1.79
EX3
0.4
km
EX3
Cover =
96.95%
LSI = 1.51
EX4
0.4
km
EX4
Cover =
92.86%
LSI = 2.02

Figure 2: Example sites and 400 m landscape extents varying in levels of grassland cover and fragmentation. The top panel shows example sites (EX 1-4) relative to the Foothills Parkland Natural Subregion. In each row, aerial imagery provided by Nature Conservancy Canada *(NCC, 2020)* is shown to the left of its land cover classification using the modified version of the 30 m resolution 2020 Annual Crop Inventory *(AAFC, 2020)*. Labels depict example site numbers matching the top panel, grassland cover as a percentage of the 400 m landscape extent, and grassland fragmentation at the 400 m landscape extent as the Landscape Shape Index (LSI).



Terrain Ruggedness
Topographic Position Index
Grass Cover (%)
Shrub Cover (%)
Forb Cover (%)
Bare Ground Cover (%)
Litter Cover (%)
Robel Obstruction (cm)
Vegetation Height (cm)
A
B
C
D
E
F
G
H
I
Value
Grassland Type
Native
Invaded
Modified
Hayland

Figure 3: Relationship of grassland type (by percent composition of non-native vegetation with native < 30%, invaded 30-70%, modified > 70% but grazed, and haylands previously cultivated and cut/bailed annually) with local topography (A, B) and vegetation structure (C to I) variables at the site (100 m) extent. All units are shown in panel headers except terrain ruggedness (A), which is measured as the standard deviation in elevation (m), and the Topographic Position Index (B), which is <0 in depressional areas, 0 in flat areas, >0 in raised areas. Points are means ± 85% confidence intervals. Based on ANOVA and Tukey HSD post-hoc tests at the 85% confidence level, different letters within panels denote significant differences between grassland types.

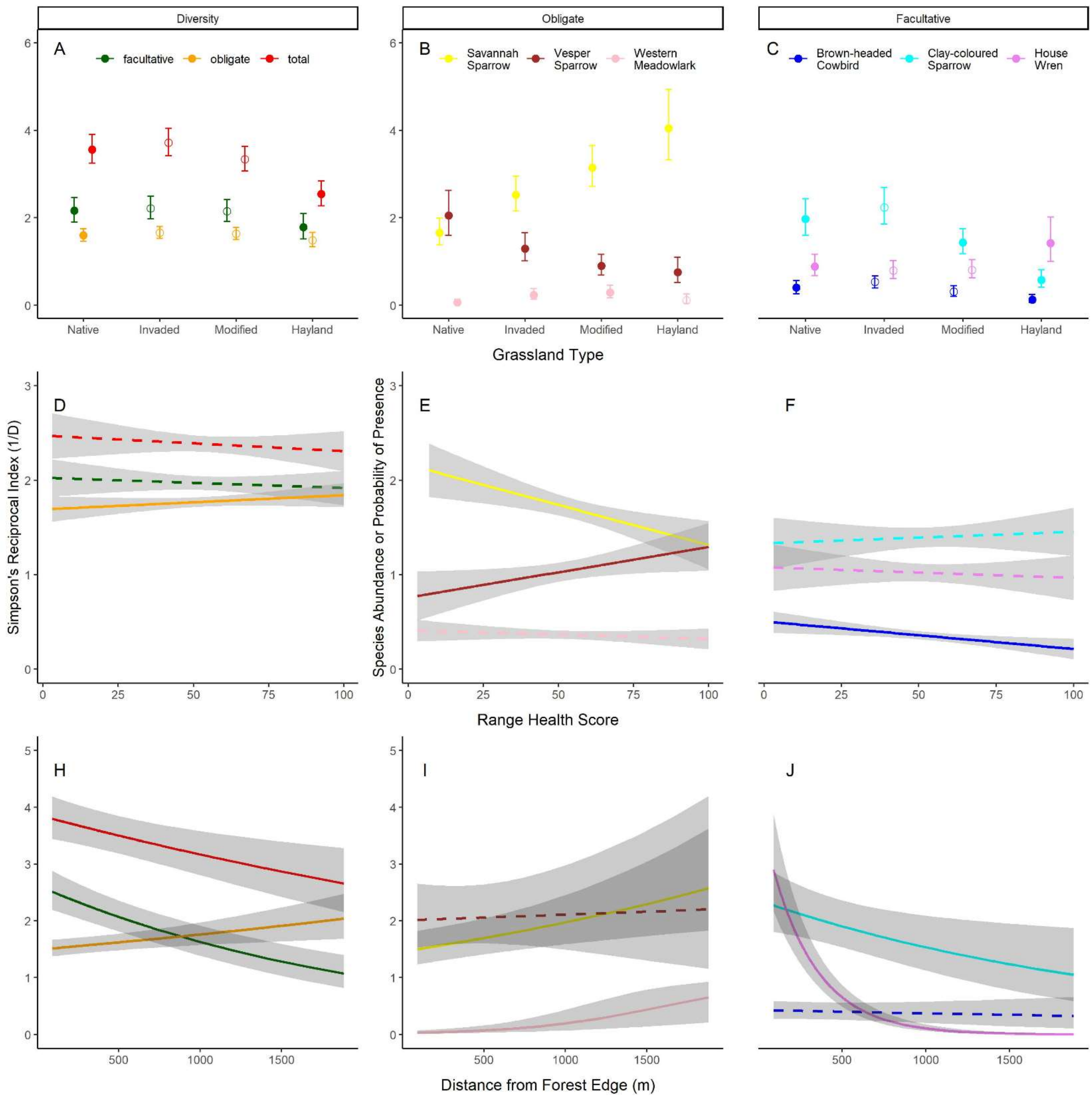

Diversity
Obligate
Facultative
A
facultative
obligate
total
B
Savannah Sparrow
Vesper Sparrow
Western Meadowlark
C
Brown-headed Cowbird
Clay-coloured Sparrow
House Wren
Native
Invaded
Modified
Hayland
Grassland Type
D
E
F
Simpson's Reciprocal Index (1/D)
Species Abundance or Probability of Presence
Range Health Score
H
I
J
Distance from Forest Edge (m)

Figure 4: Model predictions ± 85% CIs for the effects of different grassland types (A, B, C), range health (D, E, F; separately modelled from the other variables), and distance from forest edge (H, I, J) on the diversity of grassland bird groups (A, D, H) and the individual responses of obligate (B, E, I) and facultative (C, F, J) grassland bird species. Filled circles and solid lines depict estimates with 85% CIs not overlapping zero ('influential' predictors). Open circles and dashed lines indicate estimates with 85% CIs overlapping zero (non-influential predictors). Only Western Meadowlark and Brown-headed Cowbird models represent the probability of presence instead of abundance.

