

**Wildfires and climate change: their effects on moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) winter habitat in the boreal mixedwoods of Alberta, Canada**

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Wildlife Ecology and Management

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## ABSTRACT

Understanding how species respond to wildfires and climate change is fundamental for land use management and biodiversity conservation. Wildfires provide generalist ungulates, such as moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*), with high quantity and quality of winter browse. Climate change, however, is expected to reduce winter severity by creating milder winter conditions and increasing winter food availability for ungulates through changes in vegetation and fire regime.

The goal of this thesis was to investigate the effects of wildfires and climate change on moose and white-tailed deer winter forage and habitat quality in the boreal mixedwoods of northeastern Alberta, Canada. First, I examined the changes in winter browse richness, evenness, abundance, and community composition, as well as their use (browse levels) by moose and white-tailed deer, in post-wildfire upland and lowland forests over a 150-year post-wildfire period. In the summer of 2019, I collected vegetation and ungulate browsing data from 164 upland and lowland forest sites in northeastern Alberta. I used analysis of covariance (ANCOVA) and ordinal logistic regression to examine changes in browse measures. Second, I assessed the long-term effects of climate-induced wildfires and vegetation change on the distribution and quality of moose and white-tailed deer winter habitat in the boreal mixedwoods. I developed a winter habitat quality model for moose and white-tailed deer based on predicted changes in vegetation (i.e., static and fire-mediated) and fire regime (i.e., constrained and unconstrained) under an RCP 8.5 climate scenario in the 2020s, 2050s and 2080s.

Species richness and evenness peaked at both 10 – 25 years and 90 years post-wildfire in mixedwood forests, as a result of fluctuations in preferred and highly palatable browse species, while browse abundance remained constant. Black spruce and lowland forests had similar species

richness, evenness, and abundance over the 150-year chronosequence. Browse abundance in lowland forests was higher than mixedwood forests, but consisted of low palatable browse. Therefore, wildfires in boreal mixedwoods provided higher foraging availability for ungulates in upland forests for far longer than reported in other boreal forests, whereas wildfires in lowland forests do not recruit preferred winter browse species consumed by ungulates. In the absence of vegetation change, moose and white-tailed deer winter habitat is projected to remain similar to baseline conditions; thus, climate-induced wildfires will continue to provide high amounts of winter forage resulting in higher moose populations and continuous expansion of white-tailed deer populations in northeastern Alberta. However, the expansion of deciduous forests in the boreal mixedwoods in the 2050s is projected to decrease moose and white-tailed deer winter habitat quality. Deciduous forests will further provide high quantity and quality forage, but the absence of coniferous cover will result in higher wolf predation risk for moose and white-tailed deer. Finally, the transition between deciduous and mixedwood forests to grasslands in the 2080s is projected to significantly reduce winter habitat quality as moose and white-tailed deer do not have the capacity to incorporate high amount of grasses, sedges and forbs in their winter diets.

## PREFACE

This thesis is an original work by Mélanie Rachel Routh.

Chapter 2 of this thesis has been published as: Routh, M.R., and Nielsen, S.E. (2021) “Dynamic patterns in winter ungulate browse succession in the Boreal Plains of Alberta”. *Forest Ecology and Management*, 492: 119242. I contributed to the concept formation and study design, and led field data collection, data analysis, and manuscript composition. Scott E. Nielsen contributed to the concept formation, study design, data analysis, and manuscript edits.

Findings from Chapter 3 are intended for publication in *Ecological Applications* along with co-authors Scott E. Nielsen and Diana Stralberg. I contributed to the concept formation, study design, and led data analysis and manuscript composition. Scott E. Nielsen contributed to the concept formation, study design, data analysis, and manuscript edits. Diana Stralberg contributed to the study design, data analysis, and manuscript edits.

This thesis follows the formatting style of the *Journal of Wildlife Management*. No additional manuscript has been submitted for publication to date.

## ACKNOWLEDGEMENTS

I'd like to express my appreciation to my supervisor, Scott Nielsen, for the opportunity to be involved in this project. Scott is a great mentor who gave thoughtful and constructive feedback on my work, which I am grateful for. I would like to thank Diana Stralberg for her mentorship and expertise, but also for generously providing me with her previous vegetation modeling work that was used as the framework for Chapter 3. Thank you to my committee member, Evelyn Merrill, for her support during this research, as well as her expertise on deciduous shrub and sapling palatability consumed by ungulates needed for Chapter 2.

A special thank you to my field assistants who made fieldwork endurable and amusing: Ryleigh VanderSchee, Amanda Kadatz, and Aidan Sheppard. Also, thank you to Victoria Colyn and Sara Peterson for their support in the field. This project would not have been possible without their hard work and dedication in the field. They were always ready for the challenges of bushwhacking in burned areas, but most importantly, they always had a positive and excited attitude; I am beyond grateful to have had the opportunity to work with all of you.

I would like to thank Jason Fisher and Wylie Fuller for their useful advice on white-tailed deer distribution in northern Alberta, as well as Joe Silva for his comments and suggestions that improved this thesis. A special thanks to the members of the Applied Conservation Ecology (ACE) Lab who were always willing to offer advice and assistance, whether it was personal or related to the peskiest ArcGIS and R statistical issues. I will forever miss our lengthy discussions and ranting sessions in the office, which quite frankly kept me sane throughout my Master's degree!

A massive thank you to Noah Johnson. I'm so lucky and blessed to have your continuous support and reassurance. Thank you for your ability to make difficult situations much more bearable, but also to tolerate my attitude when I was stressed or when things did not go as planned.

Thank you to my sisters, Cassandra Routh and Jessica Routh, for sacrificing their time to listen to my research even though they don't understand my research project to this day. I would also like to thank my wonderful mother Chantal Brulé; your love and endless support are always close to my heart and truly appreciated. You strive to push me harder every single day and without the years of your support and dedication for my education, I don't think I would be here writing the acknowledgements section of my Master's thesis.

Lastly, this research was supported by funding and in-kind support from Natural Sciences and Engineering Research Council of Canada (NSERC) and the University of Alberta.

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## CHAPTER 1 – GENERAL INTRODUCTION

### 1.1. Anthropogenic habitat alteration in the Canadian Boreal Plains

Boreal populations of woodland caribou (*Rangifer tarandus caribou*), a species listed as ‘Threatened’ under the Canadian *Species at Risk Act* (Environment Canada 2012, COSEWIC 2014), ranges over more than 2.3 million km<sup>2</sup> of boreal forest, from the Yukon in the west to the east coast of Quebec and Labrador (Environment Canada 2012). Historically, woodland caribou spatially separated themselves from their main predators, gray wolves (*Canis lupus*) and to a lesser extent black bears (*Ursus americanus*), by selecting mature coniferous stands and peatland complexes with abundant terrestrial and arboreal lichens (Bergerud et al. 1984, James et al. 2004, McLoughlin et al. 2005); these areas supported relatively low densities of moose (*Alces alces*) (Fuller and Keith 1980, Rettie and Messier 2000, James et al. 2004). This avoidance strategy allowed woodland caribou to coexist at larger landscape scales with moose, the primary prey species of wolves, because only early successional hardwood and mixedwood forests provide sufficient browse to support higher moose densities (Peek 2007, Street et al. 2015).

Over the past century, forestry, oil and gas exploration, and other types of industrial activities have severely altered the configuration of boreal forests in the Boreal Plains of Canada (Vors et al. 2007, Schneider et al. 2010). A meta-analysis from Environment Canada demonstrated that excessive anthropogenic disturbance in woodland caribou habitat can reduce their long-term probability of persistence (Environment Canada 2012). In Alberta, woodland caribou have been extirpated from over 60% of their historic extent of occurrence (Hummel and Ray 2008). Their populations have shown gradual declines over the past 70 years (Edmonds 1988, Dzus 2001), with some populations significantly declining since the early 2000s (McLoughlin et al. 2003, Hervieux

et al. 2013). As a result, extirpation of woodland caribou from Alberta is predicted over the next 10 to 70 years based on current population sizes and rates of decline (Schneider et al. 2010).

These constantly changing patterns of anthropogenic land use have disrupted the historical caribou–moose–wolf system in synergistic ways. First, the combination of increased small patch sizes, edge effects, and linear disturbances (Courbin et al. 2014, Pickell et al. 2015) associated with forestry activities, as well as reduced human harvest of ungulates by First Nations communities (Serrouya et al. 2011), have created more early-successional areas that favour higher density of moose and white-tailed deer (*Odocoileus virginianus*) within woodland caribou range (Bergerud 1988, Cumming 1992, James et al. 2004, Serrouya et al. 2011). Although moose and white-tailed deer do not directly compete with woodland caribou for forage and space, the increase in primary prey density for wolves has created greater spatial overlap between wolves and woodland caribou (Kuzyk et al. 2004, Dawe 2011, Latham et al. 2011b, 2013, Peters et al. 2013). Ultimately, increases in moose and white-tailed deer have led to increases in wolf populations, as predators are numerically supported by total ungulate biomass (Fuller et al. 2003), and thus unsustainable levels of predation on woodland caribou (Fuller 1989, Seip 1992, McLoughlin et al. 2005, Wittmer et al. 2005, Latham et al. 2011a). This predator-prey relationship is a form of apparent competition (Holt 1977), generally referred to as ‘habitat- or disturbance-mediated apparent competition’ (DeMars et al. 2019), and it is now the main proximate cause of woodland caribou population declines in northern Alberta (Bergerud 1974, Festa-Bianchet et al. 2011).

Secondly, linear disturbances, such as roads, railways, transmission lines, pipelines, and seismic lines, are an ubiquitous form of landscape disturbance associated with oil and gas exploration in northern Alberta (Pattison et al. 2016), where they occur at densities as high as 50 km/km<sup>2</sup> (Stern et al. 2018). Many studies have shown avoidance of linear disturbances by

woodland caribou within their range (James and Stuart-Smith 2000, Dyer et al. 2001, DeCesare et al. 2012, Mumma et al. 2017, DeMars and Boutin 2018); and most populations in northern Alberta continue to decline as they are exposed to >90% industrial footprint on some ranges (Sorensen et al. 2008). Although individuals have learned to avoid linear disturbances, peatlands no longer provide woodland caribou the necessary predation refuge from wolves (Dyer et al. 2001, James et al. 2004). A number of studies have shown that wolves frequently use linear disturbances, especially in areas with low human activities (James and Stuart-Smith 2000, Whittington et al. 2005, Hebblewhite and Merrill 2008). Linear disturbances are increasing caribou-wolf encounters by enhancing the hunting efficiency of wolves (Mckenzie et al. 2012, Dickie et al. 2017). Researchers have demonstrated that wolves use linear features to increase their daily movement rates and daily travel distances, therefore increasing their instantaneous search and kill rate (Whittington et al. 2011, DeCesare 2012). Several explanations have been used to justify these trends, mainly that linear features are enhancing wolf line-of-sight allowing more visual encounters and wolf olfactory encounters with fresh woodland caribou tracks, increasing wolf travel speeds, and altering the orientation of wolf movements thereby including a greater proportion of woodland caribou habitat in hunting forays (Latham 2009). Consequently, wolves are more likely to encounter woodland caribou, increasing wolf predation on this ungulate (James and Stuart-Smith 2000, Latham et al. 2011*b*, Whittington et al. 2011, DeCesare 2012).

Overall, there is considerable evidence that anthropogenic disturbance has led to disturbance-mediated apparent competition between moose, white-tailed deer, and woodland caribou in the Boreal Plains of Alberta (Courtois et al. 2007, Festa-Bianchet et al. 2011, Latham et al. 2011*b*, DeMars et al. 2019, Fryxell et al. 2020). Yet, researchers have paid less attention to the role of wildfires in the creation of deciduous browse capable of supporting higher densities of



moose and white-tailed deer, particularly in areas where both wildfires and anthropogenic disturbances are responsible for changes in landscape configuration.

## **1.2. Ungulate responses to boreal wildfires in the absence of anthropogenic disturbances**

The interactions between woodland caribou, moose, and white-tailed deer, are a key focus for the conservation and management of northern Alberta's boreal forests. Woodland caribou are considered a disturbance-sensitive species (Courtois et al. 2007) as they respond negatively to post-wildfire stands by avoiding early successional forests within their home range (Schaefer and Pruitt 1991, Dalerum et al. 2007, Faille et al. 2010, Lafontaine et al. 2019). Early successional forests are considered suboptimal habitat for woodland caribou as a result of poor foraging availability of terrestrial and arboreal lichens (Schaefer and Pruitt 1991, Dunford et al. 2006) and increased predation risk from wolves (Courtois et al. 2007, Courbin et al. 2013). In fact, lichens are destroyed by moderate to high severity wildfires, and often need approximately 20 to 40 years to fully recover from pre-disturbance conditions (Morneau and Payette 1989, Silva et al. 2019). Also, significant tree mortality from wildfires can impede woodland caribou movement through early successional forests and increase their energetic costs (Schaefer and Pruitt 1991). Nevertheless, it is important to note that recent studies demonstrate that wildfires may have little to no effect on woodland caribou demography, habitat selection, and population viability as woodland caribou rarely encounter recent burns ( $\leq 5$  years post-wildfire) within their home range (Dalerum et al. 2007, Johnson et al. 2020, Silva et al. 2020).

On the other hand, moose respond positively to increases in early successional post-wildfire habitat in upland forests as wildfires increase the productivity, quality, and quantity of their preferred browse, young trees and seral shrubs (Spencer and Hakala 1964, Peek 1974a, MacCracken and Viereck 1990, Loranger et al. 1991, Weixelman et al. 1998, Maier et al. 2005,

Lord and Kielland 2015, Joly et al. 2016). Although wildfires provide greater woody browse production within the first 50 years post-wildfire (LeResche and Bishop 1974, Kashian et al. 2005), moose forage availability is maximized 15–20 years post-wildfire in upland forests (Spencer and Hakala 1964, Maier et al. 2005). Fire severity is also another important factor – moose can consume a higher proportion of available browse following high severity burns because they produce over 3 times more forage than low severity burns (Lord and Kielland 2015).

In contrast with uplands, several authors have suggested that post-wildfire trajectories in lowlands do not increase preferred browse for moose (MacCracken and Viereck 1990, Brown et al. 2018), which explains why moose avoid lowlands across the boreal forest (James et al. 2004, DeMars et al. 2019). However, a recent study found that post-wildfire shrub abundance was higher in lowlands than uplands, suggesting that wildfires would increase preferred browse for moose (Mallon et al. 2016). The response of moose to wildfires is therefore likely to differ between uplands and lowlands, however, the magnitude of these differences is still unclear. One major question is whether wildfires in uplands would promote increases in moose activity in adjacent lowlands regardless of whether or not lowlands had burned. This question is especially relevant in areas that have experienced anthropogenic disturbances and increases in climate-induced wildfires.

Natural and anthropogenic disturbances aside, climate change has altered in the historical caribou–moose–wolf system in northern Alberta. Over the last half of the 20<sup>th</sup> century, white-tailed deer have been expanding their northern distribution into the boreal forest of Alberta, and the Northwest Territories (Webb 1967, Veitch 2001). Recent warmer winters are believed to have contributed this range expansion (Côté et al. 2004, Dawe 2011, Dawe and Boutin 2016). In northeastern Alberta, white-tailed deer populations have increased 17.5-fold since the 1990s due to both natural and anthropogenic disturbances; they also respond positively to early successional

post-wildfire forests (Vogl and Beck 1970, Latham et al. 2011*b*). Winter severity is considered the most important factor limiting white-tailed deer distribution in northern Alberta, however, anthropogenic disturbances have significantly increased their presence in these regions (Dawe et al. 2014, Fisher et al. 2020*a*). Overall, white-tailed deer dynamics in the boreal forest of northern Alberta are influenced by both landscape changes across space and winter severity through time. Consequently, woodland caribou have increased by 10-fold in the annual wolf diet since the white-tailed deer invasion in the 1990s, while moose have decreased by 3.44-fold, therefore replacing moose as the primary prey species (James et al. 2004, Latham et al. 2011*b*, 2013). Yet, little attention has been devoted to studying the impacts of this invasion and population increase, despite its potential importance (Latham et al. 2011*b*, 2013, Dawe et al. 2014, Fisher et al. 2020*a*).

### **1.3. Current and future changes in the Canadian boreal wildfire regime**

Wildfires are the main stand-replacing natural disturbance in the boreal forest of North America (Johnson 1992, Payette 1992). Between 2009 and 2018, an estimated 257,000 ha of forest was burned by wildfires annually in Alberta (National Forestry Database 2019). Wildfires play an important role in forest nutrient cycling by removing vegetation and organic matter through combustion (Grier 1975, Boerner 1982, Certini 2005), thus altering vegetation community composition and productivity (Reich et al. 2001, Thornley and Cannell 2004, Goulden et al. 2011). As a result, boreal animal species are adapted to specific successional stages as wildfires influence the structure and dynamics of communities, altering competition and predation (Halpern 1989).