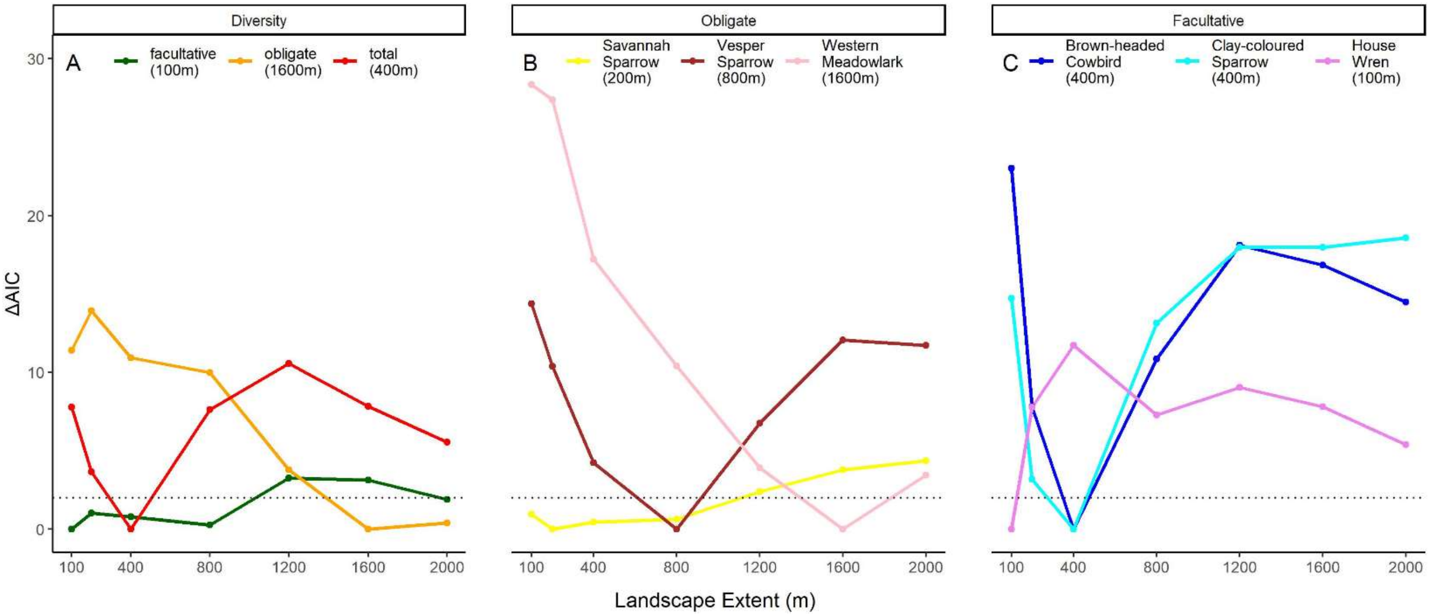


Figure 5: Difference in model fit at each landscape extent for the diversity of grassland bird groups (A) and the individual responses of obligate (B) and facultative (C) grassland bird species. The best fitting model in each panel is shown as ΔAIC = 0 and all other models are shown relatively. The best-fitting landscape extent was used for interpretations unless 100m or 200m extent models, which contained fewer variables, had ΔAIC <2 (dotted line).

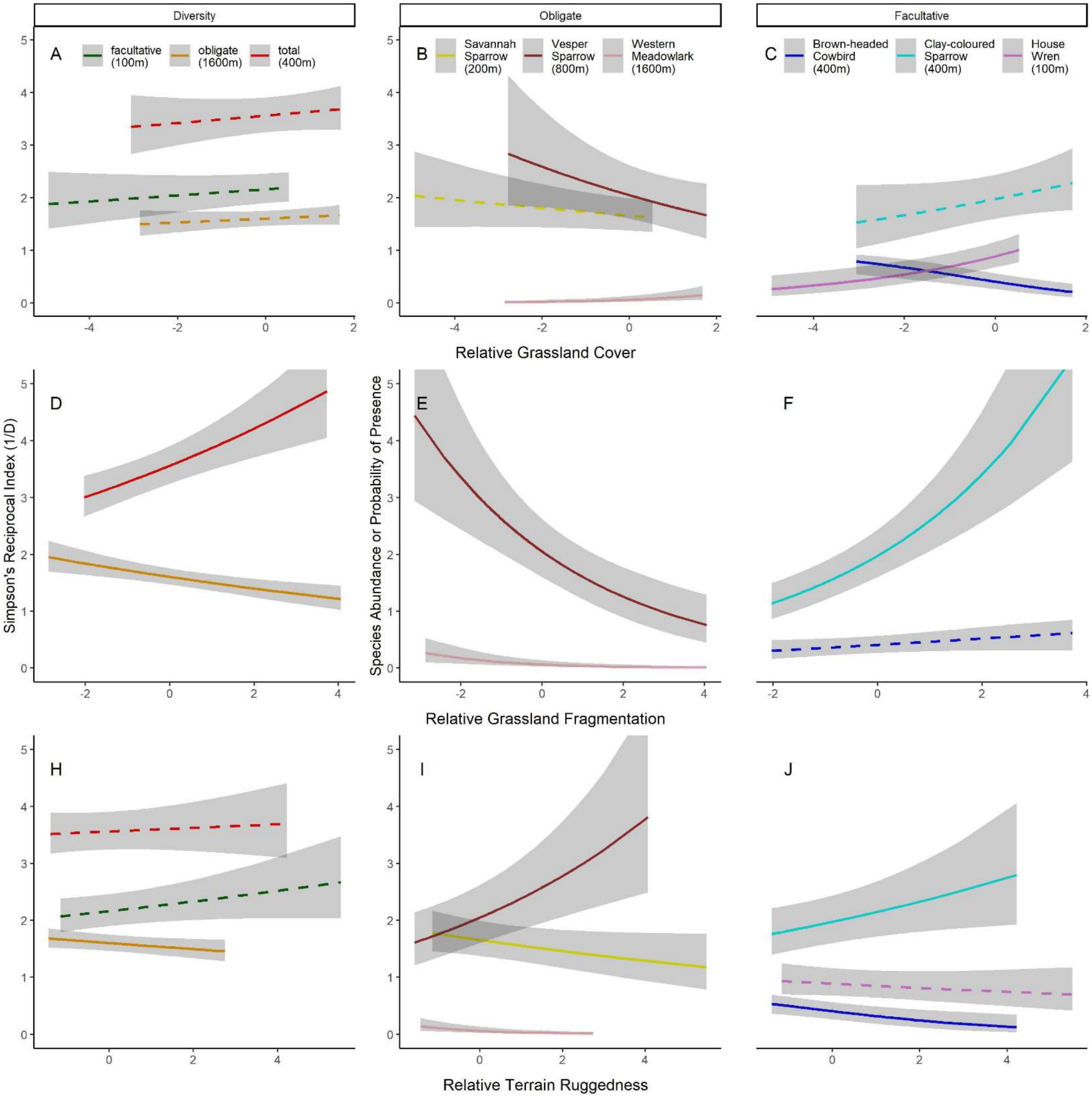

Diversity
Obligate
Facultative
A
facultative (100m)
obligate (1600m)
total (400m)
B
Savannah Sparrow (200m)
Vesper Sparrow (800m)
Western Meadowlark (1600m)
C
Brown-headed Cowbird (400m)
Clay-coloured Sparrow (400m)
House Wren (100m)
Relative Grassland Cover
D
E
F
Simpson's Reciprocal Index (1/D)
Species Abundance or Probability of Presence
Relative Grassland Fragmentation
H
I
J
Relative Terrain Ruggedness

Figure 6: Model predictions ± 85% CIs for the effects of grassland cover (A, B, C), grassland fragmentation (D, E, F), and terrain ruggedness (H, I, J) on the diversity of grassland bird groups (A, D, H) and the individual responses of obligate (B, E, I) and facultative (C, F, J) grassland bird species. All metrics are shown in standard deviations from the mean at the best-fitting landscape extent (shown under legend title). *S*olid lines depict estimates with 85% CIs not overlapping zero ('influential' predictors) and dashed lines indicate estimates with 85% CIs overlapping zero (non-influential predictors). Only Western Meadowlark and Brown-headed Cowbird models represent the probability of presence instead of abundance. Models at best fitting extents for facultative diversity, Savannah Sparrow, and House Wren did not include grassland fragmentation.

3 Summary and Management Implications

3.1 Summary

This thesis represents the first formalized study of the grassland bird community in the Waterton Foothills Parkland region. This area contains a high concentration of private conservation projects associated with the Nature Conservancy of Canada (NCC), which contributes to the protection and management of over a third of the region by area. The importance of the region for providing habitat for wide-ranging mammals such as Grizzly Bear and Elk has been long recognized, but there has been little to no other formalized bird monitoring in this region outside of the small portion within Waterton Lakes National Park.

All data associated with this thesis is included in the attached data package. This data package was provided to NCC as part of the submission of this project in conjunction with the Weston Family Conservation Science Fellowship. In addition to the results being included within this thesis and prospectively published in peer-reviewed journal articles, data from the ARU deployments will be included in the Central Grassland Avian Modeling Project (CGAMP). This project is a partnership between the Canadian Wildlife Service, United States Fish and Wildlife Service, Bird Conservancy of the Rockies, World Wildlife Fund, and the Joint Venture 8 Conservation Initiative to create spatially explicit density models of grassland birds across the Northern Great Plains. Although this area is technically outside of the definition of the Canadian Prairies (ESWG, 1995), it still represents an important transition zone where many grassland species occur and contributes valuable insight into habitat associations.

In total, I documented 138 species of birds during this project. I used ARUs to document 120 species and documented 18 additional species (mostly waterfowl) in incidental eBird surveys. 10 are ranked as Special Concern under COSEWIC (Canada, 2024), and 24 are ranked as Sensitive, May Be At Risk, or At Risk provincially (AEP, 2020). The obligate grassland bird community in this region is mostly generalist grassland species that can tolerate the complex forest-grassland mosaic landscapes in this region. Some of the notable species at risk observed in small numbers include Ferruginous Hawk (COSEWIC SC, although only on private lands not related to NCC projects further east), Bank Swallow (COSEWIC T, in a few populations throughout), Barn Swallow (COSEWIC SC, a few observations), and Long-billed Curlew (COSEWIC SC, only two observations).