Recent anthropogenic-driven climate change has increased the frequency and extent of moisture deficits in the western boreal forest of North America (Peng et al. 2011), leading to more frequent and larger wildfires (Kasischke and Turetsky 2006, Abatzoglou and Williams 2016). The boreal landscape post-wildfire is currently composed of a higher proportion of early successional

stands, resulting in more deciduous tree and shrub species colonizing these areas that were previously dominated by black spruce (*Picea mariana*), white spruce (*P. glauca*), or jack pine (*Pinus banksiana*) (Lord and Kielland 2015). This shifting vegetation mosaic will ultimately affect the habitat selection of moose and white-tailed deer, as well as their winter foraging.

Recent observations of increased fire frequency and intensity has resulted in forest ecosystem shifts towards a higher composition of deciduous stands that is expected to continue under a warming climate (Flannigan et al. 2005). It is predicted that the area burned could increase as much as five times by the end of the 21<sup>st</sup> century (Boulanger et al. 2014). Given that larger fires tend to be more severe, the average fire severity is also likely to increase (Duffy et al. 2007). Extreme fire-weather days, length of the fire season, fire ignition events, and daily fire spread are other elements of the fire regime that are expected to increase with future climate change (Flannigan et al. 2009, Wang et al. 2015, 2017). As a result, it is predicted that anthropogenic warming and increased drought frequency will lead to widespread conversion of vegetation types as the boreal forest progressively becomes drier (Mbogga et al. 2010, Stralberg et al. 2018). For example, mesic upland mixedwood forests will shift from conifer-dominated to deciduous-dominated stands with warmer temperatures and increased wildfire frequency (Johnstone et al. 2010b). High severity wildfires favour the recruitment and establishment of deciduous shrub and tree seedlings (Johnstone and Chapin 2006), which persist for several decades with further shifts from conifer-dominated to deciduous-dominated forests (Shenoy et al. 2011).

Simulation studies suggest that climate change will accelerate the shift in boreal forest vegetation, leading to a younger forest mosaic characterized by higher abundance and diversity of deciduous trees and shrubs (Stralberg et al. 2018). These predicted changes in forest composition and age structure towards greater production of deciduous browse will be advantageous to moose

and white-tailed deer populations and a disadvantage to woodland caribou. Thus, a better understanding of the spatiotemporal succession of shrubs post-wildfire is important for informing the conservation and management of ungulate habitat, especially through changes mediated by both fire regimes and climate change.

#### **1.4. Research objectives**

Under the *National Recovery Strategy* and *Woodland Caribou Policy for Alberta*, alternate prey (i.e. moose and white-tailed deer) management was identified as a key component for achieving the recovery of threatened woodland caribou populations (Government of Alberta 2011, Environment Canada 2012). Understanding the mechanisms explaining current alternate prey distribution is essential in determining the most efficient solution to manage their populations (DeCesare et al. 2010). However, browse species for moose and white-tailed deer have not been studied intensively in areas where both wildfires and anthropogenic disturbances are responsible for changes in landscape configuration and in particular how it relates to limitations in winter forage. This thesis will address this knowledge gap by assessing the successional trajectories of moose and white-tailed deer winter browse in both uplands and lowlands, as well as ungulate response to these changes in winter browse communities (Chapter 2). These data will allow me to evaluate the effects of projected fire weather, fire regime, and fuels under high climate forcing scenarios on the abundance and quality of ungulate winter habitat (Chapter 3). Failure to address the bottom-up effects of habitat alteration on alternate prey populations may contribute to continuous long-term woodland caribou population declines in northern Alberta. Together, these research questions will provide useful information on knowledge gaps of interest to other academics, land use stakeholders, and government necessary for reducing alternate prey species populations and stabilizing declining woodland caribou populations in northern Alberta.

## CHAPTER 2 – DYNAMIC PATTERNS IN WINTER UNGULATE BROWSE SUCCESSION IN THE BOREAL PLAINS OF ALBERTA

### 2.1. Abstract

Wildfires are a key driver of boreal forest structure and community composition that alter food resources affecting the behaviour and ecology of wildlife. In the first 50 years post-wildfire, woody browse availability in upland forests increase in quantity and quality for generalist ungulates, such as moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*). Greater favorable habitat for these generalist ungulates results in increases to their respective populations, and through apparent competition, leads to increases in wolf populations; thus, causing unsustainable levels of predation on threatened woodland caribou (*Rangifer tarandus caribou*) populations. However, the duration of post-wildfire browse availability is not well understood in the Boreal Plains of Alberta as previous studies are primarily from the Taiga and Boreal Shield where vegetation communities are structurally different. This study examines the changes in winter browse richness, evenness, abundance, and community composition, as well as their use (browse levels) by moose and white-tailed deer, over a 150-year post-wildfire period. In the summer of 2019, I collected vegetation and ungulate browsing data from 164 upland and lowland forest sites in northeastern Alberta, Canada. I used analysis of covariance (ANCOVA) and ordinal logistic regression to examine changes in browse measures. Species richness and evenness showed a double peak at 10 – 25 years and 90 years post-wildfire in mixedwood forests, as a result of fluctuations in browse palatability, while browse abundance was constant. In contrast, black spruce and lowland forests had similar species richness, evenness and abundance over the 150-year chronosequence. However, browse abundance in lowland forests was higher than mixedwood forests, but this consisted of low palatable browse. Browsing was significant in jack pine forests, mixedwood forests and poor fens; coniferous saplings were generally avoided, whereas 35 to 65%

of available deciduous saplings were browsed. Understanding post-wildfire succession and ungulate browsing in post-wildfire forests provides useful information for managing alternative prey populations necessary for long-term woodland caribou conservation.

## **2.2. Introduction**

Over the last 90 – 125 million years, wildfires have played a major role in the life-history strategies used by trees (He et al. 2012) and thus regulating biodiversity and ecological processes in fire-prone ecosystems, including the boreal forest of North America (Pausas and Keeley 2009). Plant diversity in fire-prone systems is often highest post-wildfire, with some ecosystems reaching a peak faster than others, due in part to differences in post-wildfire successional pathways dictated by both animal habitat preferences and the lifespan of native plants (He et al. 2019). In the southern parts of the boreal forest of Canada, successional pathways of upland forests are characterized as following the initial floristic composition model given post-wildfire regeneration strategies of serotiny (coniferous species), root suckering (broadleaf species), and wind-dispersal (Bergeron et al. 2014). Typically, early successional mixedwood stands are dominated by broadleaf shade-intolerant species, such as trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and paper birch (*Betula papyrifera*), and in some cases by shade-tolerant coniferous species, such as white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*) (Bergeron et al. 2014). Pre-wildfire coniferous stands, such as jack pine (*Pinus banksiana*) stands found in well-drained upland forests and black spruce (*Picea mariana*) stands found in poorly drained upland and lowland forests, have serotinous cones that are stimulated by wildfires; thus, these post-wildfire stands are characteristically self-replacing (Ilisson and Chen 2009a). In both cases, burned stands are gradually replaced by coniferous species over time, including black spruce, white spruce, jack pine, and balsam fir (Johnstone et al. 2010a, Bergeron et al. 2014).

Understory richness, biomass and productivity is also highest in early succession (Bond-Lamberty et al. 2002, Mack et al. 2008, Mallon et al. 2016). As a result, animals' responses to post-wildfire communities differ as a consequence of either enhanced food resources, reduced predation risk, or modified microclimate (Pausas and Parr 2018). The latter is especially true in the northwestern boreal forest of Canada, where moose (*Alces alces*), woodland caribou (*Rangifer tarandus caribou*), and recently white-tailed deer (*Odocoileus virginianus*), coexist and interact within a fire-dominated landscape. Early successional forests (10 – 35 years post-wildfire) can support higher moose densities, and theoretically higher white-tailed deer densities, because higher quality and quantity of their preferred browse, young trees and seral shrubs, are available (Spencer and Hakala 1964, Peek 1974a, MacCracken and Viereck 1990, Loranger et al. 1991, Weixelman et al. 1998, Maier et al. 2005, Lord and Kielland 2015, Joly et al. 2016). Moose and white-tailed deer are considered “generalist” browsers as they ingest moderate amounts of a wide variety of plant species, in contrast with “specialist” browsers which ingest high amounts of only a few plant species (McArthur et al. 1991).

Moose typically browse plants under 2.5 metres in height (Telfer 1974). They consume the foliage and twigs of deciduous and evergreen shrubs year-round, but their winter diet consists exclusively of twigs from deciduous shrubs and saplings (Nowlin 1978). In fact, moose can consume up to 221 plant species and/or genera in their annual diet (see Table 6 in Renecker and Schwartz 2007 for more details), but they usually eat high quantities of only a few of these species. Principal forage consumed by moose in North America by genera are willow (*Salix* spp.), birch (*Betula* spp.), and poplar (*Populus* spp.) (Peek 1974a, Renecker and Schwartz 2007). Nonetheless, moose will consume, less preferably, the following genera: maple (*Acer* spp.), dogwood (*Cornus* spp.), serviceberry (*Amelanchier* spp.), mountain-ash (*Sorbus* spp.), cherry (*Prunus* spp.), hazelnut



(*Corylus* spp.), viburnum (*Viburnum* spp.), and alder (*Alnus* spp.) (Peek 1974a, Renecker and Schwartz 2007). Coniferous tree species, such as balsam fir, subalpine fir (*Abies lasiocarpa*), Canada yew (*Taxus canadensis*), and Pacific yew (*Taxus brevifolia*), are also part of the moose diet, particularly in the winter, but they are generally not preferred and will only be consumed when hardwood availability or quality is low (Peek 1974a, Raymond et al. 1996, Newbury et al. 2007).

White-tailed deer are classified as concentrate selectors (Hofmann 1989) and browse plants under 1.5 metres in height (Miller et al. 2003). They consume the foliage and stems of deciduous shrubs, evergreen shrubs, deciduous trees, coniferous trees, forbs, and grasses, as well as hard mast (nuts and pods) and soft mast (fruits and berries) of trees and shrubs (Hewitt 2011). White-tailed deer can forage up to 100 plant species annually, but typically only a dozen species are selected in any one season (Nixon et al. 1970, Korschgen et al. 1980). Detailed information of white-tailed deer diet in the boreal forest is only available in eastern North America, more specifically in the hemi-boreal region of the Northern Great Lakes in Minnesota, United States. Within that region, preferred white-tailed deer browse are alternate-leaf dogwood (*Cornus alternifolia*), American mountain-ash (*Sorbus americanus*), eastern hemlock (*Tsuga canadensis*), eastern white cedar (*Thuja occidentalis*), and red maple (*Acer rubrum*) (Blouch 1984). Principal foods are balsam fir, beaked hazelnut (*Corylus cornuta*), eastern white pine (*Pinus strobus*), jack pine, mountain maple (*Acer spicatum*), northern red oak (*Quercus rubra*), paper birch, red pine (*Pinus resinosa*), saskatoon (*Amelanchier alnifolia*), trembling aspen, and yellow birch (*Betula alleghaniensis*) (Blouch 1984). On rare occasions, white-tailed deer can forage on speckled alder (*Alnus incana* subsp. *rugosa*), tamarack (*Larix laricina*), and white spruce as “last resort” browse (Blouch 1984).

Despite the vast literature on the effects of wildfires on moose habitat selection and foraging ecology, the duration of post-wildfire browse availability for moose and white-tailed deer is not well understood in the Boreal Plains of Canada's western boreal forest. Previous studies of browse in the boreal forest are primarily from interior Alaska, Kenai Peninsula of Alaska or central Newfoundland where anthropogenic disturbances are sparse to absent and vegetation communities are structurally different. Additionally, no studies to this date have looked at the foraging ecology of expanding white-tailed deer in the boreal forest.

The goals of this study are to improve our understanding of ungulate (moose and white-tailed deer) winter browse succession and relative use in post-wildfire upland and lowland forests in the Boreal Plains of northeastern Alberta, Canada. This study investigated winter browse as opposed to spring, summer and fall browse because northern ungulates undergo periods of negative energy balance in winter (Dumont et al. 2005) as they cannot meet their energy requirements from ingestion of woody browse (Ullrey et al. 1970, Mautz et al. 1976). Specifically, I am interested in: (1) examining changes in winter browse (deciduous shrubs and saplings) richness, evenness, abundance, and community composition consumed by ungulates, (2) determining the trajectory of winter browse, stratified by palatability, consumed by ungulates, (3) examining changes in ungulate relative use of winter browse using evidence of browsing (percentage and severity), and (4) determining ungulate relative winter diet using evidence of browsing (percentage and severity) in the first 150 years post-wildfire using a space-for-time substitution method. As a result, this chapter is divided into two sections; the first section examines winter browse succession (hereafter "Winter Browse Succession"), while the second section investigates the relative use of these browse species by ungulates (thereafter "Winter Use").

I hypothesized that wildfires increase early seral recruitment of winter browse in upland forests and promote changes in relative use of deciduous shrubs and saplings for ungulates, which maintain moose habitat and promote expansion of white-tailed deer. I predicted that: (1) early seral successional stands ( $\leq 30$  years post-wildfire) will have higher deciduous shrub and sapling richness and abundance than older successional stands ( $\geq 31$  years post-wildfire), (2) early seral upland stands will have higher deciduous and sapling richness and abundance than lowland forests, (3) early seral successional stands will have higher abundance of desirable palatable (i.e. preferred and high palatability) winter browse than older successional stands, (4) early seral upland stands will have higher abundance of desirable palatable winter browse than lowland forests, and (5) early seral successional stands will have higher relative browse use than older successional stands.

A recent study by DeMars et al. (2019) tested the prediction that moose respond positively to burns ( $\leq 40$  years post-wildfire) within and outside of woodland caribou range in Alberta and British Columbia. The authors found that moose avoided lowland forests presumably because they do not provide enough forage. However, the authors did not directly measure forage (browse), and its responses to wildfires in lowland forests within an area with different levels of anthropogenic disturbances. If the post-wildfire trajectory of burned lowland forests (peatlands) are to return to lowland forests (Johnstone et al. 2010a), then there should be insufficient winter forage to alter moose (and subsequently white-tailed deer) spatial avoidance towards lowland forests. In contrast, there are suggestions that wildfires in the southern portions of the boreal forest may be altering successional trajectories towards more upland-like conditions with recruitment of woody species that would benefit moose and white-tailed deer (Johnstone et al. 2010a, Stralberg et al. 2018, Frelich et al. 2020, Wang et al. 2020). I tested these hypotheses by examining whether: (1) early seral lowland forests recruited winter browse species consumed by moose and white-tailed deer,

and (2) there was evidence of browsing from moose and white-tailed deer in early seral lowland forests. If lowland forests are resilient post-wildfire there would be no evidence for recruitment of additional browse species and thus little evidence of browsing.

### **2.3. Study Area**

This research was conducted in the Lower Athabasca Region (LAR) south of Lake Athabasca in northeastern Alberta, Canada (Figure 2.1). This area encompasses 81,162 km<sup>2</sup> of boreal upland forest and lowland complex; including the Athabasca Plain in the northeast, parts of the Birch Mountains in the northwest, Stony Mountain in the centre, and the Lakeland and Cold Lake areas in the south. Elevation ranges from approximately 200 m along the Athabasca River to 868 m in the Birch Mountains (Natural Regions Committee 2006). The LAR is characterized by a rolling upland forest mosaic, dominated by trembling aspen, balsam poplar, and white spruce (Natural Regions Committee 2006). Shrubs typically grew up to 1.5 m in height in upland forests, but occasionally alders, willows, pin cherry (*Prunus pensylvanica*), and chokecherry (*Prunus virginiana*) grew to 5 m in height (Harper and Macdonald 2001, Guo et al. 2017). Common deciduous shrubs included prickly wild rose (*Rosa acicularis*), saskatoon, currants (*Ribes* spp.), wild red raspberry (*Rubus idaeus*), lowbush cranberry (*Viburnum edule*), common blueberry (*Vaccinium myrtilloides*), and Labrador tea (*Ledum groenlandicum*) (Harper and Macdonald 2001). Uplands were interspersed with extensive lowlands of bogs, treed fens, shrubby fens, and sedge fens (Natural Regions Committee 2006). Black spruce and tamarack were the dominant tree species in lowland forests. Understory vegetation, including shrubs that can reach up to 5 m in height for some species (Moss 1983, Guo et al. 2017), consisted mainly of Labrador tea, peat moss (*Sphagnum* spp.), sedges (*Carex* spp.), bog birch (*Betula pumila*), willows, and several species of lichens (e.g.: *Cladina* spp. and *Peltigera* spp.) (Bradshaw et al. 1995). Conversely, the Athabasca

Plain was characterized by jack pine forests occurring on dry, well-drained sandy soils (Natural Regions Committee 2006). Understory vegetation consisted mainly of bryophytes (e.g.: *Ceratodon purpureus* and *Polytrichum piliferum*) and lichens from the genus *Cladina*, but occasionally shrubs that can reach up to 0.5 m in height were present, notable common blueberry, bearberry (*Arctostaphylos uva-ursi*), and woolly beach-heather (*Hudsonia tomentosa*) (Pinno and Errington 2016).

The climate in the LAR is characterized as dry continental with long cold winters and short warm summers with mean temperatures ranging from 17.1°C and -17.4°C (Environment Canada 2019). Mean annual precipitation was 419 mm, through which 60% was received in the growing season (Environment Canada 2019). Average snow depth between November and March was 22 cm, but reached a maximum of 30 cm in February (Environment Canada 2019).

Large, infrequent, and intense wildfires are the main stand-replacing natural disturbance in the LAR (Kasischke and Turetsky 2006, Erni et al. 2020). Approximately 42,077 km<sup>2</sup> (51.84%) of the region has burned within the past 48 years (1970 – 2018; Routh 2021, unpublished data), and the fire return interval is estimated between 59–180 years (Larsen 1997, De Groot et al. 2013). Yet, 8.2% of the LAR is designated as agriculture, forest harvesting, oil and gas exploration, and other rural and industrial activities (Campos-Ruiz et al. 2018). Oil and gas exploration are a significant economic activity, as the LAR includes a significant portion of the Athabasca Oil Sands area (Government of Alberta 2012). Linear disturbances, mainly roads and seismic lines that consist of 2 – 8 m wide clear-cut lines, make up 0.36% and 0.70% of the anthropogenic disturbances in the LAR, and reach densities of 0.5 km/km<sup>2</sup> and 1.49 km/km<sup>2</sup>, respectively (Schneider et al. 2010, Campos-Ruiz et al. 2018). Forestry is the second most significant economic development in the LAR with 2.61% of the land harvested (Campos-Ruiz et al. 2018).

Moose, white-tailed deer, and woodland caribou occur throughout most of the LAR, whereas elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) occurred at very low densities in only the southern part of the study area (Latham 2009). Based on ungulate aerial survey locations conducted by the Government of Alberta from 2013 to 2018, moose density and white-tailed deer density ranged from 0–0.13 moose/km and 0–3.06 deer/km, respectively (Government of Alberta 2020). While historically wolves occurred at low densities (0.6 wolves/100 km<sup>2</sup>; Fuller and Keith 1980), the population was recently estimated at 0.77–1.15 wolves/100 km<sup>2</sup> (Latham et al. 2011b, Burgar et al. 2019). In addition to these species, beavers (*Castor canadensis*), snowshoe hares (*Lepus americanus*), black bears (*Ursus americanus*), Canada lynx (*Lynx canadensis*), red foxes (*Vulpes Vulpes*), and coyotes (*Canis latrans*) were present in the study area (Latham et al. 2011b, Burgar et al. 2019).

## **2.4. Methods**

### *2.4.1. Study design*

A total of 164 field plots were surveyed between June 1 and August 19, 2019. Prior to field data collection, I used a factorial sampling design, where field plot locations were preselected based on drainage class (upland and lowland), landcover type (upland: jack pine, black spruce and mixedwood forests; lowland: bogs, rich and poor fens), and stand age (young: 0 – 30 years; intermediate: 31 – 70 years; mature: ≥71 years). Specifically, drainage class and landcover type were determined using the Ducks Unlimited Canada Enhanced Wetland Classification (Ducks Unlimited Canada 2018), while stand age was derived from wildfire polygons from the Spatial Wildfire Data (1931 – 2018) by Alberta Wildfire (Alberta Wildfire 2019). This stand age stratum was used to ensure landcover types were sampled across a chronosequence of ages, not as a categorical treatment variable in statistical models. I sampled at least three replicates for each

combination of landcover type and stand age class. The resulting sampling design consisted of 31 jack pine forest, 22 black spruce forest, 39 mixedwood forest, 33 bog, 22 poor fen, and 17 rich fen field plots (Appendix 2.1). Field plots were at least 100 metres from a road and 25 metres from other linear disturbances (some places have seismic lines spaced in a grid pattern at 50-m distances) or forest edges to minimize edge effects on shrub communities. Despite some geographic differences in the distribution of field plots across the study area, plot locations are representative of major landcover types in the region and follow areas of past wildfires which limit sampling locations. Thus, the stratified design used in this study ensures a more even distribution of samples in environmental space rather than geographic space (Peterson et al. 2011).

#### *2.4.2. Field data collection*

Field plots consisted of 50 m belt transects ( $50 \times 2$  m;  $100 \text{ m}^2$ ) with geographic coordinates recorded in UTM's (NAD 1983, Zone 12) at the start of the 50 m transect. Locations were selected based on stratifying both forest type and forest age (time since wildfire). Geographic Information System (GIS) data from the Ducks Unlimited Canada Enhanced Wetland Classification was used to identify forest types and Spatial Wildfire Data by Alberta Wildfire was used for identifying forest ages during stratification. Empirical measurements of depth of the organic soil layer and tree age in the field was used to verify stand type as either an upland or a lowland, and stand age by using dendrochronology. Field plots were classified as uplands when organic matter was absent or less than 10 cm in depth, whereas lowland forests had over 38 cm of organic matter. Stand age was estimated from tree rings obtained from a tree core of the largest conifer stem or deciduous stem if no conifer species were big enough to be representative of the stand age (Appendix 2.2). Boring at a predetermined height above ground requires a height correction ( $h_c$ ), an estimate of the number of years for a tree species to grow to coring height within a given landcover type (Wong

and Lertzman 2001). Height corrections were implemented for a coring height of 55 cm based on the equation from Wong and Lertzman (2001):

$$Age_{total} = Age_{measured\ at\ coring\ height} + h_c + e_{estimate\ of\ years\ to\ pith} \\ + e_{estimate\ of\ missing/false\ rings}$$

Given that all tree cores intersected the pith, an estimate for years to the pitch and missing or false rings were not needed. For example, trembling aspen requires on average two years ( $h_c$ ) to reach core height in uplands forests (Brinkman and Roe 1975, DeByle and Winokur 1985); therefore, if the number of tree rings counted in the field ( $Age_{measured\ at\ coring\ height}$ ) was 55, then stand age was corrected to 57 years post-wildfire. Stand age was only verified in sites that had burned prior to 1980 due to fire polygon errors in older wildfires using the Spatial Wildfire Data from Alberta Wildfire (Alberta Wildfire 2019), as well as areas that had not burned since 1940.

All deciduous shrub stems  $\geq 30$  cm in height (Fort McMurray average snow depth; Environment Canada 2019), as well as sapling stems  $\geq 30$  cm in height and  $< 2$  cm in diameter found within 1 m on the right side of the 50 m transect line ( $50 \times 1$  m;  $50\ m^2$ ) were identified and counted. However, the length of the transect line was reduced for species that were abundant and its abundance was homogenous throughout the length of the transect. Specifically, if 25 or more stems of a species were counted in the first 10 or 25 m of the transect line, plot size was decreased to either 10 or  $25\ m^2$ , respectively. Density of all species was later standardized to  $100\ m^2$  for analysis. Estimates of winter ungulate percent browse by species were measured in the field using ordinal categories of browsing rates ranging from 0 to 5 (0: 0%; 1: 1 – 5%; 2: 6 – 20%; 3: 21 – 50%; 4: 51 – 90%; 5: 91 – 100%). Ungulate percent browse corresponded to the visually estimated ratio of the number of browsed branches to the total number of branches off the main stem. Estimates of winter ungulate browse severity by species were also quantified by using an ordinal



category ranging from 0 to 4 (0: None; 1: Low; 2: Medium; 3: High; 4: Extreme). Ungulate browse severity used qualitative visual assessments of individual shrubs and saplings based on the amount of leader and secondary growth, hedging and amount of dead wood (Appendix 2.3). For example, a browsed branch with no dead wood and some healthy leader growth was considered to be ‘low’ browse severity, while a browsed branch with substantial secondary growth (hedging) and excessive dead wood was classified as ‘high’ browse severity. Both ungulate browse percentage and ungulate browse severity were independently estimated for each deciduous shrub and sapling species identified in the field based on active browse from the previous winter (Appendix 2.3).

#### 2.4.3. Winter browse species

A total of 32 deciduous shrub and 8 sapling species were considered and measured in the field (Appendix 2.4). However, five deciduous shrub species and one sapling species were later removed as they were not observed or were too rare for statistical analyses. These species were common wild rose (*Rosa woodsii*), Greene’s mountain-ash (*Sorbus scopulina*), common snowberry (*Symphoricarpus albus*), buckbrush (*Symphoricarpus occidentalis*), dwarf blueberry (*Vaccinium cespitosum*), and balsam fir (*Abies balsamea*).

Due to the lack of scientific knowledge of ungulate winter browse diet in northeastern Alberta, deciduous shrub and sapling species were classified into palatability categories based on ungulate browsing prevalence recorded in the field, which were later standardized with scientific literature on moose foraging ecology in western Canada and white-tailed deer foraging ecology in the hemi-boreal region of the Northern Great Lakes in Minnesota, as well as expert opinion (see Table 2.1 and 2.2 for more details). Note that palatability represents an indirect measure of browse quality through evidence of browsing; thus, a deciduous shrub and sapling species is more palatable for moose and white-tailed deer when its browsing prevalence is higher (i.e., higher

percentage of stems are browsed by these two ungulates). Palatability in this study does not consider the nutritional value of winter browse species (i.e., forage quality) which is a more quantitative and robust representation of browse selection or avoidance by moose and white-tailed deer (see Mautz et al. 1976 and Renecker and Hudson 1988).

Browsing prevalence was calculated individually for each deciduous shrub and sapling species by dividing the total number of browsed stems across all field plots with the total number of stems of that species across all field plots. As a result, palatability categories were stratified into four levels, where low palatable winter browse species had 1 to 20% browsing prevalence, medium palatable winter browse species had 21 to 50% browsing prevalence, highly palatable winter browse species had 51 to 90% browsing prevalence, and preferred winter browse species had 91 to 100% browsing prevalence. Unless otherwise stated, winter browse species were pooled for statistical analyses, but the latter were done separately for deciduous shrub and sapling species.

#### *2.4.4. Statistical analyses*

##### *2.4.4.1. Winter browse succession*

Winter browse succession was assessed with six two-way analysis of covariance (ANCOVA; three models with deciduous shrub species and three models with sapling species) with one of the three diversity metrics as the response variable: species richness (number of species/100 m<sup>2</sup>), Hill's Shannon-Weaver Index (hereafter referred to as Hill's Index), and species abundance (stem density: number of stems/100 m<sup>2</sup>). Hill's Index was used to measure the changes in equitability among winter browse species over time as the Shannon-Weaver Index does not correctly reflect the changes in species diversity and abundance within a community (Jost 2007). The Hill's number represents the numbers of species expected in a community with the same level of diversity, but with equally abundant species (Hill 1973). For example, a Hill's Index of 65

suggests the diversity of the community is equivalent to a community with 65 evenly abundant species. Successional trajectories of ungulate winter browse by palatability was also assessed for deciduous shrub and sapling species separately (one model with deciduous shrub species and one model with sapling species) using a three-way ANCOVA with species abundance as the response variable.

Stand age (in years) and landcover types (upland: jack pine, black spruce and mixedwood forests; lowland: bogs, rich and poor fens) were included as fixed effects in the two-way ANCOVAs, while palatability categories (preferred, high, medium and low) were included in the three-way ANCOVAs. The two-way interactions (stand age  $\times$  landcover; stand age  $\times$  palatability) and three-way interaction (stand age  $\times$  landcover  $\times$  palatability) were also considered as predictor variables, and were removed if shown to be insignificant in ‘anova’ analyses in the “stats” package (R Core Team 2018). Specifically, the ‘anova’ function determined if the most complex model (model with two-way or three-way interactions) captured the data significantly better than the simplest model (model without two-way or three-way interactions). If the resulting p-value was less than 0.05, the most complex model was favored over the simplest model, whereas if the p-value was greater than 0.05, the simplest model was favored over the complex model. To meet assumptions of normality, response variables were either log transformed or square root transformed. All other assumptions and diagnostics for linear models were analyzed and met before running statistical analyses, which were fitted using the ‘lm’ function in the “stats” package (R Core Team 2018).

Changes to winter browse community composition in uplands and lowlands over time were graphically illustrated using a two dimensions ( $k = 2$ ; stress values = 0.07 – 0.16) Multidimensional Non-Metric Scaling (NMDS) with the ‘metaMDS’ function in the “vegan” package (Oksanen et

al. 2019). The NMDS attempts to represent the pairwise dissimilarity between field plots in a low-dimensional space (Legendre and Legendre 2012). A total of eight NMDS (four with deciduous shrub species and four with sapling species) were performed with the following stand age categories: young forests (0 – 10 years post-wildfire, and 11 – 30 years post-wildfire), intermediate forests (31 – 70 years post-wildfire), and mature forests ( $\geq 71$  years post-wildfire). Bray-Curtis distance was used in the NMDS because it is suitable for analyzing count data (stem density: number of stems/100 m<sup>2</sup>) with a high number of zeros (Clarke 1993).

#### 2.4.4.2. Winter use

Winter use was assessed with four ordinal logistic regression (OLR; two models with deciduous shrub species and two models with sapling species) with either ungulate browse percentage or ungulate browse severity as the ordinal response variable. Winter browse species (deciduous shrubs or saplings), stand age (in years), and landcover types (upland: jack pine, black spruce and mixedwood forests; lowland: bogs, rich and poor fens) were included as fixed effects. The two-way interaction of stand age  $\times$  landcover was also added as a predictor variable, and was removed if shown to be insignificant using the ‘anova’ function in the “stats” package (R Core Team 2018). Specifically, the ‘anova’ function determined if the most complex model (model with two-way interaction) captured the data significantly better than the simplest model (model without two-way interaction). If the resulting p-value was less than 0.05, the most complex model was favored over the simplest model, whereas if the p-value was greater than 0.05, the simplest model was favored over the complex model. Deciduous shrub and sapling species detected in less than 10 field plots ( $N \leq 10$ ) were removed from the analysis, which included speckled alder, saskatoon, beaked hazelnut (*Corylus cornuta*), red-osier dogwood (*Cornus sericea*), alder-leaved buckthorn (*Endotropis alnifolia*), chokecherry, and balsam poplar (*Populus balsamifera*). All assumptions

and diagnostics for the OLR were analyzed and met before running statistical analyses, which were fitted using the ‘polr’ function in the “MASS” package (Venables and Ripley 2002). All statistical analyses were conducted in R version 3.5.0 with a significance threshold of  $\alpha = 0.05$  (R Core Team 2018).

## 2.5. Results

### 2.5.1. Winter browse succession

All diversity metrics examining the change in winter browse (deciduous shrubs and saplings) consumed by ungulates over the first 150 years post-wildfire were best explained by landcover type (Table 2.3). In fact, landcover explained a substantial amount of variation in deciduous shrub richness (adjusted  $R^2 = 0.275$ ), Hill’s Index (adjusted  $R^2 = 0.320$ ), and abundance (adjusted  $R^2 = 0.253$ ). Landcover type also explained a moderate amount of sapling richness (adjusted  $R^2 = 0.099$ ), Hill’s Index (adjusted  $R^2 = 0.136$ ), and abundance (adjusted  $R^2 = 0.171$ ). Stand age had no significant effect on deciduous shrub and sapling diversity metrics, except for sapling abundance that was inversely related to stand age ( $\beta_{\text{sapling}} = -0.087$ ,  $SE = 0.026$ ,  $p < 0.001$ ).

Interestingly, deciduous shrub richness and Hill’s Index in mixedwood forests peaked in the first 10 years post-wildfire at 10 species/100 m<sup>2</sup> and dropped to approximately 2.5 species/100 m<sup>2</sup> at 50 – 60 years post-wildfire, but increased with a second peak at 90 years post-wildfire (Figure 2.2). This double peak pattern was also observed with sapling richness and Hill’s Index, where they peaked in the first 25 years post-wildfire at 6 species/100 m<sup>2</sup>, decreased to 2 species/100 m<sup>2</sup> at 60 – 70 years post-wildfire, and increased slightly for a second peak of 3 species/100 m<sup>2</sup> at 80 – 90 years post-wildfire (Figure 2.2). The double peak pattern was not detected in lowland forests (i.e., bogs and poor fens) as deciduous shrub richness and Hill’s Index decreased linearly in bogs over time from 3 species/100 m<sup>2</sup> to 2 species/100 m<sup>2</sup>, but remained constant in poor fens at

approximately 5 species/100 m<sup>2</sup> (Figure 2.2). Sapling richness and Hill's Index in poor fens, however, peaked in the first 20 years post-wildfire at 6 species/100 m<sup>2</sup>, but dropped and remained constant at approximately 2.5 species/100 m<sup>2</sup> over time, while sapling richness and Hill's Index remained constant at approximately 1.5 species/100 m<sup>2</sup> in bogs (Figure 2.2).