3.2 Management Implications

Examining the configuration and classification of grasslands in parcel-based management units (sections and quarter sections) will provide key insights into the grassland bird community. Of the nine ecological responses measured, only two (Western Meadowlark occurrence and obligate species diversity) were best predicted at extents greater than 800 m (outside of sections). Because this region has such a reduced diversity of obligate grassland birds, higher amounts of grassland are unlikely to have higher obligate species diversity unless they are closer to the more open landscapes in the Foothills Fescue Natural Subregion. On the periphery of the study region, there were the only observations of some mixedgrass species such as Baird's Sparrow and higher probability of Western Meadowlark occurring. Within this regional context, more fragmented and smaller patches of grassland will likely support similar overall levels of obligate species and will support more facultative grassland species. Parcels with higher terrain ruggedness will likely support more microhabitat diversity, including native grasslands on hills and shrubby depressional areas. These factors are key determinants of the abundances of Vesper and Clay-coloured Sparrow, and likely other species dependent on these habitats as well (e.g. Lincoln's Sparrow, *Melospiza lincolnii*).

The types of grassland present will likely be the largest determinant of the species comprising the grassland bird community. Savannah Sparrow, Vesper Sparrow, and Clay-coloured Sparrow are all present in similar abundances in native grasslands, but Savannah Sparrow and Western Meadowlark were more prevalent in more altered grasslands. Savannah Sparrows were most dominant in haylands, although there were additional observations in these habitats of Bobolink and Grasshopper Sparrow in low numbers. When determining types of grassland, 'invaded' (30-70% non-native composition) grasslands served had distinct responses in presence and abundance as compared to native and modified grasslands for all three of the common obligate grassland birds modelled. I would recommend the inclusion of invaded grasslands into ecosystem mapping initiatives to gain insights into areas at risk of potentially shifting into modified vegetation communities and presenting distinct habitat conditions for obligate grassland birds. This recommendation is in line with efforts to conduct a national grassland inventory using similar categories: native (>75% native), tame (<25% native) and mixed (25-75% native; B. Robinson, pers. comm.).

Range health proved to be a reasonable predictor of grassland communities as it was associated with levels of grassland alteration. Vesper Sparrow was more abundant in native, high range health sites, and Savannah Sparrow was more abundant in modified, lower range health grasslands. Brown-headed Cowbird occurrence also decreased in higher range health sites, and this obligate brood parasite is a major cause of lower nest productivity in other grassland habitats (Lipsey & Naugle, 2017). The mechanism behind the relationship between Brown-headed Cowbird occurrence is unclear but may be related to litter cover as this is a large portion of the range health score and has been shown to affect abundance of this species negatively (Lipsey & Naugle, 2017). Because of these associations, range health could serve as a strong source of common language between managers and the ecology of birds in this region with higher range health sites having more Vesper Sparrows and lower probability of Brown-headed Cowbirds occurring.

3.3 Notes on Future Research

3.3.1 Bobolink

An interesting note is that the relative abundance of Bobolink (*Dolichonyx oryzivorus*) has been modelled to be highest in this region within Alberta (ABMI, 2024). Despite this, Bobolink was only observed 19 times in the two years of surveys conducted across nearly all available grassland patches (9 point counts and 10 incidental observations). I observed very high abundances of this species on the more recently secured Yarrow Creek NCC Project in 2020 while conducting surveys with the Alberta Conservation Association as part of their Multiple Species at Risk (MULTISAR) monitoring program. Unfortunately, this study could not include these areas due to timing. It is unclear why the study sites surveyed did not have high observed abundances of this species as they are known to prefer dense and tall modified or cultivated grasslands (ABMI, 2024), which were included in many sites. It is possible that Bobolink require higher patch sizes of modified/hayland to persist in this region as active edge avoidance has been documented in this species (Fletcher & Koford, 2003).

3.3.2 Common Nighthawk

There were many observations of Common Nighthawk (*Chordeiles minor*; COSEWIC SC) throughout the Waterton Foothills Parkland. Common Nighthawk was detected in evening and overnight ARU recordings 47 times and were just short of thresholds (50 observations) to model habitat preferences. They were particularly well documented on the Wellman, Jenkins, LB Bruder, and Birdseye Ranch projects. Tentative models could be produced predicting occurrence using the data procured for this research.

3.3.3 Underrepresented Bird Assemblages

In this research, the use of ARUs limited the scope of bird communities able to be assessed. Raptors and waterfowl are prevalent and diverse throughout these habitats but were unable to be studied because they were not reliably detectable or countable using the ARU methods employed. These assemblages are quite diverse in foothills and parkland habitats (nearly 50 species of water-associated or raptor species detected incidentally throughout surveys), meaning that their exclusion here presents a limitation to understanding the grassland bird community regionally. Examining habitat use and the composition of these assemblages may provide greater insight into aspects of habitat securement and management considering avian diversity.

3.3.4 Nest Productivity

Although species persist across multiple habitat types, it is unclear how breeding success varies. Species may avoid edges when establishing nests, but this behaviour does not always positively affect nesting success (Renfrew et al., 2005). Additionally, species can be abundant in non-native-dominated grasslands, but in some cases can have reduced nesting success (Davis et al., 2016). Nest searching would be exceedingly difficult in the hilly native habitats here (pers. obs.) but would provide insight into the value of altered and fragmented habitats for grassland birds in this region.

3.3.5 Implications of Range Health versus Topography on Grassland Alteration

The results of this study support that there are complex interactions between topography, grazing, and grassland alteration. Human cultivation has been shown to be more prevalent in flatter areas (Simonson & Johnson, 2005), and invasions of non-native species have been shown to be more common in flatter areas here and elsewhere (Gennet et al., 2017; Pasinelli, 2016; Reino et al., 2013) by affecting the distribution of vegetation communities based on slope, aspect, and topographic position. Topography also affects cattle access and grazing preferences, with hills being less accessible in general (Collins & Calabrese, 2012; Fuhlendorf et al., 2006; Hartnett et al., 1996). Grassland modification is generally considered to be a consequence of too much or too little cattle disturbance (Adams et al., 2016), but the role of topography in influencing non-native vegetation invasions has implications for grassland conservation. For example, if the alteration of grasslands is primarily caused by factors related to topography regardless of grazing disturbance (e.g. exposure, hydrology, and soils), then management and restoration interventions would have little success at preventing (or reversing) modification. Alternatively, if lower lying areas are simply more susceptible to modification following disturbance and more accessible to cattle, then modifying cattle stocking rates in lower-lying native grasslands might be able to prevent (or reverse) alteration in flatter areas that are more susceptible to invasions. Determining the relative impacts of cattle and topography in grassland alteration through non-native species invasions could have important implications for the conservation of native grassland in this region.

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Appendix 1: Comparing Land Cover Datasets

Introduction

Despite the importance of remotely sensed land cover datasets for environmental research, few studies have compared the accuracies of different remotely sensed datasets at regional scales. To better understand the accuracy of the available remotely sensed data in the Rocky Mountain Foothills, I sought answers to two questions: (1) Which of three openly available datasets – the North American Land Change Monitoring System (NALCMS), the Annual Crop Inventory (ACI), or the Alberta Biodiversity Monitoring Institute (ABMI) Wall-to-Wall Land Cover inventory – most accurately assesses grassland cover in the Waterton Foothills Parkland, and (2) whether any of these datasets were able to distinguish between native grasslands and non-native grasslands, especially cultivated lands for tame forage species (haylands). Together, the answers to these questions informed the selection of a land cover dataset used in this thesis.

Methods

Study Region & Validation Sites

I used sites selected and surveyed as part of a study of avian communities in the Waterton Foothills Parkland of Alberta, Canada (113.71°W, 49.11°N) to assess the accuracy of land cover datasets (Figure 1). This region is a mosaic of *Populus tremuloides* forest interspersed amongst grasslands, with frequent wetlands and depressions with high shrub cover dominated by *Dasiophora fruticosa, Symphyocarpus occidentalis*, *Amelancier alnifolia*, and *Salix* species. Grasslands are primarily dominated by native bunchgrasses including *Festuca campestris*, *Festuca idahoensis*, *Danthonia parryi*, and *Koeleria* *macrantha* interspersed with high forb diversity. There are many other areas with historical or active cultivation to agronomic grasses including *Phleum pratense*, *Poa pratensis*, *Dactylis glomera*, and *Bromus inermis*. In many places, these agronomic species have invaded native grasslands, creating ‘modified’ communities where cultivation may or may not have occurred previously (Adams et al., 2005, 2016; DeMaere et al., 2012).