Deciduous shrub and sapling abundance in lowland forests (i.e., bogs and poor fens) were constantly higher than mixedwood forests over the first 150 years post-wildfire, with the exception of sapling abundance in the first 10 years post-wildfire (Figure 2.2). Deciduous shrub abundance in mixedwood forests remained constant at an average of 400 stems/100 m<sup>2</sup>, while sapling abundance decreased exponentially from approximately 1,600 stems/100 m<sup>2</sup> to 25 stems/100 m<sup>2</sup> over this period (Figure 2.2). Bogs showed similar trends to mixedwood forests with constant deciduous shrub abundance at an average of 785 stems/100 m<sup>2</sup> (Figure 2.2). Poor fens, however, showed a linear decrease in deciduous shrub abundance from approximately 900 stems/100 m<sup>2</sup> to 400 stems/100 m<sup>2</sup> (Figure 2.2). Sapling abundance in bogs increased to an average of 225 stems/100 m<sup>2</sup>, whereas in poor fens, sapling abundance peaked at 400 stems/100 m<sup>2</sup> at 20 years post-wildfire and decreased to 25 stems/100 m<sup>2</sup> (Figure 2.2). Additional details on the changes in deciduous shrub and sapling richness favored by ungulates, Hill's Index, and stem abundance for jack pine forests, black spruce forests, and rich fens can be found in Appendix 2.5.

The NMDS ordination demonstrated that winter browse composition used by ungulates in upland (black spruce, jack pine, and mixedwood forests) and lowland (bogs, poor and rich fens) forests became dissimilar with increasing stand age (Figure 2.3 and Appendix 2.6). In the first 10 years post-wildfire, deciduous shrub composition in all six landcover types were similar and overlapped (Figure 2.3). Sapling composition in the first 10 years post-wildfire were already dissimilar between upland and lowland forests (Appendix 2.6). Segregation of deciduous shrub

composition was evident between 11 to 30 years post-wildfire as lowland forests were further apart than uplands (Figure 2.3). The segregation of deciduous shrub and sapling communities were evident for mature stands ( $\geq 71$  years post-wildfire) as landcover types weren't overlapping, suggesting different community compositions (Figure 2.3 and Appendix 2.6).

Successional trajectories of ungulate winter browse (deciduous shrubs and saplings) differed significantly by palatability (Table 2.4). When adding palatability to the model, stand age had a significant and negative effect on deciduous shrub abundance, but was non-significant for sapling abundance (Table 2.4). All palatability categories were statistically significant for deciduous shrub and sapling abundance (Table 2.4), except for moderate sapling palatability ( $\beta_{\text{sapling}} = -0.174$ ,  $SE = 0.095$ ,  $p = 0.067$ ; Table 2.4). Regardless of landcover types, highly palatable sapling abundance decreased significantly over time, while low palatable deciduous shrub abundance increased significantly over time (Table 2.4).

However, three-way interactions between stand age, landcover type, and palatability were significant demonstrating that successional trajectories for browse abundance differed between uplands and lowland forests (Table 2.4, Figure 2.4 and Appendix 2.7). Indeed, abundance of highly palatable deciduous shrubs differed significantly over time within jack pine forests, mixedwood forests, and rich fens (Table 2.4). Abundance of moderately palatable deciduous shrubs changed significantly over time in poor fens and rich fens, whereas low palatable deciduous shrubs varied in mixedwood forests and rich fens (Table 2.4). Three-way interactions were less prominent with sapling abundance as only highly palatable saplings in mixedwood forests, as well as low palatable saplings in bogs and mixedwood forests had significant changes over time (Table 2.4).

Changes in winter browse palatability were apparent within the first 150 years post-wildfire that were absent in the two-way ANCOVAs (Figure 2.4 and Appendix 2.7). For example,

abundance of deciduous shrubs in mixedwood forests remained constant at 400 stems/100 m<sup>2</sup> over time regardless of palatability categories (Figure 2.2). Yet, abundance of preferred and highly palatable deciduous shrubs peaked in the first 20 years post-wildfire, dropping at 50 – 60 years, and then peaking a second time at 90 years post-wildfire, similarly to trends detected in species richness and Hill's Index (Figure 2.4). Abundance of highly palatable saplings was high in the first 10 – 20 years post-wildfire thereafter decreasing exponentially in black spruce forests and mixedwood forests (Appendix 2.7). Lastly, abundance of low palatable browse was constantly higher than preferred, highly, and moderately palatable browse in black spruce forests, and lowland forests (i.e., bogs, poor fens, and rich fens) (Figure 2.4 and Appendix 2.7).

#### 2.5.2. *Winter use*

Browse percentage and browse severity on deciduous shrub species were best explained by stand age, landcover type, and the presence of deciduous shrub species consumed by ungulates over the first 150 years post-wildfire (Table 2.5). Both browse percentage and browse severity on deciduous shrubs were statistically significant in jack pine forests, mixedwood forests, and poor fens (Table 2.5; Figure 2.5 and 2.6). Given that the other predictor variables in the model were held constant, the odds of moving from 0 (unbrowsed) to 1 – 5 (browsed) were 3.136 and 2.567 times greater in jack pine forests, 1.860 and 1.903 times greater in mixedwood forests, as well as 2.216 and 1.906 times greater in poor fens for browse percentage and browse severity, respectively (Table 2.5).

The presence of deciduous shrub species had significant effects on both browse percentage and browse severity (Table 2.5; Figure 2.5 and 2.6). Twining honeysuckle, bracted honeysuckle, currants & gooseberries, wild red raspberry and Canada buffaloberry were avoided by ungulates (Table 2.5; Figure 2.5 and 2.6). Only currants & gooseberries were significantly avoided ( $\beta_{\text{percentage}}$



= -1.395, SE = 0.669,  $p = 0.037$ ;  $\beta_{\text{severity}} = -1.391$ , SE = 0.672,  $p = 0.039$ ; Table 2.5), but wild red raspberry was nearly, but not statistically significant ( $\beta_{\text{percentage}} = -1.548$ , SE = 0.857,  $p = 0.071$ ;  $\beta_{\text{severity}} = -1.641$ , SE = 0.857,  $p = 0.056$ ; Table 2.5). Green alder, dwarf birch, northern bog birch, Labrador tea, fly mountain honeysuckle, pin cherry, prickly wild rose, willows, and common blueberry were all selected by ungulates (Table 2.5; Figure 2.5 and 2.6). These deciduous shrub species were browsed significantly with the exception to green alder, fly mountain honeysuckle, and pin cherry (Table 2.5). When the other predictor variables were held constant, the odds of moving from 0 (unbrowsed) to 1 – 5 (browsed) were 9.673 and 13.440 times greater with dwarf birch, 2.748 and 3.310 times greater with northern bog birch, 2.981 and 2.957 times greater with Labrador tea, 4.263 and 4.220 times greater with prickly wild rose, 5.153 and 4.918 times greater with willows, as well as 4.151 and 3.923 times greater with common blueberry for browse percentage and browse severity, respectively (Table 2.5).

Stand age, landcover type, and the presence of sapling species consumed by ungulates failed to explain both browse percentage and browse severity on saplings species, in exception to mixedwood forests ( $\beta_{\text{severity}} = 0.800$ , SE = 0.821,  $p = 0.030$ ; Table 2.6). The odds of moving from 0 (unbrowsed) to 1 – 5 (browsed) were 2.226 times greater in mixedwood forests, given that the other predictor variables in the model were held constant (Table 2.6). Coniferous sapling species were not browsed or could be browsed up to 15% in all landcover types, regardless of the percentage and severity, whereas approximately 35 to 65% of available deciduous sapling stems were browsed in upland forests and bogs (Appendix 2.8).

## 2.6. Discussion

Plant diversity is typically highest post-wildfire, with some ecosystems reaching a peak faster than others, and gradually decreases over time (He et al. 2019). In the western and central

Canadian boreal forest, most tree species re-establish immediately post-wildfire (Gutsell and Johnson 2002, Chen et al. 2009, Ilisson and Chen 2009*b*). Understory biomass and productivity have been reported to be highest in early succession (10 – 35 years post-wildfire) (Bond-Lamberty et al. 2002, Mack et al. 2008, Mallon et al. 2016), including deciduous shrub and sapling species consumed by ungulates (Spencer and Hakala 1964, Weixelman et al. 1998, Chapin et al. 2006). Yet, in the Boreal Plains of Alberta, this paradigm of browse succession patterns was only detected with deciduous shrub and sapling species consumed by ungulates in jack pine forests. Black spruce forests, bogs, poor fens, and rich fens had relatively constant species richness, evenness (Hill's Index) and abundance (number of stems/100 m<sup>2</sup>) across a chronosequence of stand ages post-wildfire. Lowland forests are known to be resilient to wildfires (Thompson and Waddington 2013) and to burn less severely in comparison to upland forests (Whitman et al. 2018). Negative hydrological feedback allow lowland forests to minimize water loss during dry conditions, therefore wildfires normally consume the top of a few centimetres of peat (Zoltai et al. 1998, Benschoter et al. 2011). The latter suggests that early seral lowland forests do not recruit winter browse species consumed by ungulates in the Boreal Plains of Alberta, as predicted, which means that early seral successional stands do not always have higher deciduous shrub and sapling richness and abundance as expected in other regions in the western and central Canadian boreal forest.

Despite little to no patterns in the previous landcover types investigated in this study, mixedwood forests showed dynamic patterns of winter browse succession. Both deciduous shrub and sapling richness and evenness peaked at 10- and 25-years post-wildfire, respectively. However, a clear second peak was evident at 80 – 90 years post-wildfire that has not been detected in previous studies. The second peak of species richness and evenness is likely attributed to the die-off of early successional species, such as trembling aspen and paper birch. These two species

are root suckering broadleaf species known to grow in high numbers immediately post-wildfire (Bergeron et al. 2014). The lifespan of deciduous saplings is relatively short compared to late successional coniferous species (Bergeron 2000, Auger et al. 2004), and die-off usually occurs 75 – 125 years post-wildfire in boreal mixedwood forests (Harvey et al. 2002). This die-off of deciduous saplings allows more sunlight to reach the forest floor, creating small patch disturbances (referred to as “gap dynamics”), allowing shade-tolerant coniferous saplings to grow within these new abiotic conditions (Chen and Popadiouk 2002). However, it is also common for deciduous shrubs to outgrow the shade-tolerant coniferous saplings depending on local site conditions (Waldron 1959, Kneeshaw and Bergeron 1996, Aubin et al. 2000, Chen and Popadiouk 2002), permitting new deciduous shrub species to persist following these canopy openings.

Interestingly, deciduous shrub abundance in mixedwood forests remained constant over time, regardless of the observed sinuous changes in species richness and evenness. While abundance did not change, there were dynamic fluctuations in the palatability of these species consumed by ungulates. As predicted, the abundance of highly palatable deciduous shrubs decreased, whereas low palatable deciduous shrubs increased over time, with the relationship being significant in jack pine forests, mixedwood forests and rich fens. These results support previous studies who reported that moose selected jack pine forests (or coniferous forests) and mixedwood forests in winter (Forbes and Theberge 1993, Gillingham and Parker 2008, Jung et al. 2009, Street et al. 2015). In fact, moose generally selected mixedwood forests in early winter and progressively shifted into conifer dominated habitats as winter progresses (Timmermann and McNicol 1988, Bjørneraas et al. 2011). Particularly in northeastern Alberta, moose were found to strongly select deciduous hardwood forests and mixedwood forests in winter (Nowlin 1978, Osko et al. 2004). However, these studies speculated that ungulates selected these habitat types for

foraging purposes without directly measuring this. This study quantified ungulate browse percentage and severity on deciduous shrubs and saplings, and revealed that ungulates significantly browsed preferred species in jack pine and mixedwood forests.

The abundance of preferred and highly palatable deciduous shrubs showed a second peak at 80 – 90 years post-wildfire, similarly to the second peak in deciduous shrub richness and evenness. Numerous studies have documented that prime moose habitat ranged between 11 and 30 years post-wildfire (first observed peak in this study) as moose densities have shown to peak during that time period (LeResche and Bishop 1974) and moose select habitat with high canopy cover characterized by having abundant forage (Maier et al. 2005, Joly et al. 2016). No studies to this date have documented a second peak in prime moose habitat at 80 – 90 years post-wildfire, however, it has been previously highlighted that moose and white-tailed deer selected winter habitat over 120 years post-wildfire in the boreal mixedwoods of Alberta (Stelfox et al. 1995). The lack of evidence of a second peak could be due to four non-mutually exclusive reasons: 1) previous studies have investigated specific time periods post-wildfire (i.e. 11 to 30 years post-wildfire) (MacCracken and Viereck 1990, Weixelman et al. 1998, Maier et al. 2005), 2) past studies have classified stand age into decadal categories which does not allow proper visualizations of changes in winter browse (Maier et al. 2005, Newbury et al. 2007), 3) previous studies were conducted in the Taiga Plains or Alaska Boreal Interior which have structurally different vegetation communities (i.e. black spruce dominated forests with low amounts of mixedwood forests) than the Boreal Plains of Alberta (Spencer and Hakala 1964, Peek 1974*a*, MacCracken and Viereck 1990, Loranger et al. 1991, Weixelman et al. 1998, Maier et al. 2005, Lord and Kielland 2015, Joly et al. 2016), and 4) information supporting the second peak in ungulate winter habitat has

been buried in grey literature, whether it has not been published through a peer-review process or has not been easily retrieved by the scientific community (Stelfox et al. 1995).

Previous studies have suggested that moose and white-tailed deer do not forage in lowland forests. In fact, moose in northeastern British Columbia and northern Alberta avoided burned lowlands more than any other burned habitat types (DeMars et al. 2019), while moose in central Labrador avoided open habitats, such as conifer-lichen woodlands, bogs, fens, burned forests and barren areas (Jung et al. 2009). However, a recent study found that moose selected areas with high availability of willow biomass (i.e. low severity sites) rather than habitats with the most total available woody browse biomass (i.e. high severity sites) in the winter (Brown et al. 2018). Indeed, mean willow abundance was greater in poor and rich fens ( $270 \pm 256$  stems/100 m<sup>2</sup> and  $302 \pm 331$  stems/100 m<sup>2</sup>, respectively), which can be considered as low severity sites as these wet habitats are less likely to be burned severely (Whitman et al. 2018). Nonetheless, lowland forests also had the highest winter browse density (bogs:  $985 \pm 658$  stems/100 m<sup>2</sup>; poor fens:  $851 \pm 395$  stems/100 m<sup>2</sup>; rich fens:  $1024 \pm 612$  stems/100 m<sup>2</sup>) and constantly higher abundance of low palatable browse throughout the boreal lowland forest succession. Similarly, Mallon et al. (2016) found greater understory biomass, including shrub biomass, and productivity in boreal lowlands in northern Ontario across all stand age classes as a result of low canopy density and greater light availability. Yet, the authors did not investigate ungulate responses to higher winter browse availability in lowlands. As predicted, this study found no significant evidence of ungulate browsing in lowland forests, with the exception of browsing on deciduous shrubs in poor fens, likely as a result of high willow abundance. Lowland forests seem to provide ungulates with high quantity of low quality forage, and while evidence of browsing was found in lowland forests, the lack of significance suggests that ungulates select these habitats for other reasons than forage availability, such as

vegetation cover for thermoregulation purposes (reduction in wind velocities and subsequently heat loss), protection against deep snow or shelter from predators and hunters (Timmermann and McNicol 1988). Altogether, this study partly supports the hypothesis that moose and white-tailed deer do not forage in lowland forests due to poor forage quality; yet, it is important to note that lowland forests could still be utilized in greater proportions if moose and white-tailed deer had low quantity of high-quality forage in surrounding uplands.

As previously noted, many aspects of winter diet selection by moose and white-tailed deer remain unresolved, particularly in their responses to wildfires in an anthropogenic landscape. Ungulates were found to avoid all sapling species, twining honeysuckle, bracted honeysuckle, currants & gooseberries, wild red raspberry and Canada buffaloberry, whereas green alder, dwarf birch, northern bog birch, Labrador tea, fly mountain honeysuckle, pin cherry, prickly wild rose, willows, and common blueberry were selected by ungulates in the Boreal Plains of Alberta. Willows and paper birch make up the majority of moose winter diet throughout its geographic range (Regelin et al. 1987, Risenhoover 1989, Weixelman et al. 1998, Newbury et al. 2007, Renecker and Schwartz 2007), however, its importance in northeastern Alberta is much lower (Nowlin 1978). In fact, the author found no evidence of browsing on paper birch and willows accounted for 30% of their winter diet. While direct measurements of ungulate winter diet were not conducted in this study, the avoidance of paper birch and the selection of willows support the findings from Nowlin (1978). Moose are known to avoid bracted honeysuckle, Canada buffaloberry, currants & gooseberries, and wild red raspberry (Renecker and Schwartz 2007), which were also avoided in this study. A study investigating white-tailed deer winter diet in the Pohémégamook area of the Lower Saint-Lawrence in Quebec, Canada, found opposite evidence than reported in the Boreal Plains of Alberta, where balsam fir, paper birch, honeysuckles, balsam

poplar, trembling aspen, willows, and lowbush cranberry were significantly utilized in proportion to their availability (Dumont et al. 2005). The latter suggest that white-tailed deer winter diet in northeastern Alberta is considerably different than other regions of its geographic distribution, and more research should be conducted to fully understand this ungulate's selection of winter browse.

Coniferous species are generally known to be consumed by ungulates when deciduous shrub and sapling availability or quality is low (Peek 1974a, Raymond et al. 1996, Newbury et al. 2007). In fact, coniferous needles are poor in nutrition compared to other woody browse species, and their consumption in high levels can lead to malnutrition, starvation, and even death (Dahlberg and Guettinger 1956, Wetzel 1972). It has been estimated that balsam fir can negatively affect rumen functioning beyond a threshold of 15 to 20% of their winter diet (Crête and Jordan 1982, Crête 1989, Crête and Courtois 1997). In this study, coniferous saplings were rarely browsed in exception to white spruce in mixedwood forests where up to 15% of stems were browsed, suggesting that ungulates in the Boreal Plains of Alberta are not limited by deciduous shrub and deciduous sapling availability in the winter. The latter has been supported by previous findings that balsam fir does not represent a highly nutritive species for moose and white-tailed deer (Ullrey et al. 1968, Crête and Jordan 1982, Crête 1989, Dumont et al. 2005).

Lastly, chronosequences (i.e., space-for-time substitution) offer invaluable insights into temporal dynamics of vegetation communities over time that cannot be achieved from direct and repeated post-wildfire observations (Morneau and Payette 1989, Bergeron 2000, Kashian et al. 2005, Mallon et al. 2016). Yet, there are still limitations associated with this indirect approach despite its popularity for reconstructing successional pathways extending beyond several decades (Walker et al. 2010). There are two fundamental assumptions about chronosequences: 1) vegetation communities found in young forests (e.g.,  $\leq 30$  years post-wildfire) are developing in a

temporal pattern to resemble vegetation communities of mature forests (e.g.,  $\geq 71$  years post-wildfire) (Walker et al. 2010), and 2) pre-disturbance vegetation, environmental conditions, and post-disturbance establishment are uniform among sites (Halpern 1989). However, differences in vegetation communities may result from differences in vegetation histories due to climatic, landscape or stochastic factors (Walker and del Moral 2003). Generally, chronosequences have been found to be suitable for “studying successional trajectories that are convergent, have low diversity and are infrequently disturbed than for trajectories that are divergent, more diverse and frequently disturbed” (Walker et al. 2010). This is the case with the Boreal Plains of Alberta where early successional deciduous and mixedwood forests typically converge to coniferous forests over time (Chen and Popadiouk 2002), have low vegetation diversity (Bergeron et al. 2014), and experience infrequent stand-replacing wildfires (Larsen 1997, Erni et al. 2020). Readers must understand the limitations surrounding chronosequences (i.e., space-for-time substitution) and the possible effects it may have on the dynamic trends found in this study.

## **2.7. Conclusion**

Moose have extended their geographic distribution northward by 200 – 700 km since 1875 (Hatter 1950), and most recently, white-tailed deer have extended into the boreal forests of Alberta and the Northwest Territories (Webb 1967, Veitch 2001). Comprehensive and detailed data on moose and white-tailed deer foraging ecology throughout most of the boreal successional pathway are sparse, yet highly important to assess the feasibility of managing alternative prey population and expansion as a management tool. Moose density is associated with species richness within a given habitat, due to the fact that moose prefer habitats with diverse food items (Maier et al. 2005). The latter suggests that wildfires can provide higher winter forage availability for ungulates residing in the upland forests of the Boreal Plains of Alberta for longer periods of time than initially



reported by the scientific community. The greater availability of high quality winter browse in uplands through wildfires could be an additional reason for higher numbers of moose populations and expanding populations of white-tailed deer in northern Alberta, aside from the known effects of anthropogenic disturbances and climate change (Latham et al. 2011*b*, 2013, Dawe et al. 2014, Fisher et al. 2020*a*).

This study is also the first to test the paradigm prediction that lowland forests provide insufficient winter browse to alter moose spatial behavior towards lowland forests. Despite lowland forests having higher winter browse abundance, the lack of winter browse recruitment consumed by moose and white-tailed deer following wildfires and the lack of significant browsing suggests that lowland forests are not high-quality habitats for these ungulates. However, researchers must be cautious in their wording of the avoidance of lowland forests by moose and white-tailed deer due to insufficient winter browse. Lowland forests do provide enough forage for ungulates, as seen by constantly higher abundance of deciduous shrubs over time, but the available forage is of poor quality and undesirable to moose and white-tailed deer, particularly given the availability of forage in adjacent upland forests.

Research on ungulate winter foraging ecology should examine winter diet at finer scales, particularly with microhistological analyses of feces to fully separate the species of deciduous shrubs and saplings consumed by either moose and white-tailed deer throughout the boreal succession. A better understanding of specific species consumed by these ungulates in northern Alberta will allow appropriate land-use management of high quality ungulate winter habitat within woodland caribou range. Additionally, researchers must prioritize understanding white-tailed deer habitat selection, foraging ecology, and population demographics in northeastern Alberta as they've recently replaced moose as the primary prey species of wolves (James et al. 2004, Latham

et al. 2011*b*, 2013). Overall, given the substantial increase in the frequency and extent of wildfires in the boreal forests as a result of recent anthropogenic climate change (Kasischke and Turetsky 2006), more researchers need to focus on the bottom-up effects of wildfires on ungulate habitat selection and foraging ecology in the Boreal Plains of Alberta, and particularly how these changes in winter browse are impacting declining threatened woodland caribou populations.

## Tables

**Table 2.0.1.** Summary of the number of deciduous shrub detections, abundance (stem density/100 m<sup>2</sup>), and winter ungulate browsing prevalence (in percentage) from 164 vegetation plots conducted in the summer of 2019 in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada. Shrub species are listed alphabetically by species code.

Shrub Species	Species Code	Number of detections	Prevalence (%)	Average Stem Density $\pm$ SD (per 100 m <sup>2</sup> )	Total number of stems	Number of browsed stems	Browse Prevalence (%)	Winter Browse Species	Ungulate Palatability Category <sup>1</sup>	Ungulate Palatability Category <sup>2</sup>
Salix	Salix	103	62.8	129.5 $\pm$ 224.7	13,336	8,530	64.0	Yes	High	Preferred <sup>3</sup>
Speckled Alder	AlnInc	5	3.1	12.8 $\pm$ 15.5	64	58	90.6	Yes	Preferred	High <sup>4</sup>
Green Alder	AlnVir	23	14.0	90.5 $\pm$ 103.4	2,082	1,304	62.6	Yes	High	High
Saskatoon	AmeAln	10	6.1	42.0 $\pm$ 81.7	420	396	94.3	Yes	Preferred	Preferred
Dwarf Birch	BetGla	22	13.4	195.1 $\pm$ 209.5	4,292	4,288	99.9	Yes	Preferred	Medium <sup>5</sup>
Northern Bog Birch	BetPum	40	24.4	254.4 $\pm$ 404.1	10,174	8,956	88.0	Yes	High	Medium <sup>5</sup>
Beaked Hazelnut	CorCor	2	1.2	11.0 $\pm$ 9.9	22	22	100.0	Yes	Preferred	Preferred
Red-osier Dogwood	CorSer	3	1.8	28.0 $\pm$ 31.2	84	76	90.5	Yes	Preferred	Preferred
Alder-leaved Buckthorn	EndAln	5	3.1	47.2 $\pm$ 70.1	236	216	91.5	Yes	Preferred	Preferred
Labrador Tea	LedGro	130	79.3	359.8 $\pm$ 451.7	46,768	40,022	85.6	Yes	High	Low <sup>6</sup>
Twining Honeysuckle	LonDio	11	6.7	23.6 $\pm$ 17.4	260	60	23.1	Yes	Medium	Medium
Bracted Honeysuckle	LonInv	11	6.7	10.7 $\pm$ 9.2	118	44	37.3	Yes	Medium	Medium
Mountain Fly Honeysuckle	LonVil	12	7.3	39.2 $\pm$ 59.7	470	68	14.5	Yes	Low	Medium <sup>7</sup>
Pin Cherry	PruPen	11	6.7	23.8 $\pm$ 21.3	262	104	39.7	Yes	Medium	High <sup>8</sup>
Chokecherry	PruVir	3	1.8	10.0 $\pm$ 9.2	30	2	6.7	Yes	Low	High <sup>8</sup>
Prickly Wild Rose	RosAci	73	44.5	70.8 $\pm$ 93.4	5,176	4,248	82.1	Yes	High	High
Common Wild Rose	RosWoo	0	0.0	0.0 $\pm$ 0.0	0	0	0.0	No		
American Black Currant	RibAme	0	0.0	0.0 $\pm$ 0.0	0	0	0.0	No		
Skunk Currant	RibGla	6	3.7	25.0 $\pm$ 24.6	150	0	0.0	No		

Swamp Gooseberry	RibHir	1	0.6	4.0 ± 0.0	4	0	0.0	No		
Northern Black Currant	RibHud	7	4.3	8.3 ± 4.4	58	22	37.9	Yes	Medium	
Bristly Black Currant	RibLac	3	1.8	6.0 ± 3.5	18	10	55.6	Yes	High	
Canada Gooseberry	RibOxy	14	8.5	7.3 ± 5.5	102	8	7.8	Yes	Low	
Swamp Red Currant	RibTri	9	5.5	33.3 ± 21.1	300	10	3.3	Yes	Low	
Currants & Gooseberries	RibSpp	29	17.7	21.8 ± 23.8	632	122	19.3	Yes	Low	Low
Wild Red Raspberry	RubIda	16	9.8	97.3 ± 227.5	1,556	1,168	75.1	Yes	High	Medium <sup>9</sup>
Canada Buffaloberry	SheCan	22	13.4	65.0 ± 78.6	1,430	472	33.0	Yes	Medium	Medium
Greene's Mountain-ash	SorSco	0	0.0	0.0 ± 0.0	0	0	0.0	No		
Common Snowberry	SymAlb	1	0.6	8.0 ± 0.0	8	0	0.0	No		
Buckbrush	SymOcc	4	2.4	12.5 ± 9.2	50	0	0.0	No		
Dwarf Blueberry	VacCes	2	1.2	58.0 ± 0.0	116	0	0.0	No		
Common Blueberry	VacMyr	79	48.2	71.5 ± 106.5	5,646	5,000	88.6	Yes	High	Low <sup>6</sup>
Lowbush Cranberry	VibEdu	34	20.7	63.7 ± 90.7	2,166	762	35.2	Yes	Medium	High <sup>8</sup>

<sup>1</sup> Ungulate palatability category based on browse prevalence: None – 0% browsed prevalence; Low – 1 to 20% browsed prevalence; Medium – 21 to 50% browsed prevalence; High – 51 to 90% browsed prevalence; Preferred – 91 to 100% browsed prevalence.

<sup>2</sup> Ungulate palatability category standardized with findings in the literature and expert opinion on ungulate foraging ecology.

<sup>3</sup> Multiple publications have shown that willows are considered the universal preferred food for moose (*Alces alces*) as they are consumed whenever and wherever they are available on the landscape (Peek 1974a, Risenhoover 1989, Renecker and Schwartz 2007). Therefore, willows will be considered as a preferred winter browse species.

<sup>4</sup> Moose and white-tailed deer (*Odocoileus virginianus*) have been shown to forage on speckled alder in the winter (Rogers et al. 1981, Blouch 1984, Renecker and Schwartz 2007), but the number of detections and total number of observed stems are too low to justify the 'preferred' palatability category derived from the browse prevalence. Speckled alder will be considered as a highly palatable winter browse species.

<sup>5</sup> Nowlin (1978) reported low browsing quantities of dwarf birch and northern bog birch from moose. No information is currently known about white-tailed deer preference for these two species. Given that elk (*Cervus canadensis*) consider these two species of birch as low palatable winter browse (pers. comm. by Dr. Evelyn Merrill), the high ungulate browse prevalence must be from either moose and/or white-tailed deer. As a result, dwarf birch and northern bog birch will be compromised as a medium palatable winter browse species.

<sup>6</sup> High browse prevalence percentage is likely to be associated with snowshoe hare (*Lepus americanus*) winter browsing; these species are generally at snow pack level and may not be heavily accessible to moose and white-tailed deer. However, white-tailed deer has been shown to consume Labrador tea and blueberries in low quantities in the Upper Great Lakes region (Rogers et al. 1981). Therefore, these species will be considered as low palatable winter browse.

<sup>7</sup> Despite the fact that moose and white-tailed deer have not been shown to consume honeysuckles in the scientific literature, both ungulates occasionally consume honeysuckles in their winter diet in northern Alberta (pers. comm. by Dr. Evelyn Merrill). Therefore, mountain fly honeysuckle will be considered as a medium palatable winter browse species (as with twining honeysuckle and bracted honeysuckle).

<sup>8</sup> Pin cherry, chokecherry, and lowbush cranberry are fruiting shrubs highly favoured by moose and white-tailed deer. This has been documented in the scientific literature (Rhude and Hall 1977, Rogers et al. 1981, Renecker and Schwartz 2007), and confirmed by an expert specialized in ungulate foraging ecology in northern Alberta (pers. comm. by Dr. Evelyn Merrill). All three species will be considered as a highly palatable winter browse.

<sup>9</sup> Moose and white-tailed deer forage on wild red raspberries in the summer (mostly the berries themselves); they do not consume raspberries as heavily in the winter (pers. comm. by Dr. Evelyn Merrill). Wild red raspberry will be considered as a medium palatable winter browse species.

**Table 2.0.2.** Summary of the number of sapling detections, sapling abundance (stem density/100 m<sup>2</sup>), and winter ungulate browsing prevalence (in percentage) from 164 vegetation plots conducted in the summer of 2019 in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada. Sapling species are listed alphabetically by species code.

Sapling Species	Species Code	Number of detections	Prevalence (%)	Average Stem Density $\pm$ SD (per 100 m <sup>2</sup> )	Total number of stems	Number of browsed stems	Browse Prevalence (%)	Winter Browse Species	Ungulate Palatability Category <sup>1</sup>	Ungulate Palatability Category <sup>2</sup>
Trembling Aspen	Aw	68	41.5	40.1 $\pm$ 147.3	6,614	1,034	15.6	Yes	Low	High <sup>3</sup>
Balsam Poplar	Ab	11	6.7	0.4 $\pm$ 1.9	68	14	20.6	Yes	Medium	Medium
Paper Birch	Bw	42	25.6	1.3 $\pm$ 5.7	426	194	45.5	Yes	Medium	Preferred <sup>4</sup>
Balsam Fir	Fb	1	0.6	0.04 $\pm$ 0.5	12	0	00.0	No		
Tamarack	Lt	32	19.5	2.3 $\pm$ 7.2	818	176	21.5	Yes	Medium	Low <sup>5</sup>
Jack Pine	Pj	52	31.7	19.4 $\pm$ 102.4	3,204	540	16.9	Yes	Low	Low
Black Spruce	Sb	109	66.5	48.7 $\pm$ 72.9	8,036	6	0.1	Yes	Low	Low
White Spruce	Sw	23	14.0	2.3 $\pm$ 7.7	376	52	13.8	Yes	Low	Low

<sup>1</sup> Ungulate palatability category based on browse prevalence: None – 0% browsed prevalence; Low – 1 to 20% browsed prevalence; Medium – 21 to 50% browsed prevalence; High – 51 to 90% browsed prevalence; Preferred – 91 to 100% browsed prevalence.

<sup>2</sup> Ungulate palatability category standardized with findings in the literature and expert opinion on ungulate foraging ecology.

<sup>3</sup> Moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) have been shown to significantly forage on trembling aspen in the winter (Peek 1974a, Blouch 1984, Renecker 1987, Renecker and Schwartz 2007). Trembling aspen will be considered as a highly palatable winter browse species.

<sup>4</sup> Multiple publications have shown that paper birch is considered the universal principal food for moose as it is the most available and palatable winter browse species on the landscape (Peek 1974a, Regelin et al. 1987, Newbury et al. 2007, Renecker and Schwartz 2007). Paper birch has also been shown to be one of the many principal foods for white-tailed deer (Blouch 1984). Therefore, paper birch will be considered as a preferred winter browse species.

<sup>5</sup> Coniferous tree species can be part of moose winter diet, but they are generally not preferred and will only be consumed when hardwood availability or quality is low (Peek 1974a, Raymond et al. 1996, Newbury et al. 2007). White-tailed deer will forage on tamarack on rare occasions as “last resort” browse (Blouch 1984). In fact, coniferous needles are very low in nutrients and their consumption in high levels can lead to malnutrition, starvation, and death (Dahlberg and Guettinger 1956, Wetzell 1972). As a result, tamarack will be considered as a low palatable winter browse species.

**Table 2.0.3.** Summary of two-way ANCOVA models testing the effects of stand age and landcover types on deciduous shrub and sapling richness, Hill's Index, and abundance (number of stems/100 m<sup>2</sup>) preferred by ungulates. Beta coefficients ( $\beta$ ), standard errors (SE), and p-values ( $p$ ) are presented with black spruce forest as the reference category for landcover types. Statistically significant variables ( $p < 0.05$ ) are highlighted in bold.