I defined ‘sites’ as the 100 m buffer around a centre point in grassland habitat for the avian habitat study included in Chapter 2 of this thesis. Sites contained >75% of a single grassland community type, <10% cover of trees or shrubs taller than 2m and were >250 m from other sites (average ± standard deviation distance between sites: 505 ± 196 m). In total, I identified and surveyed 187 unique sites across 2021 and 2022. For this analysis, I only included 152 sites that were within the Foothills Parkland because I had originally included additional objectives associated with describing grassland cover in this region, and because it seemed reasonable to limit examination of accuracy to a regional unit as defined by the Natural Subregion. I classified each grassland site as native (<30% non-native vegetation), invaded (30-70% non-native vegetation), modified (>70% non-native vegetation), or hayland (actively cultivated for harvesting tame grasses; modified from Adams et al., 2016) during rangeland health assessments conducted in July and August 2021 and 2022.

Datasets Compared

I compared three freely available land cover products covering the study region (Table 1; Figure 2). The first was the 2015 Land Cover of Canada layer produced as part of the North American Land Change Monitoring System (NALCMS; NRC, 2015). The NALCMS covered the United States, Canada, and Mexico and classified land cover into 19 categories at 30 m resolution by classifying specific spectral bands in satellite imagery. This dataset was produced in 2010, 2015, and 2020 using methods independently applied in the United States, Canada, and Mexico (CEC, 2024). This dataset is produced in Canada from the Operation Land Imager (OLI) Landsat sensor and was reported to have an accuracy of 80% (NRC, 2015). The 2020 version of this dataset was available with a reported 87% accuracy, but upon initial examination, was much less accurate than the 2015 version in this region (Figure 3). The second dataset was the 2020 Annual Crop Inventory (ACI; AAFC, 2020). This dataset is also a remotely sensed 30 m raster but is produced by the Government of Canada annually and only covers the agricultural areas of southern Canada (AAFC, 2020). In addition to identifying spectral bands from satellite imagery, this dataset included ground truthing by agricultural producers and identified 72 categories of land cover, 58 of which are different crop types (AAFC, 2020). In Alberta, this version of the dataset was assessed with 92% accuracy for crop classes and 67% accuracy for other land cover (AAFC, 2020). Finally, I compared the Alberta Biodiversity Monitoring Institute (ABMI) Wall-2-Wall land cover inventory, which is a polygon layer based on 30 m satellite resolution land cover maps but with extensive ground-truthing and manual validation efforts across 11 cover classes (ABMI, 2010). Polygons were delineated with 5000 m^2 patch size minimum for water and 20,000 m^2 minimums for other covers and reported an overall accuracy of 75% based on validation datasets, with the caveats that roads and shrubland covers were overestimated (ABMI, 2010).

To compare these three datasets, I converted the ABMI dataset into a 30 m resolution raster and I reclassified the land cover types in each to the same schema. This reclassification included 7 cover classes: ‘grassland’, ‘shrubland’, ‘forest’, ‘water’, ‘wetlands’, ‘agriculture’, and ‘other’ (Table 2). All cases of reclassification were clear based on this schema. It should be expected that this more generalized classification schema should increase the accuracy of each dataset relative to their more specific categorizations (ABMI, 2010), and facilitate comparison between datasets.

Accuracy Assessment

To compare the accuracy of the three datasets, I calculated the percent cover of each of the reclassified land cover types in each of the 152 sites using the *landscapemetrics* package in R (Hesselbarth et al., 2019; R Core Team, 2024). Because each of these sites were > 90% grassland cover, accuracy would be expected to be > 90% grassland for each site on average. To compare the datasets, I averaged the percent cover of grassland across the sites for each land cover type and compared means and standard errors between datasets. I also examined the accuracy of land cover classification by the ground-truthed grassland type (native, invaded, modified, or cultivated), to determine if any of these datasets consistently identified cultivated grasslands as ‘agriculture’. I concluded that the dataset with the highest predicted cover of grassland across the validation sites was the most accurate.

Results

The 2020 ACI dataset was the most accurate grassland cover predictor in this region (Table 3; Figure 4). The ACI classified the 152 ground-truthed grassland sites as 91.8 ±

1.3% (average grassland cover ± SE) ‘grassland’ as compared to 71.6 ± 3.3% in the ABMI dataset and 40.6 ± 2.9% in the NALCMS dataset. The ACI was more accurate at identifying grasslands in this region than its published non-crop-class accuracy (92% versus 67%; AAFC, 2020), while the NALCMS was less accurate than its published accuracy (41% versus 80%; NRC, 2015) and the ABMI dataset was close to its published accuracy (72% versus 75%; ABMI, 2010).

None of the datasets consistently identified cultivated grasslands as ‘agriculture’ (Table 3; Figure 5). The ACI classified the 19 cultivated grassland sites primarily as ‘grassland’ (average cover = 63.8 ± 6.7% standard error [SE]) with a lower proportion of ‘agriculture’ (23.0 ± 7.2% SE). The ABMI classified cultivated grasslands primarily as ‘shrubland’ (39.5% ± 11.1% SE) with lower proportions of ‘grassland’ (24.6 ± 9.5% SE) and ‘agriculture’ (30.7 ± 10.7% SE). The NALCMS dataset was most accurate at identifying cultivated grasslands as ‘agriculture’ (38.8 ± 11.0% SE), but also classified high proportions of the cultivated grasslands as ‘forest’ (28.5 ± 8.2% SE) and ‘shrubland’ (25.0 ± 5.9% SE).

Conclusion

Of the three datasets examined, the ACI most accurately classified the 152 grassland validation sites as ‘grassland’ and was highly accurate in doing so. It did not, however, classify cultivated grasslands consistently as ‘agriculture’. All the ‘agriculture’ cover overlapping cultivated grasslands was originally classified as ‘pasture’ in the published ACI dataset, supporting that this classification should be considered as ‘grassland’ in the study region.

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Tables

Table 1: Dataset information. Datasets are as described in text (AAFC, 2020; ABMI, 2010; NRC, 2015)

Dataset Information	NALCMS	ACI	ABMI
Name	North American Land Change Monitoring System	Annual Crop Inventory	Alberta Biodiversity Monitoring Institute Wall to Wall Cover Inventory
Year Produced	2015	2020	2010
Citation	NRC 2015	AAFC 2020	ABMI 2010
Data Format	30 m raster	30 m raster	polygon layer converted to 30m raster for comparison
Published Land Cover Classes	19	72	11
Reclassified Land Cover Classes	7	7	7
Published Accuracy	80%	92% for agricultural cover classes, 62% for non-agricultural cover classes	75% with caveat that shrublands and roads are inflated
Geographic Extent	North America, but created separately between Canada, US and Mexico.	Southern Canada (Agricultural Areas)	Alberta
Ground-Truthing	Limited	High in Agricultural Areas	Extensive throughout

Table 2: Reclassified land cover dataset definitions.

Original Classification			Reclassified Values	
Raster Cell Value	**Name**	**Description**	**Raster Cell Value**	**Name**
2010 Alberta Biodiversity Monitoring Institute (ABMI) Wall-2-Wall Cover Inventory (ABMI 2010)				
210	Coniferous Forest	Treed areas with at least a 10% crown closure of trees, where coniferous trees (spruce, pine, fir, larch) are 75% or more of the crown closure. Providing crown closure is more than 10% and dominated by conifers, young plantations or regenerating cutblocks, and treed wetlands (e.g. black spruce bogs and fens) are included in this class providing mean tree height exceeds 2 m.	1	forest
220	Broadleaf Forest	Treed areas with at least a 10% crown closure of trees, where broadleaf trees (trembling aspen, balsam poplar and white birch) are 75% or more of the crown closure. Providing crown closure is more than 10% and dominated by broadleaf trees, young plantations or regenerating cutblocks, and treed swamps along floodplains or wetlands are included in this class providing mean tree height exceeds 2 m.	1	forest
230	Mixed Forest	Treed areas with at least a 10% crown closure of trees, where neither coniferous nor broadleaf trees account for 75% or more of crown closure.	1	forest
50	Shrubland	At least 20% ground cover which is at least one-third shrub, with no or little presence of trees (<10% crown closure). Examples of plants belonging to this class are alder, willow, juniper, and sagebrush. Shrubby fens and other non-treed woody wetlands, usually associated with floodplains and the shores of lakes and streams, belong to this class. Includes cutblocks where trees are still < 2m height, and recently burned forest areas.	2	shrubland
110	Grassland	Predominantly native grasses and other herbaceous vegetation with a minimum of 20% ground cover; may include some shrub cover (but less than a third of the vegetated area) or a few trees (but the tree cover cannot exceed 10%). Land used for range or native unimproved pasture (e.g., rough fescue) is included in this class. Alpine meadows fall into this class. Marshes and other non-woody wetlands with at least 20% vegetation cover (sedges, cattails, or moss) belong to this class. Note: A forestry cutblock harvested more than a year ago containing seedlings with less than 10% cover, belongs to this class. If the cutblock had no successful regeneration and is covered by more than 20% shrubs, it would belong to the 'Shrubland' class.	3	grassland
120	Agriculture	Annually cultivated cropland, tame pastures (fields planted or sown with non-native grasses/legumes where livestock is directly grazing on them), forage crops (same as tame pasture, but instead cut for hay) and woody perennial crops (fruit orchards and vineyards). Includes annual field crops, vegetables, summer fallow, orchards and vineyards. Bare agricultural soil (i.e., tilled) belongs to this class.	4	agriculture
20	Water	Lakes, lagoons, rivers, canals, and artificial water bodies. Shallow open water is included in this category, unless	5	water

Table 2 Continued.

Original Classification			Reclassified Values	
Raster Cell Value	**Name**	**Description**	**Raster Cell Value**	**Name**
		there is more than 20% vegetation cover, in which case it belongs to the relevant vegetated class.		
34	Developed	Urban and built-up areas (including industrial sites), impervious artificial surfaces (e.g. airport runaways), railways and roads. Acreages and farmsteads are included in this class. Oil and gas well pads are included in this class if connected to a road and not abandoned or under reclamation. Urban terrain under development is included in this class, even if the land is exposed. Urban green areas are excluded from this class if larger than 2 ha and if they have less than 2 buildings per hectare.	5	developed
31	Snow/Ice	Areas permanently covered by snow or ice, including glaciers.	7	other
32	Rock/Rubble	Bedrock, rubble, talus, blockfield, lava beds, or other natural impervious surfaces.	7	other
33	Exposed Land	Bare soil (barren, non-agricultural), river sediments and cut banks, pond or lake sediments, reservoir margins, beaches, landings, recently burned areas, mudflat sediments, surface mining, or other nonvegetated (less than 6% trees, or less than 20% shrub/herb) surfaces.	7	other
		2015 North American Land Change Monitoring System (NALCMS; NRC 2015)		
0	no value	no value	0	none
1	Temperate or sub-polar needleleaf forest	RGB 0 61 0;	1	forest
2	Sub-polar taiga needleleaf forest	RGB 148 156 112;	1	forest
3	Tropical or sub-tropical broadleaf evergreen forest	RGB 0 99 0;	1	forest
4	Tropical or sub-tropical broadleaf deciduous forest	RGB 30 171 5;	1	forest
5	Temperate or sub-polar broadleaf deciduous forest	RGB 20 140 61;	1	forest
6	Mixed forest	RGB 92 117 43;	1	forest
7	Tropical or sub-tropical shrubland	RGB 179 158 43;	2	shrubland
8	Temperate or sub-polar shrubland	RGB 179 138 51;	2	shrubland
11	Sub-polar or polar shrubland-lichen-moss	RGB 156 117 84;	2	shrubland
9	Tropical or sub-tropical grassland	RGB 232 220 94;	3	grassland
10	Temperate or sub-polar grassland	RGB 225 207 138;	3	grassland
12	Sub-polar or polar grassland-lichen-moss	RGB 186 212 143;	3	grassland
15	Cropland	RGB 230 174 102;	4	agriculture
18	Water	RGB 76 112 163;	5	water
14	Wetland	RGB 107 163 138;	6	wetland
13	Sub-polar or polar barren-lichen-moss	RGB 64 138 112;	7	other

Table 2 Continued.

Original Classification			Reclassified Values	
Raster Cell Value	**Name**	**Description**	**Raster Cell Value**	**Name**
16	Barren lands	RGB 168 171 174;	7	other
17	Urban	RGB 220 33 38;	7	other
19	Snow and Ice	RGB 255 250 255.	7	other
2020 Annual Crop Inventory (ACI; AAFC 2020)				
200	Forest (undifferentiated)	RGB 0 153 0	1	forest
210	Coniferous	RGB 0 102 0	1	forest
220	Broadleaf	RGB 0 204 0	1	forest
230	Mixedwood	RGB 204 153 0	1	forest
50	Shrubland	RGB 255 255 0	2	shrubland
110	Grassland	RGB 204 204 0	3	grassland
122	Pasture/forages	RGB 255 204 51	4	agriculture
120	Agriculture (undifferentiated)	RGB 204 102 0	4	agriculture
130	Too wet to be seeded	RGB 120 153 246	4	agriculture
131	Fallow	RGB 255 153 0	4	agriculture
132	Cereals	RGB 102 0 0	4	agriculture
133	Barley	RGB 218 227 29	4	agriculture
134	Other grains	RGB 153 204 0	4	agriculture
135	Millet	RGB 210 219 37	4	agriculture
136	Oats	RGB 209 213 43	4	agriculture
137	Rye	RGB 202 206 50	4	agriculture
138	Spelt	RGB 195 198 58	4	agriculture
139	Triticale	RGB 185 188 68	4	agriculture
140	Wheat	RGB 167 179 77	4	agriculture
141	Switchgrass	RGB 185 198 78	4	agriculture
142	Sorghum	RGB 153 153 0	4	agriculture
143	Quinoa	RGB 233 226 177	4	agriculture
145	Winter wheat	RGB 128 151 105	4	agriculture
146	Spring wheat	RGB 146 165 91	4	agriculture
147	Corn	RGB 255 255 153	4	agriculture
148	Tobacco	RGB 152 136 124	4	agriculture
149	Ginseng	RGB 121 155 147	4	agriculture
150	Oilseeds	RGB 94 162 99	4	agriculture
151	Borage	RGB 82 174 119	4	agriculture
152	Camelina	RGB 65 191 122	4	agriculture
153	Canola/rapeseed	RGB 214 255 112	4	agriculture
154	Flaxseed	RGB 140 140 255	4	agriculture
155	Mustard	RGB 214 204 0	4	agriculture
156	Safflower	RGB 255 127 0	4	agriculture
157	Sunflower	RGB 49 84 145	4	agriculture
158	Soybeans	RGB 204 153 51	4	agriculture
160	Pulses	RGB 137 110 67	4	agriculture
161	Other pulses	RGB 153 102 51	4	agriculture
162	Peas	RGB 143 108 61	4	agriculture
163	Chickpeas	RGB 182 164 114	4	agriculture
167	Beans	RGB 130 101 74	4	agriculture
168	Fababeans	RGB 163 144 105	4	agriculture
174	Lentils	RGB 184 89 0	4	agriculture
175	Vegetables	RGB 183 75 21	4	agriculture
176	Tomatoes	RGB 255 138 138	4	agriculture
177	Potatoes	RGB 255 204 204	4	agriculture
178	Sugarbeets	RGB 111 85 202	4	agriculture
179	Other vegetables	RGB 255 204 255	4	agriculture
180	Fruits	RGB 220 84 36	4	agriculture
181	Berries	RGB 208 90 48	4	agriculture
182	Blueberry	RGB 210 0 0	4	agriculture

Table 2 Continued.