	Deciduous shrubs			Saplings		
	$\beta$	SE	$p$	$\beta$	SE	$p$
<b>Species richness</b>						
Intercept	3.256	0.426	<b>&lt;0.001</b>	1.787	0.276	<b>&lt;0.001</b>
Stand age	-0.001	0.003	0.717	-0.003	0.002	0.140
Bog	-0.525	0.484	0.279	-0.132	0.314	0.675
Jack pine forest	-0.311	0.497	0.532	0.451	0.323	0.164
Mixedwood forest	2.229	0.473	<b>&lt;0.001</b>	0.701	0.307	<b>0.024</b>
Poor fen	1.694	0.537	<b>0.002</b>	1.003	0.348	<b>0.005</b>
Rich fen	0.915	0.581	0.117	0.335	0.377	0.375
<b>Hill's Index<sup>1</sup></b>						
Intercept	0.470	0.029	<b>&lt;0.001</b>	1.093	0.055	<b>&lt;0.001</b>
Stand age	-0.0003	0.0002	0.169	-0.0002	0.0004	0.585
Bog	-0.080	0.033	<b>0.018</b>	0.025	0.062	0.687
Jack pine forest	-0.003	0.034	0.924	0.146	0.064	<b>0.024</b>
Mixedwood forest	0.156	0.032	<b>&lt;0.001</b>	0.224	0.061	<b>&lt;0.001</b>
Poor fen	0.078	0.037	<b>0.037</b>	0.268	0.069	<b>&lt;0.001</b>
Rich fen	0.015	0.040	0.706	0.184	0.075	<b>0.015</b>
<b>Abundance<sup>2</sup></b>						
Intercept	16.844	2.247	<b>&lt;0.001</b>	13.744	1.956	<b>&lt;0.001</b>
Stand age	-0.0005	0.018	0.980	-0.087	0.026	<b>&lt;0.001</b>
Bog	10.688	2.552	<b>&lt;0.001</b>	-5.772	2.396	<b>0.017</b>
Jack pine forest	-2.735	2.624	0.299	-3.596	2.473	0.148
Mixedwood forest	2.377	2.496	0.343	1.437	2.387	0.548
Poor fen	9.921	2.833	<b>&lt;0.001</b>	-4.354	2.562	0.091
Rich fen	12.686	3.069	<b>&lt;0.001</b>	-4.994	2.834	0.080
Stand age $\times$ Bog	–	–	–	0.115	0.032	<b>&lt;0.001</b>
Stand age $\times$ Jack pine	–	–	–	0.024	0.043	0.574
Stand age $\times$ Mixedwood	–	–	–	-0.038	0.037	0.301
Stand age $\times$ Poor fen	–	–	–	0.055	0.043	0.203
Stand age $\times$ Rich fen	–	–	–	0.077	0.048	0.107

<sup>1</sup>  $\beta$  and SE are log transformed for deciduous shrub Hill's Index, but square root transformed for sapling Hill's Index.

<sup>2</sup>  $\beta$  and SE are square root transformed for both deciduous shrub and sapling abundance.

**Table 2.0.4.** Summary of three-way ANCOVA model testing the effects of stand age, landcover, and palatability categories on abundance of deciduous shrubs and saplings (log(number of stems/100 m<sup>2</sup>)). Beta coefficients ( $\beta$ ), standard errors (SE), and p-values ( $p$ ) are presented with black spruce forest and preferred winter browse as the reference category for landcover categories and palatability, respectively. Statistically significant variables ( $p < 0.05$ ) are highlighted in bold.

	Deciduous shrubs			Saplings		
	$\beta$	SE	$p$	$\beta$	SE	$p$
Intercept	1.194	0.176	<b>&lt;0.001</b>	0.337	0.124	<b>0.007</b>
Stand age	-0.011	0.004	<b>0.008</b>	-0.003	0.003	0.265
Bog	0.065	0.190	0.732	-0.330	0.134	<b>0.014</b>
Jack pine forest	-0.416	0.187	<b>0.027</b>	-0.170	0.132	0.198
Mixedwood forest	0.411	0.182	<b>0.024</b>	0.098	0.128	0.444
Poor fen	0.708	0.197	<b>&lt;0.001</b>	0.003	0.139	0.984
Rich fen	0.541	0.211	<b>0.011</b>	-0.203	0.148	0.172
High	-0.464	0.135	<b>&lt;0.001</b>	0.747	0.095	<b>&lt;0.001</b>
Moderate	-0.296	0.135	<b>0.029</b>	-0.174	0.095	0.067
Low	0.380	0.135	<b>0.005</b>	1.089	0.095	<b>&lt;0.001</b>
Stand age $\times$ High	0.006	0.005	0.228	-0.012	0.003	<b>0.001</b>
Stand age $\times$ Moderate	-0.002	0.005	0.762	0.0009	0.003	0.803
Stand age $\times$ Low	0.020	0.005	<b>&lt;0.001</b>	0.003	0.003	0.401
Stand age $\times$ Bog $\times$ Preferred	0.0006	0.005	0.912	0.004	0.003	0.283
Stand age $\times$ Jack pine $\times$ Preferred	0.005	0.005	0.347	0.004	0.004	0.270
Stand age $\times$ Mixedwood $\times$ Preferred	-0.003	0.005	0.533	0.003	0.003	0.443
Stand age $\times$ Poor fen $\times$ Preferred	0.007	0.006	0.268	-0.001	0.004	0.911
Stand age $\times$ Rich fen $\times$ Preferred	0.008	0.006	0.158	0.003	0.004	0.530
Stand age $\times$ Bog $\times$ High	-0.004	0.005	0.460	0.005	0.003	0.173
Stand age $\times$ Jack pine $\times$ High	0.012	0.005	<b>0.024</b>	0.002	0.004	0.612
Stand age $\times$ Mixedwood $\times$ High	0.019	0.005	<b>&lt;0.001</b>	0.014	0.003	<b>&lt;0.001</b>
Stand age $\times$ Poor fen $\times$ High	-0.009	0.006	0.135	-0.001	0.004	0.910
Stand age $\times$ Rich fen $\times$ High	-0.013	0.006	<b>0.030</b>	0.003	0.004	0.536
Stand age $\times$ Bog $\times$ Moderate	0.006	0.005	0.244	0.005	0.003	0.180
Stand age $\times$ Jack pine $\times$ Moderate	0.006	0.005	0.290	0.003	0.004	0.472
Stand age $\times$ Mixedwood $\times$ Moderate	0.007	0.005	0.127	-0.001	0.003	0.880
Stand age $\times$ Poor fen $\times$ Moderate	0.012	0.006	<b>0.049</b>	0.001	0.004	0.828
Stand age $\times$ Rich fen $\times$ Moderate	0.029	0.006	<b>&lt;0.001</b>	0.003	0.004	0.480
Stand age $\times$ Bog $\times$ Low	0.006	0.005	0.190	0.014	0.003	<b>&lt;0.001</b>
Stand age $\times$ Jack pine $\times$ Low	0.008	0.005	0.115	0.002	0.004	0.607
Stand age $\times$ Mixedwood $\times$ Low	-0.012	0.005	<b>0.011</b>	-0.010	0.003	<b>0.002</b>
Stand age $\times$ Poor fen $\times$ Low	-0.008	0.006	0.216	0.003	0.004	0.546
Stand age $\times$ Rich fen $\times$ Low	-0.020	0.006	<b>&lt;0.001</b>	0.007	0.004	0.088



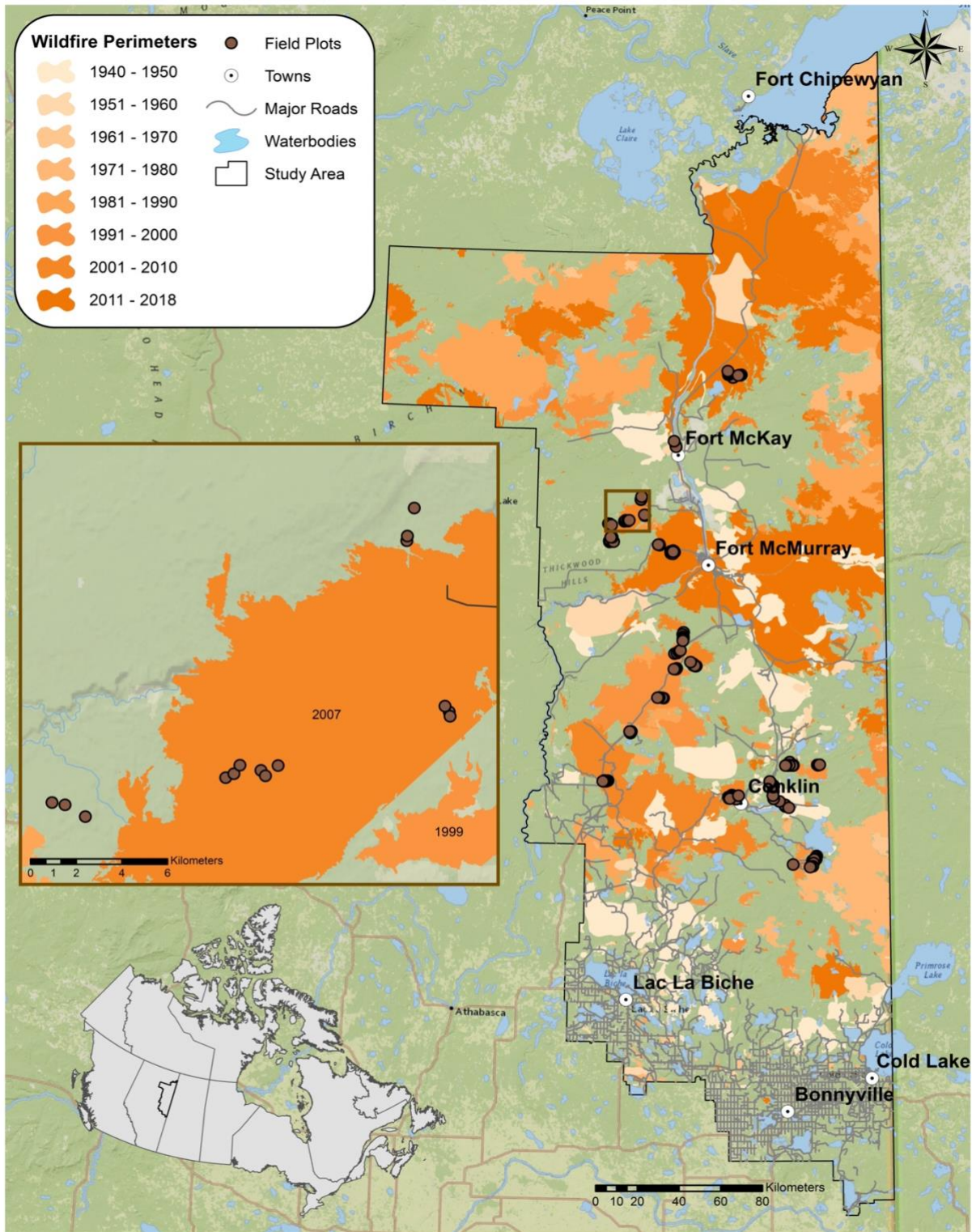
**Table 2.0.5.** Summary of the ordinal logistic regression models testing the effects of stand age, landcover, and presence of deciduous shrubs on winter browse percentage and browse severity. Odd ratios (OR), beta coefficients ( $\beta$ ), standard errors (SE), and p-values ( $p$ ) are presented with black spruce forest as the reference category for landcover categories. Statistically significant variables ( $p < 0.05$ ) are highlighted in bold. List of species code can be found in Appendix 4.

	Browse Percentage				Browse Severity			
	OR	$\beta$	SE	$p$	OR	$\beta$	SE	$p$
Stand age	1.013	0.013	0.002	<b>&lt;0.001</b>	1.014	0.014	0.002	<b>&lt;0.001</b>
Bog	1.387	0.327	0.314	0.298	1.312	0.272	0.321	0.396
Jack pine forest	3.136	1.143	0.307	<b>&lt;0.001</b>	2.567	0.943	0.310	<b>0.002</b>
Mixedwood forest	1.860	0.621	0.285	<b>0.029</b>	1.903	0.643	0.291	<b>0.027</b>
Poor fen	2.216	0.796	0.316	<b>0.012</b>	1.906	0.645	0.321	<b>0.045</b>
Rich fen	1.051	0.049	0.366	0.893	1.059	0.057	0.370	0.877
AlnVir	1.581	0.458	0.522	0.380	1.732	0.549	0.529	0.300
BetGla	9.673	2.269	0.571	<b>&lt;0.001</b>	13.440	2.598	0.576	<b>&lt;0.001</b>
BetPum	2.748	1.011	0.484	<b>0.037</b>	3.310	1.197	0.493	<b>0.015</b>
LedGro	2.981	1.092	0.415	<b>0.009</b>	2.957	1.084	0.421	<b>0.010</b>
LonDio	0.374	-0.985	0.868	0.257	0.384	-0.958	0.877	0.275
LonInv	0.569	-0.563	0.770	0.465	0.548	-0.601	0.775	0.438
LonVil	1.036	0.035	0.696	0.960	1.137	0.128	0.699	0.854
PruPen	1.941	0.663	0.731	0.364	2.439	0.892	0.744	0.231
RibSpp	0.248	-1.395	0.669	<b>0.037</b>	0.248	-1.391	0.672	<b>0.039</b>
RosAci	4.263	1.450	0.435	<b>&lt;0.001</b>	4.220	1.440	0.439	<b>0.001</b>
RubIda	0.213	-1.548	0.857	0.071	0.194	-1.641	0.857	0.056
Salix	5.153	1.640	0.425	<b>&lt;0.001</b>	4.918	1.593	0.429	<b>&lt;0.001</b>
SheCan	0.622	-0.474	0.629	0.451	0.623	-0.474	0.634	0.455
VacMyr	4.151	1.423	0.431	<b>&lt;0.001</b>	3.923	1.367	0.436	<b>0.002</b>
0   1	–	1.536	0.464	<b>&lt;0.001</b>	–	1.531	0.469	<b>0.001</b>
1   2	–	2.248	0.469	<b>&lt;0.001</b>	–	3.222	0.482	<b>&lt;0.001</b>
2   3	–	2.972	0.475	<b>&lt;0.001</b>	–	4.178	0.494	<b>&lt;0.001</b>
3   4	–	4.000	0.486	<b>&lt;0.001</b>	–	5.553	0.529	<b>&lt;0.001</b>
4   5	–	5.614	0.525	<b>&lt;0.001</b>	–	–	–	–

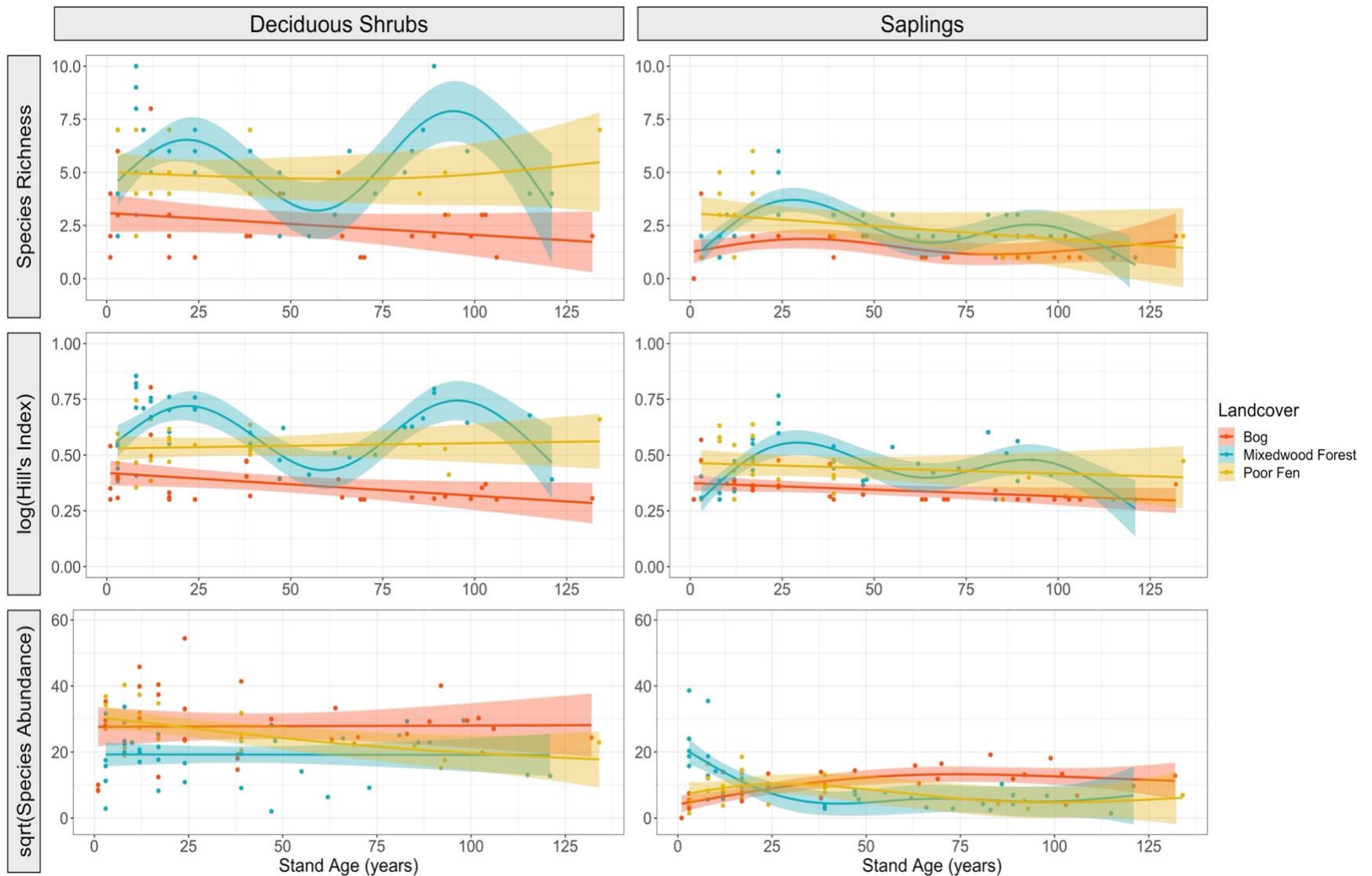
**Table 2.0.6.** Summary of the ordinal logistic regression models testing the effects of stand age, landcover, and the presence of saplings on winter browse percentage and browse severity. Odds ratios (OR), beta coefficients ( $\beta$ ), standard errors (SE), and p-values ( $p$ ) are presented with black spruce forest as the reference category for landcover categories. Statistically significant variables ( $p < 0.05$ ) are highlighted in bold. List of species code can be found in Appendix 4.

	Browse Percentage				Browse Severity			
	OR	$\beta$	SE	$p$	OR	$\beta$	SE	$p$
Stand age	1.006	0.006	0.006	0.343	1.007	0.006	0.006	2862
Bog	1.455	0.375	0.998	0.707	1.443	0.367	1.001	0.714
Jack pine forest	2.675	0.984	0.855	0.250	2.457	0.899	0.855	0.293
Mixedwood forest	2.234	0.804	0.819	0.326	2.226	0.800	0.821	<b>0.030</b>
Poor fen	0.754	-0.282	1.003	0.778	0.735	-0.308	1.004	0.759
Rich fen	1.240	0.215	1.161	0.853	1.238	0.213	1.160	0.854
Aw	2.645	0.973	0.694	0.161	2.725	1.003	0.695	0.149
Bw	3.586	1.277	0.723	0.078	3.731	1.317	0.724	0.069
Lt	0.740	-0.301	1.144	0.792	0.740	-0.301	1.144	0.792
Pj	0.467	-0.762	0.905	0.400	0.492	-0.709	0.907	0.434
Sb	0.150	-1.895	1.016	0.062	0.152	-1.882	1.019	0.065
0   1	–	2.765	1.038	<b>0.008</b>	–	2.794	1.041	<b>0.007</b>
1   2	–	3.334	1.050	<b>0.002</b>	–	4.109	1.070	<b>&lt;0.001</b>
2   3	–	3.803	1.061	<b>&lt;0.001</b>	–	4.368	1.079	<b>&lt;0.001</b>
3   4	–	4.677	1.093	<b>&lt;0.001</b>	–	6.139	1.255	<b>&lt;0.001</b>
4   5	–	6.100	1.250	<b>&lt;0.001</b>	–	–	–	–

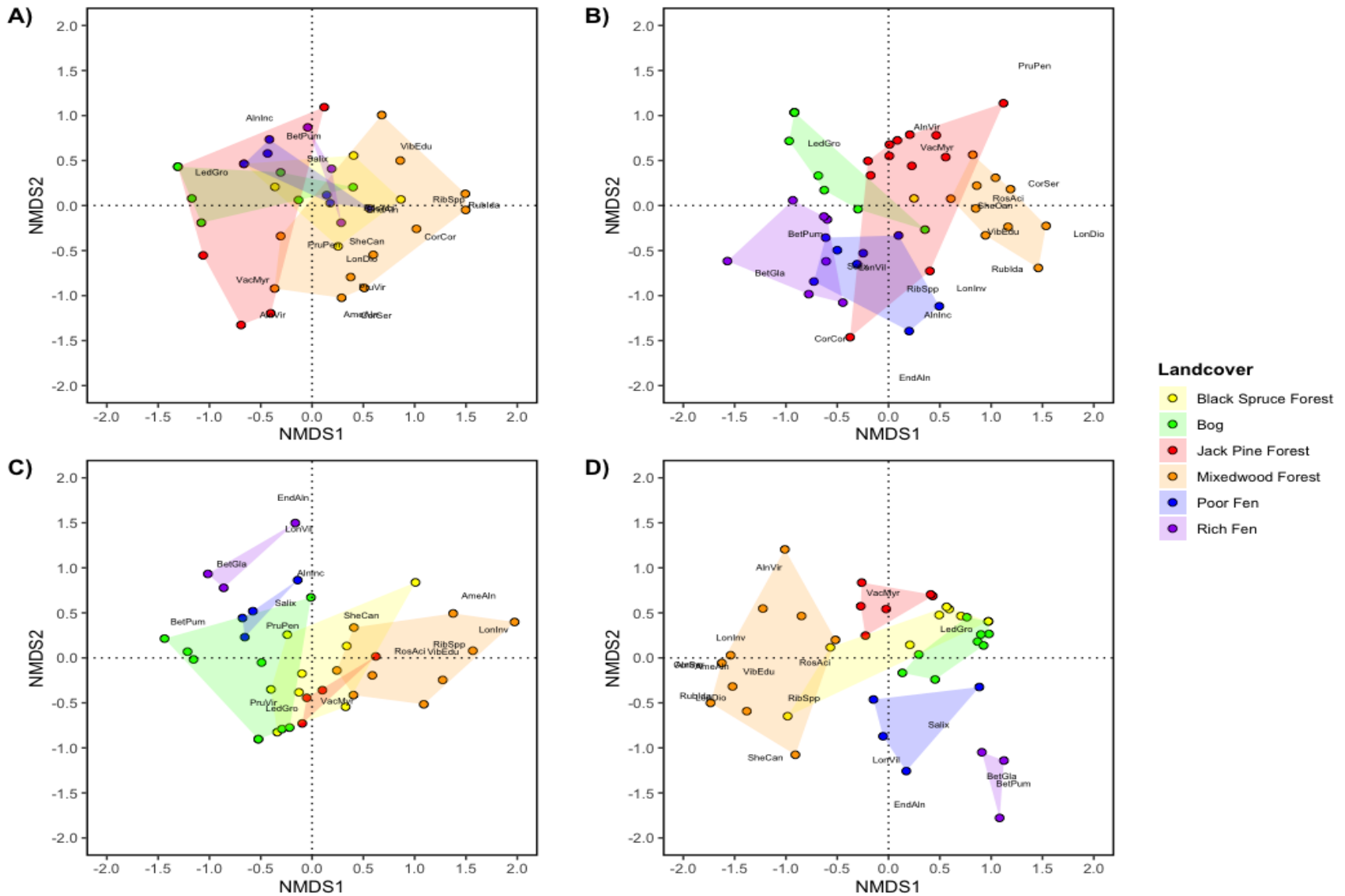
## Figures



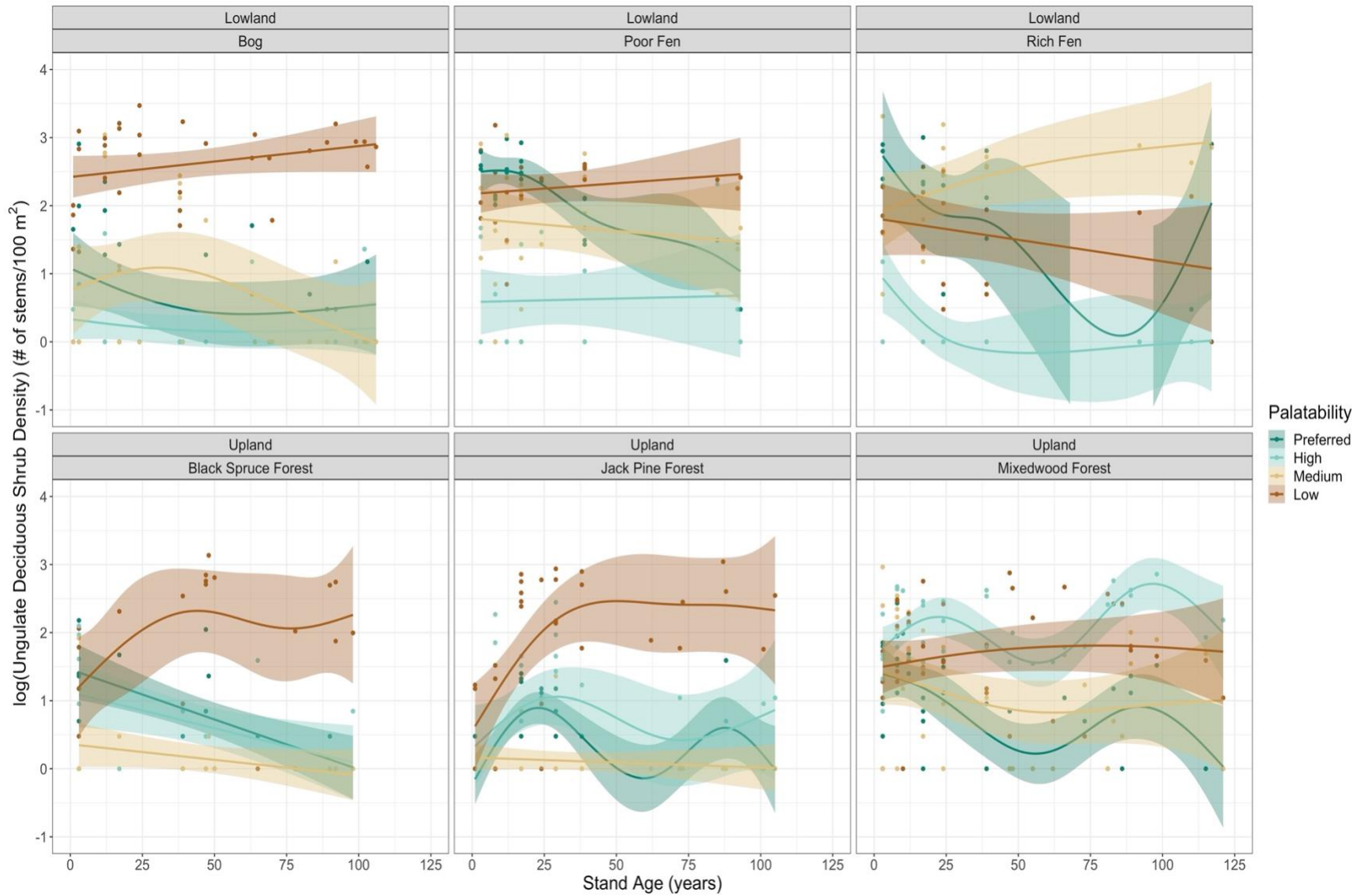
**Figure 2.0.1.** Location of 164 field plots sampled in the summer of 2019 in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada (Fort McMurray is located at  $56^{\circ}43'N$ ,  $111^{\circ}23'W$ ). Inset map of Canada in the lower left with outline of study area.



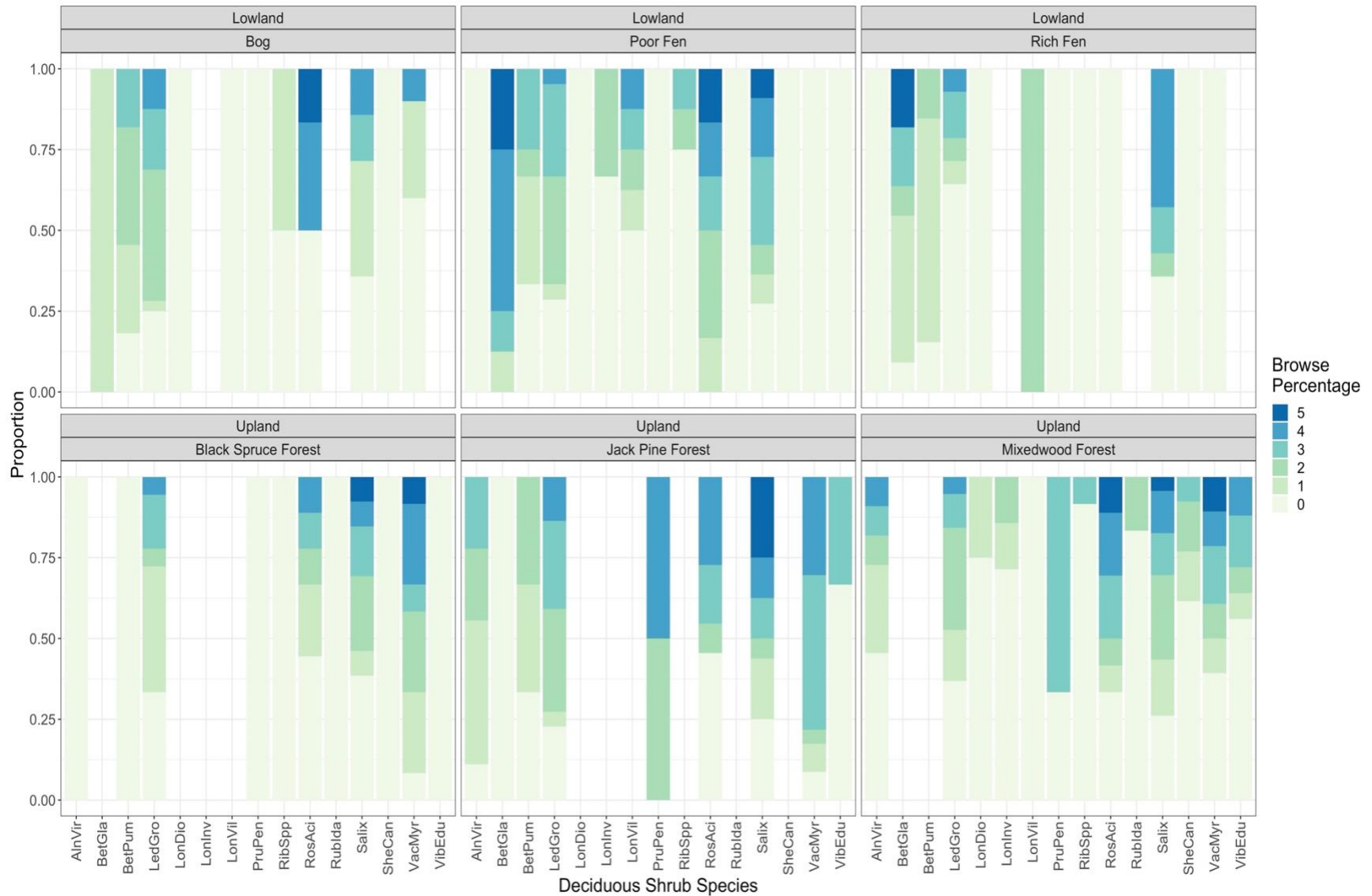
**Figure 2.0.2.** Comparison of temporal changes (stand age) in deciduous shrub and sapling richness consumed by moose and white-tailed deer, Hill's Index, and abundance (number of stems/100 m<sup>2</sup>) in mixedwood forests, bogs and poor fens in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