Original Classification			Reclassified Values	
Raster Cell Value	Name	Description	Raster Cell Value	Name
183	Cranberry	RGB 204 0 0	4	agriculture
185	Other berry	RGB 220 50 0	4	agriculture
188	Orchards	RGB 255 102 102	4	agriculture
189	Other fruits	RGB 197 69 59	4	agriculture
190	Vineyards	RGB 116 66 189	4	agriculture
191	Hops	RGB 255 204 153	4	agriculture
192	Sod	RGB 181 251 5	4	agriculture
193	Herbs	RGB 204 255 5	4	agriculture
194	Nursery	RGB 7 249 140	4	agriculture
195	Buckwheat	RGB 0 255 204	4	agriculture
196	Canaryseed	RGB 204 51 204	4	agriculture
197	Hemp	RGB 142 118 114	4	agriculture
198	Vetch	RGB 177 149 79	4	agriculture
199	Other crops	RGB 116 154 102	4	agriculture
20	Water	RGB 51 51 255	5	water
80	Wetland	RGB 153 51 153	6	wetland
10	Cloud	RGB 0 0 0	7	other
30	Exposed land/barren	RGB 153 102 102	7	other
34	Urban/developed	RGB 204 102 153	7	other
35	Greenhouses	RGB 225 225 225	7	other
85	Peatland	RGB 80 27 80	7	other

Table 3: Accuracy of the three compared datasets showing means and standard errors (SE) for the 152 >90% grassland validation sites by cover class and grassland type. Cover classes 'Water', 'Wetland', and 'Other' are not shown. Grassland types were classified according to management and percent non-native vegetation composition where 'Native' was <30% non-native vegetation, 'Invaded' was 30-70%, 'Modified' was >70% but not actively cultivated, and 'Cultivated' was actively cultivated for harvesting non-native, agronomic grasses. Datasets are as described in the text (AAFC, 2020; ABMI, 2010; NRC, 2015).

Dataset and Grassland Type	Number of Sites	% of Sites	'Agriculture' Mean % Cover	'Agriculture' SE	'Forest' Mean % Cover	'Forest' SE	'Grassland' Mean % Cover	'Grassland' SE	'Shrubland' Mean % Cover	'Shrubland' SE
ABMI	**152**	**100**	**7.5**	**2.1**	**1.5**	**0.7**	**71.6**	**3.4**	**16.2**	**2.9**
Cultivated	19	13	30.7	10.7	0.0	0.0	24.6	9.5	39.5	11.1
Modified	48	32	9.6	4.2	0.3	0.3	64.9	6.6	23.2	5.9
Invaded	47	31	2.0	2.0	4.5	2.3	76.4	5.4	12.5	4.5
Native	38	25	0.0	0.0	0.0	0.0	97.8	1.4	0.2	0.2
ACI	**152**	**100**	**2.9**	**1.1**	**1.2**	**0.2**	**91.8**	**1.3**	**3.1**	**0.6**
Cultivated	19	13	23.0	7.2	1.5	0.6	63.8	6.7	8.6	3.4
Modified	48	32	0.0	0.0	1.7	0.5	93.1	1.5	3.3	0.9
Invaded	47	31	0.0	0.0	1.0	0.3	96.8	0.8	2.1	0.6
Native	38	25	0.0	0.0	0.6	0.4	98.0	0.8	1.3	0.7
NALCMS	**152**	**100**	**9.4**	**2.2**	**8.3**	**1.8**	**40.6**	**2.9**	**41.6**	**2.7**
Cultivated	19	13	38.8	11.0	28.5	8.2	7.7	4.5	25.0	5.9
Modified	48	32	6.3	3.1	7.7	2.9	46.4	5.5	39.4	5.0
Invaded	47	31	6.5	3.3	6.8	2.9	34.7	4.5	52.1	4.8
Native	38	25	2.2	2.2	0.9	0.4	57.0	5.7	39.8	5.4

Figures

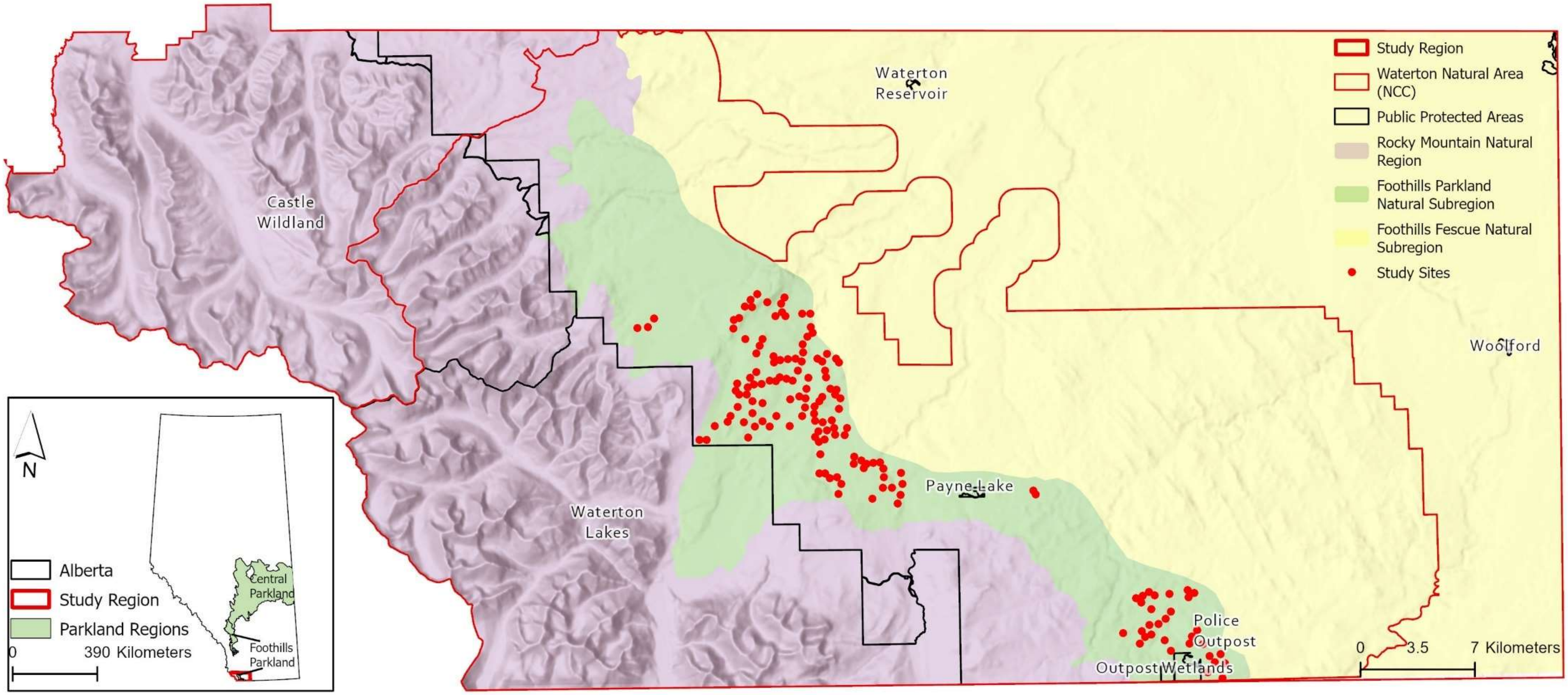


Figure 1: Overview of the 152 grassland validation sites showing Alberta Natural Region (NR) and Natural Subregion (NSR) designations (Natural Regions Committee, 2006), protected areas (Alberta, 2020), and sites for this study. Inset shows study region within Alberta, Canada. All 152 study sites were located on private land.

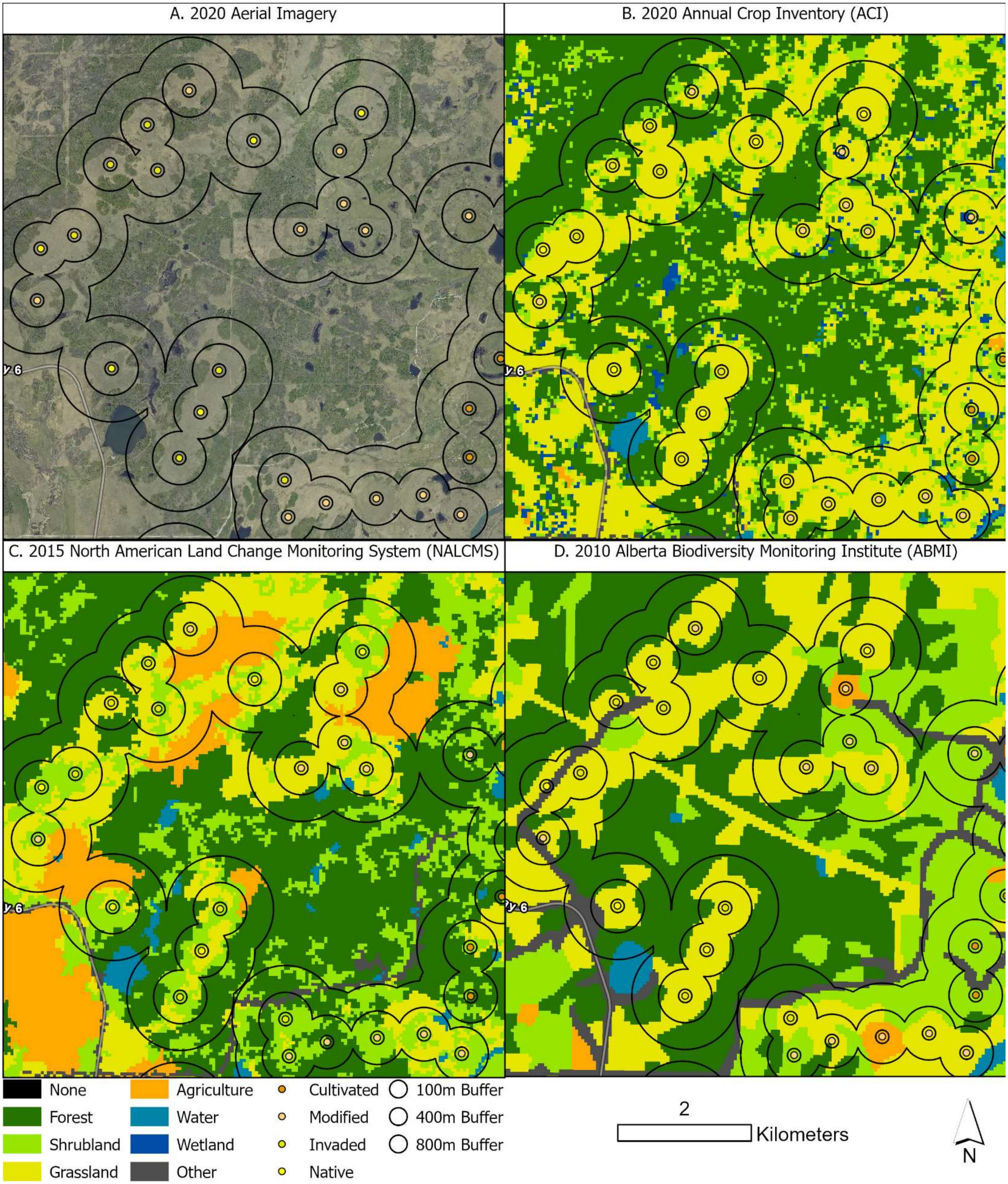
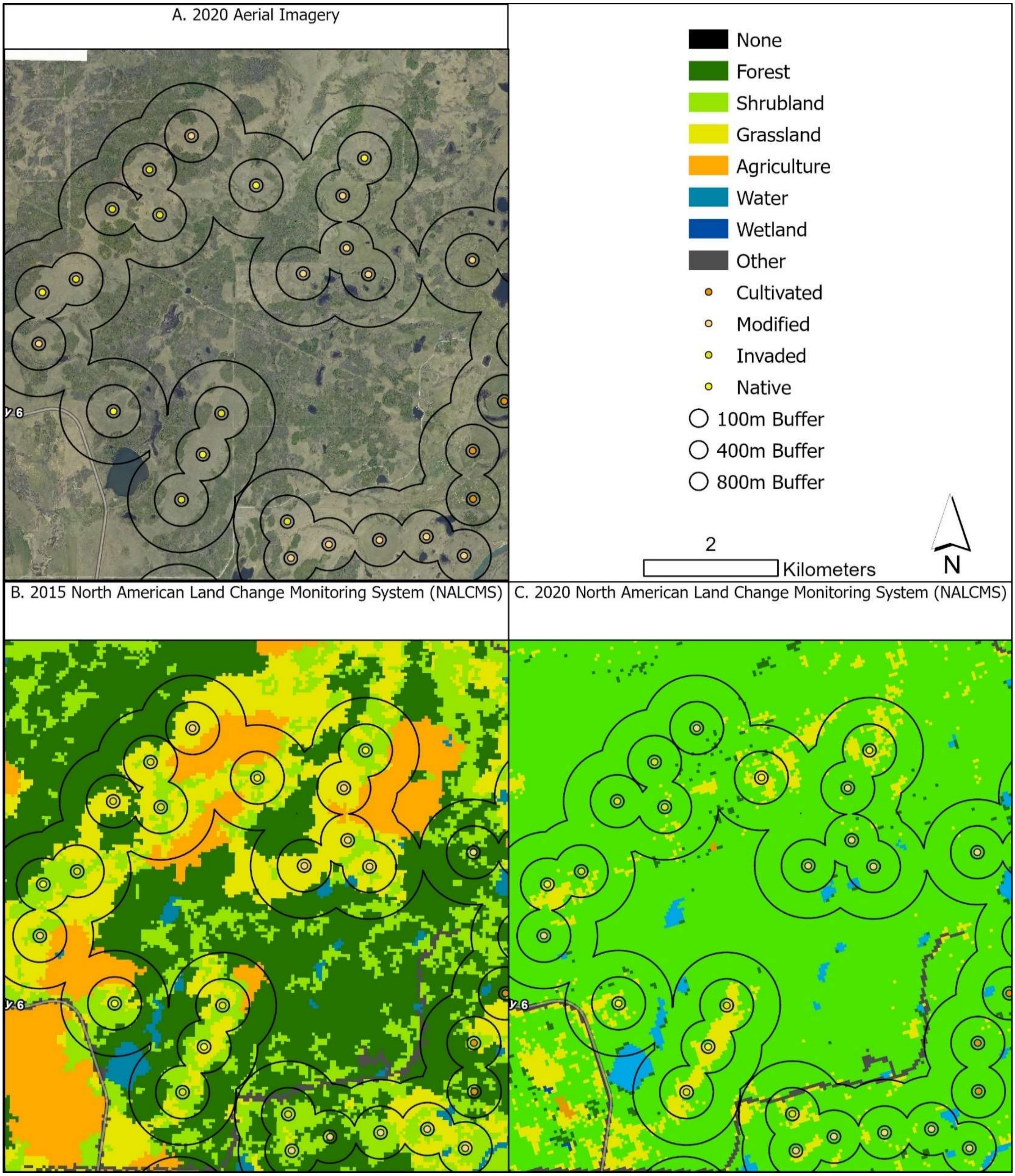

A. 2020 Aerial Imagery
B. 2020 Annual Crop Inventory (ACI)
C. 2015 North American Land Change Monitoring System (NALCMS)
D. 2010 Alberta Biodiversity Monitoring Institute (ABMI)
y 6
None
Forest
Shrubland
Grassland
Agriculture
Water
Wetland
Other
Cultivated
Modified
Invaded
Native
100m Buffer
400m Buffer
800m Buffer
2
Kilometers
N

Figure 2: Comparison of land covers by dataset using arbitrary example extent. Panel A shows aerial imagery (NCC, 2020) for comparison against raster data from the 2020 Annual Crop Inventory (AAFC, 2020; B), the 2015 North American Land Change Monitoring System (NALCMS; NRC, 2015; C), and the 2010 Alberta Biodiversity Monitoring Institute Wall-2-Wall Land Cover Inventory (ABMI, 2010; D). Study sites are visualized in a gradient from Native Grassland to Cultivated within the 100m site definition buffer (see Table 1). Dissolved buffers at 400m and 800m extents are shown to illustrate how each data set impacts interpretations of landscape structure.


A. 2020 Aerial Imagery
None
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Shrubland
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Water
Wetland
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Cultivated
Modified
Invaded
Native
100m Buffer
400m Buffer
800m Buffer
2
Kilometers
N
B. 2015 North American Land Change Monitoring System (NALCMS)
C. 2020 North American Land Change Monitoring System (NALCMS)

Figure 3: Comparison of land covers by dataset using arbitrary example extent. Panel A shows aerial imagery (NCC, 2020) for comparison against two versions of the North American Land Change Monitoring System (NALCMS; B and C; NRC 2015, 2020). Study sites are visualized in a gradient from Native Grassland to Cultivated within the 100m site definition buffer (see Table 1). Dissolved buffers at 400m and 800m extents are shown to illustrate how each data set impacts interpretations of landscape structure. This figure demonstrates how the 2020 NALCMS misclassifies both grassland and forest as 'shrubland' while the 2015 NALCMS is more accurate based on comparisons with aerial imagery.

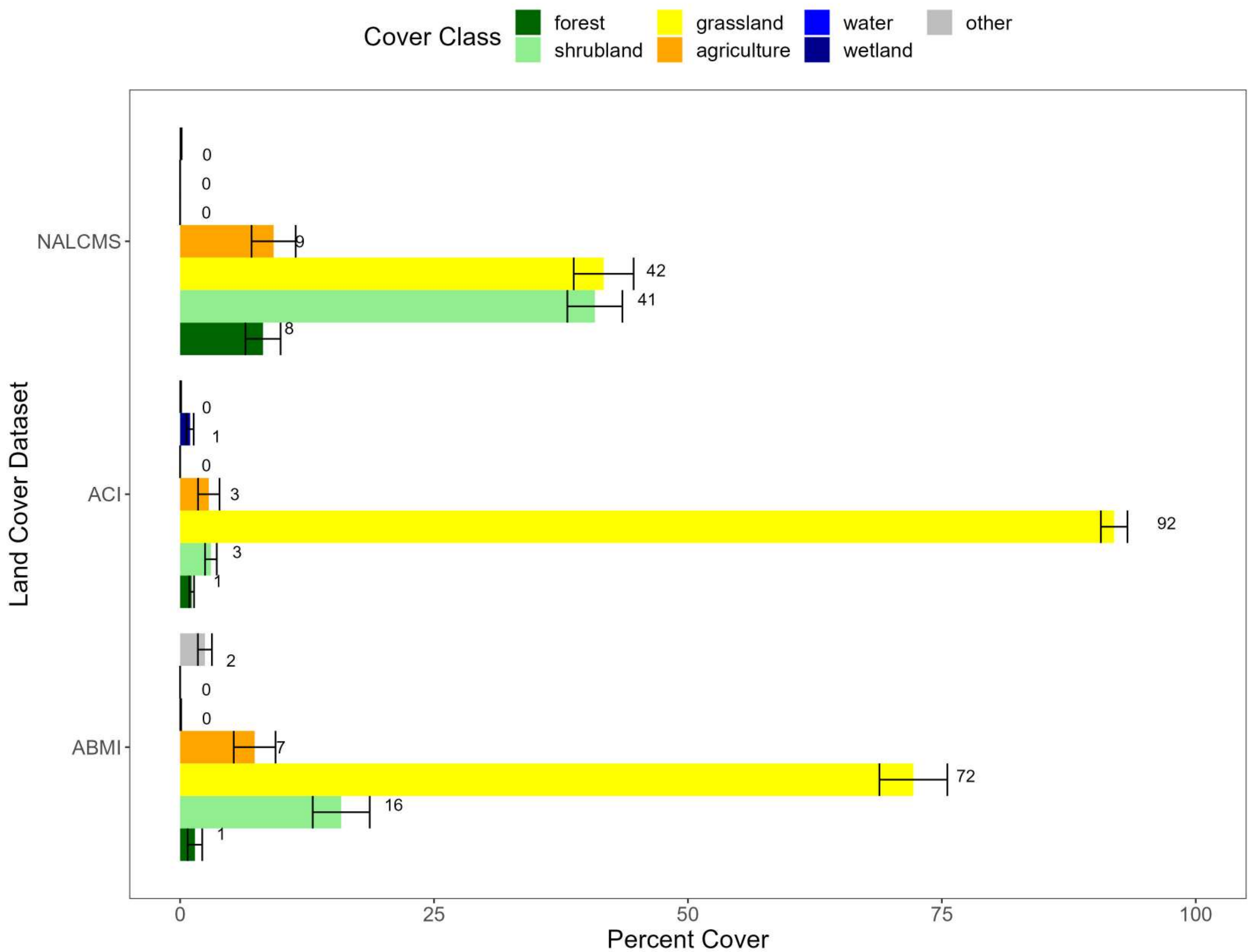

Figure 4: Mean percent cover ± 1 standard error for the 152 validation sites by reclassified land cover type and dataset. 'NALCMS' is the 2015 North American Land Change Monitoring System 30m raster (NRC, 2015), 'ACI' is the 2020 Annual Crop Inventory 30m raster (AAFC, 2020), and 'ABMI' is the 2010 Alberta Biodiversity Monitoring Institute Wall-2-Wall Land Cover Inventory 30m raster created from vectorized data (ABMI, 2010). The ACI dataset had the highest accuracy in classifying known grassland sites.

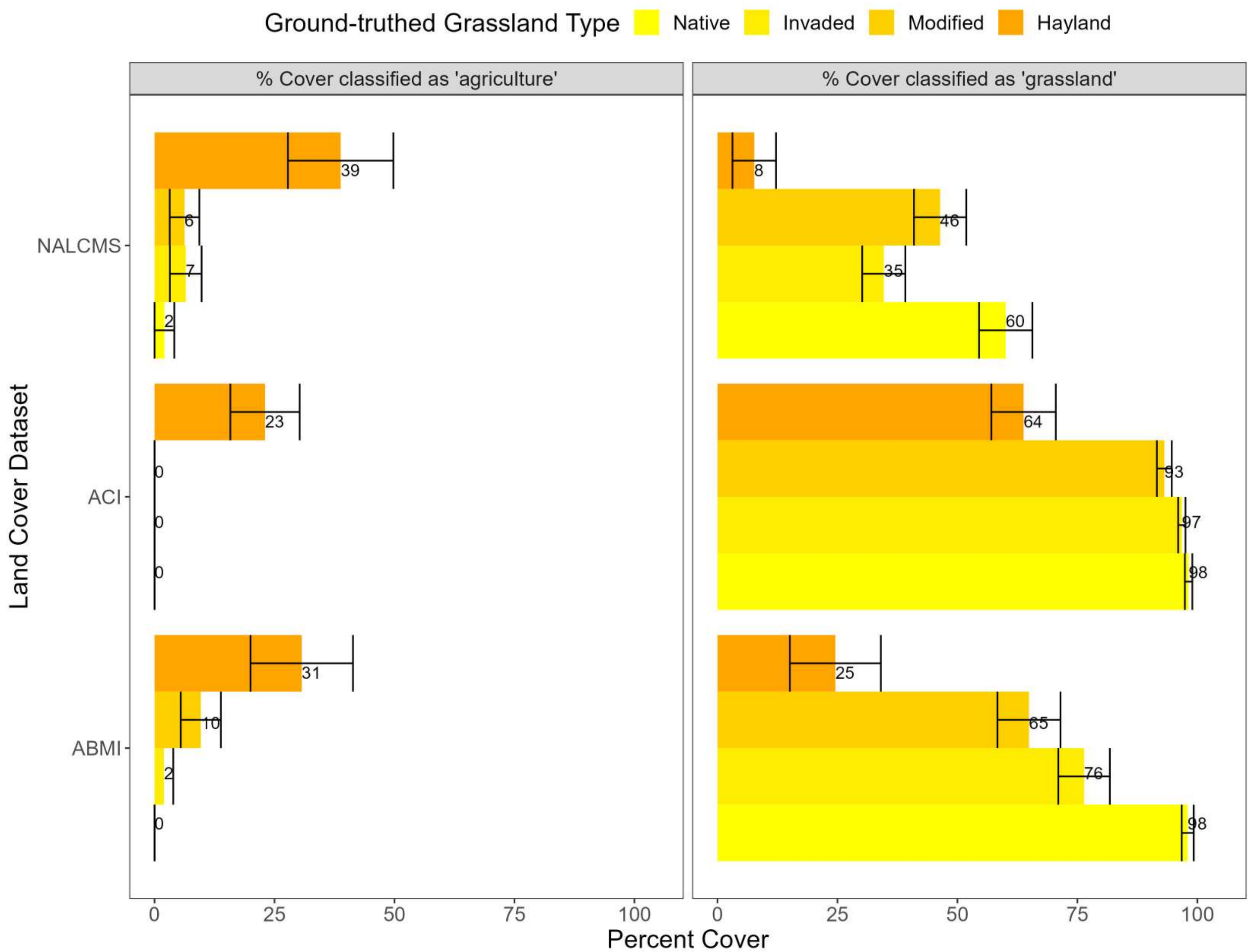

Figure 5: Mean percent cover ± 1 standard error for the 152 validation sites by reclassified land cover type ('grassland' or 'agriculture' only), dataset, and grassland type. 'NALCMS' is the 2015 North American Land Change Monitoring System 30m raster (NRC, 2015), 'ACI' is the 2020 Annual Crop Inventory 30m raster (AAFC, 2020), and 'ABMI' is the 2010 Alberta Biodiversity Monitoring Institute Wall-2-Wall Land Cover Inventory 30m raster created from vectorized data (ABMI, 2010). No datasets consistently identified 'haylands' as 'agriculture'.