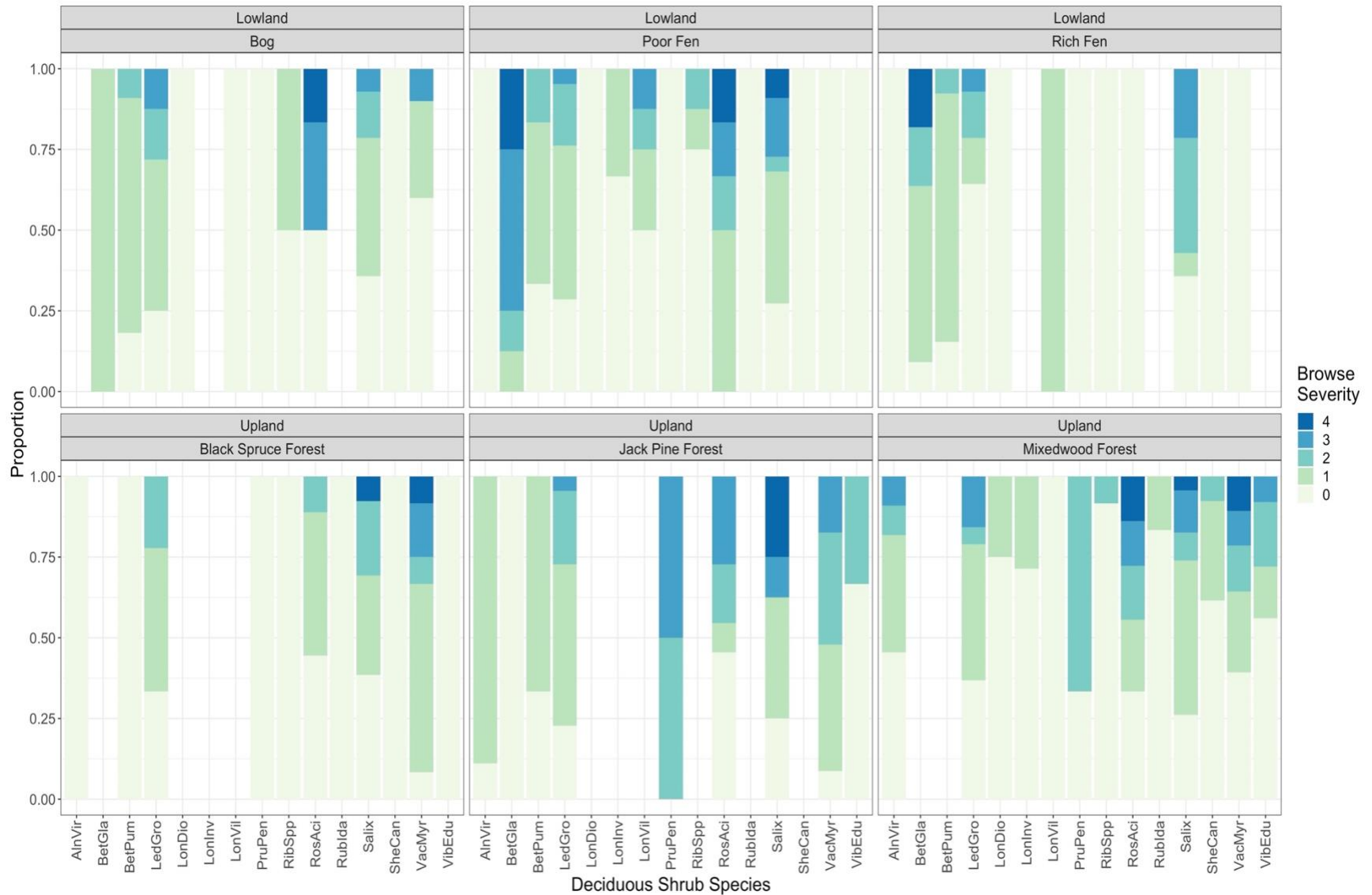
**Figure 2.0.3.** Temporal changes (stand age) in deciduous shrub composition for species consumed by moose and white-tailed deer in A) 0 – 10 years post-wildfire (young forest), B) 11 – 30 years post-wildfire (young forest), C) 31 – 70 years post-wildfire (intermediate forest), and D)  $\geq 71$  years post-wildfire (mature forest) in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



**Figure 2.0.4.** Temporal changes (stand age) in deciduous shrub abundance (number of stems/100 m<sup>2</sup>) by palatability categories in six landcover types in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



**Figure 2.0.5.** Proportion of winter browse category (by percentage) for each deciduous shrub species consumed by moose and white-tailed deer in six landcover types in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



**Figure 2.0.6.** Proportion of winter browse category (by severity) for each deciduous shrub species consumed by moose and white-tailed deer in six landcover types in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



## **CHAPTER 3 – MAKE-OR-BREAK: WILL FUTURE WINTER HABITAT CONDITIONS BE SUITABLE FOR TWO NORTHERN UNGULATES?**

### **3.1. Abstract**

Changes in climate and wildfire are altering the distribution and composition of vegetation in the western boreal forest of North America. Climate change is also reducing winter severity for ungulates through milder winter conditions and reduced snow cover. Likewise, winter browse availability for generalist ungulates, such as moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*), are expected to increase following more frequent wildfires. Recent studies have focused on climate-change responses of woodland caribou (*Rangifer tarandus caribou*), but the spatial and temporal consequences of changing wildfire regimes, vegetation types, and winter severity on the distribution and quality of moose and white-tailed deer winter habitat are much less understood. Here, I developed a winter nutritional habitat index for moose and white-tailed deer for the boreal forest of northern Alberta, Canada, based on projected changes in vegetation and fire regime in 2040, 2070 and 2100. Contrary to my expectations, projected changes in vegetation in the 21<sup>st</sup> century were predicted to decrease nutritional resources by 13–72% for both moose and white-tailed deer due to the potential replacement of deciduous and mixedwood forests with more grass-dominated systems. Predation risk and winter habitat for both moose and white-tailed deer would decrease slightly under climate-change scenarios that assume current vegetation persists. However, under fire-mediated vegetation change scenarios, predation risk was projected to increase by 105–126% for moose, and decrease by 40–43% for white-tailed deer by 2100. Depending on the relative contribution of predation risk to the habitat index, moose could experience from a 74% reduction to a 77% increase in winter habitat, while winter habitat for white-tailed deer could decrease between 33–76% by 2100. Without major vegetation change, winter habitat conditions for moose and white-tailed deer will remain similar to current conditions,

but climate-induced changes in vegetation could compromise the long-term persistence of moose and white-tailed deer in the boreal forest of Alberta.

### **3.2. Introduction**

Boreal ecosystems are experiencing higher rates of warming than any other forested region on the planet (Gauthier et al. 2015). Consequently, boreal forests are predicted to experience major changes in forest composition and age structure over the 21<sup>st</sup> century (Price et al. 2013, Gauthier et al. 2015, Boulanger et al. 2017). Although wildfire is a frequent and widespread natural disturbance in the boreal forest of North America (Stocks et al. 2002, Bergeron et al. 2014), recent anthropogenic climate change has increased the frequency and extent of moisture deficits (Peng et al. 2011), leading to more frequent and larger wildfires, especially in western North America (Kasischke and Turetsky 2006, Hanes et al. 2019). In fact, wildfires have burned 2.1 Mha of boreal forests in North America every year over the last decade (Rogers et al. 2015). Combined changes in temperature and precipitation are expected to shift boreal tree species' distributions northward by hundreds of kilometres (McKenney et al. 2007, Rehfeldt et al. 2012).

Under a stable climate and fire regime, composition of boreal vegetation is highly resilient at the landscape scale (Johnstone et al. 2010a). Thus, boreal forests have the ability to return to the same state (i.e., vegetation composition) after natural disturbances (Johnstone et al. 2010a). However, changing climate conditions may lead to multiple quasi-equilibria within the historical range of variability in vegetation composition and structure (Holling 1973, Nikinmaa et al. 2020). Longer and more severe droughts caused by reductions in moisture availability (Hogg and Hurdle 1995, Price et al. 2013), coupled with increased wildfire frequency and severity (Boulanger et al. 2014), ultimately favour the development of alternate successional pathways by transforming coniferous forests and conifer-dominated mixedwood forests into deciduous forests, shrublands,

or grasslands (Johnstone et al. 2010b, 2020, Scheffer et al. 2012, Stralberg et al. 2018). In fact, this phenomenon has already been detected in approximately 13.6% of the boreal forest of western North America within the last three decades (1984–2014) (Wang et al. 2020).

Additionally, increased wildfire frequency in the boreal forest leads to shorter disturbance intervals that may disrupt coniferous dominance (Johnstone et al. 2010a, Whitman et al. 2019). Frequent wildfires have been found to lower seed availability and regeneration of serotinous conifers (i.e., black spruce [*Picea mariana*], lodgepole pine [*Pinus contorta*], and jack pine [*Pinus banksiana*]) because these species rely on aerial seed banks stored in serotinous cones that take several decades to develop (Greene and Johnson 1999). In fact, upland forests that burned twice within a 30-year fire interval in the Northwest Territories, Canada, had lower coniferous regeneration post-wildfire than upland forests that had a longer fire-free interval, resulting in a shift to a deciduous-dominated forest (Whitman et al. 2019). Thus, higher severity fires and, to a lesser extent, shorter fire intervals, alter post-wildfire boreal successional pathways by inhibiting coniferous recruitment and facilitating deciduous recruitment in the western boreal forest.

Consequently, understanding the direct and indirect effects of climate change, and subsequently climate-induced wildfires, on species' ranges are fundamental for land use management and biodiversity conservation (Chen et al. 2011, Gilbert et al. 2020). Wildfires provide moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) with increased quantity and quality of their preferred browse for up to 50 years post-wildfire (MacCracken and Viereck 1990, Weixelman et al. 1998, Lord and Kielland 2015), although recent evidence suggests that it is even longer in the southern portion of the boreal forest (see Chapter 2). Greater forage availability from wildfires is directly linked with ungulate abundance (Peek 1974b, Schwartz and Franzmann 1989, Loranger et al. 1991); therefore, it is expected that climate-induced wildfires

will increase browse quantity and quality, potentially resulting in higher ungulate densities. However, climate is also known to influence ungulate life-history traits and population dynamics (Post and Stenseth 1998, Garroway and Broders 2005, Weiskopf et al. 2019). Deep snow and cold temperatures negatively impact winter survival in northern ungulates by increasing energetic costs (Parker et al. 1984, DelGiudice et al. 2002, Dumont et al. 2005, Kautz et al. 2020). In fact, winter severity is the most important predictor of white-tailed deer distribution and expansion in the western boreal forest (Dawe et al. 2014, Dawe and Boutin 2016, Kennedy-Slaney et al. 2018), although landscape change (i.e., forage subsidies) also helps increase abundance of this species (Fisher et al. 2020a).

Mean daily minimum temperature in the southern boreal forest is expected to increase up to 6.5°C in winter (Price et al. 2013), and temperature increases have already been evident in northern Alberta, Canada, as mild winters have become more frequent since 1950 (Kienzle 2018). Climate change will continue to reduce winter severity by creating milder winter conditions and reduced snow cover (Shabbar and Bonsal 2003, Brown and Mote 2009, Jeong et al. 2016), while climate-induced wildfires will increase winter food availability for ungulates. Given that moose are limited by winter forage availability, climate-induced wildfires could benefit this species; however, warmer winter temperatures may increase winter heat stress by increasing metabolism, heart rate, and respiration rate, thereby reducing food intake, body weight, and body condition (Renecker and Hudson 1986a). Thus, seasonal differences in climate change may offset any benefits of increased forage availability leading to moose population declines in the southern portion of their boreal range (Rempel 2011, Weiskopf et al. 2019). In contrast, white-tailed deer are limited by cold winter temperatures and deep snow, and it appears inevitable that white-tailed deer expansion will continue in the southern boreal forest (Dawe and Boutin 2016, Weiskopf et al.

2019). This expansion has management and conservation implications as intensive management efforts will be needed to maintain densities low enough to minimize apparent competition (through increased wolf densities) with woodland caribou (*Rangifer tarandus caribou*), as well as fatal disease spread from white-tailed deer to other ungulates.

The purpose of this study is to use landscape change simulations to assess the long-term effects of climate-induced wildfires on the distribution and quality of moose and white-tailed deer winter habitat in the boreal mixedwood forests of northern Alberta, Canada. This study investigated winter habitat as opposed to other seasons because northern ungulates undergo periods of negative energy balance in winter (Dumont et al. 2005), as they cannot meet their energy requirements from ingestion of woody browse (Ullrey et al. 1970, Mautz et al. 1976). Because of this limitation, winter strongly influences ungulate life-history traits and population dynamics (Post and Stenseth 1998, Garroway and Broders 2005, Weiskopf et al. 2019). Landscape change simulation models have recently been used to capture broad-scale ecosystem shifts in a climate change context in northern Alberta (Stralberg et al. 2018). Researchers have built on these models to predict changes in habitat components (i.e., nutritional resources and predation risk) of ungulate habitat suitability (Whitman et al. 2017, Barber et al. 2018). This is particularly useful for wildlife management and conservation given the novel habitat conditions that ungulates will experience as a consequence of altered fire regimes and climate-vegetation decoupling. The objective of this study is to use new models for deciduous shrub and sapling density to develop a winter habitat index for moose and white-tailed deer, and to use this index to predict changes in fire weather, fire regime, and fuels under high-end climate-change scenarios for the 21<sup>st</sup> century. I hypothesized that climate-induced wildfires would promote changes in the quality of moose and white-tailed deer winter habitat. I predicted that climate-induced wildfires and associated vegetation changes would

increase available winter habitat for both moose and white-tailed deer throughout the 21<sup>st</sup> century (i.e. 2020s < 2050s < 2080s). Although this has been predicted, it has not been adequately tested and directly measured with respect to winter forage, which is the focus of this work.

### **3.3. Study Area**

This research took place in the boreal mixedwoods of the Boreal Plains Ecozone of northern Alberta, Canada (Figure 3.1), specifically within the Central Mixedwood and Lower Boreal Highland Subregions of Alberta (Natural Regions Committee 2006). This area encompassed 113,044 km<sup>2</sup> of boreal upland forest and peatland complex; including the Birch Mountains and Peerless Lake Uplands in the north, Utikuma Lake Uplands and parts of the Buffalo Head Hills in the west, Stony Mountain and parts of Pelican Mountains in the southeast, and the Firebag Hills in the northeast. Elevation ranged from approximately 200 m along the Athabasca River to 868 m in the Birch Mountains. The boreal mixedwoods are characterized as dry continental with long cold winters and short warm summers with mean temperatures ranging from 15.9 °C and -18.7 °C and mean annual precipitation at 478 mm (Natural Regions Committee 2006).

The study area is characterized by a rolling upland forest mosaic interspersed with extensive peatlands of bogs, treed fens, shrubby fens, and sedge fens (Natural Regions Committee 2006). Upland forests are primarily characterized by mixedwood forests composed of trembling aspen, balsam poplar, and white spruce. However, coniferous forests of black spruce and jack pine are also common in some upland forests. Common shrub species in upland forests are alders (*Alnus* spp.), lowbush cranberry (*Viburnum edule*), prickly wild rose (*Rosa acicularis*), Canada buffaloberry (*Shepherdia canadensis*), common blueberry (*Vaccinium myrtilloides*), and Labrador tea (*Ledum groenlandicum*). Black spruce and tamarack (*Larix laricina*) are the dominant species in peatlands. Understory vegetation consist mainly of Labrador tea, peat moss (*Sphagnum* spp.),

sedges (*Carex* spp.), bog birch (*Betula pumila*), and several species of lichens (e.g.: *Cladina* spp. and *Peltigera* spp.). Grasslands occupy less than 1% of the study area, occurring only as small patches in jack pine on dry, coarse, and well-drained soils (Natural Regions Committee 2006). Grasslands are mainly composed of northern rice grass (*Piptatherum pungens*), Rocky Mountain fescue (*Festuca saximontana*), sedges, and plains wormwood (*Artemisia campestris*) (Natural Regions Committee 2006).

Northern Alberta's boreal wildfire regime is characterized by large, infrequent, and intense stand-renewing wildfires (Kasischke and Turetsky 2006, Erni et al. 2020). In the boreal mixedwoods, wildfires are initiated by both lightning strikes and humans (51.1% lightning and 48.9% human-caused; Erni et al. 2020) and peak wildfire season occurs from April to June, although wildfires in July, August, and September are common (Erni et al. 2020). Mean wildfire size in the boreal mixedwood is 392 ha and the fire return interval is estimated between 63–180 years (Larsen 1997, De Groot et al. 2013, Erni et al. 2020). The boreal mixedwoods contain little urban development and agricultural activities (<1%); however, the industrial footprint is quite extensive as a result of forest harvesting, oil and gas exploration, mines, and linear disturbances (Schneider et al. 2003). Linear disturbances, such as roads, railways, transmission lines, pipelines, and seismic lines (2–8 m wide clear-cut lines), are an ubiquitous form of landscape disturbance associated with oil and gas exploration in northern Alberta (Pattison et al. 2016). In the boreal mixedwoods, linear disturbances occur at mean densities of 1–5 km/km<sup>2</sup>, but can be as high as 40 km/km<sup>2</sup> in some areas (Schneider et al. 2010, Stern et al. 2018).

### **3.4. Methods**

#### *3.4.1. Habitat components*

Winter habitat for moose and white-tailed deer were modified from a framework described by Whitman et al. (2017) and Barber et al. (2018). Winter habitat was divided into three habitat components: (1) nutritional resources, (2) predation risk, and (3) winter survival. The nutritional resources and predation risk habitat components were matrices with weight values ranging from 0 to 1 that estimate winter habitat quality for a landcover type and age class (Appendix 3.1). A weight of 1 represented a landcover type and age class with the greatest use for nutritional purposes (i.e., forage availability and quality), but with the lowest risk of predation (i.e., low relative probability of encountering a wolf). Likewise, a weight of 0 corresponded to landcover types and age classes with poor nutritional resources and high predation risk. On the other hand, the winter survival component represented a winter severity index (WSI) combining daily snow-water equivalent ( $\text{kg/m}^2$ ) and minimum air temperature ( $^{\circ}\text{C}$ ) with values ranging from 0 to 1 irrespective of a landcover type and age class. Therefore, a weight of 1 represented an area with low WSI values (i.e., highest winter survival), whereas a weight of 0 corresponded to areas with high WSI values, and low winter survival.

##### *3.4.1.1. Nutritional resources*

Contrary to Whitman et al. (2017) and Barber et al. (2018) who used coefficients from previous Resource Selection Function (RSFs) studies, estimation of nutritional resources for moose and white-tailed deer within each landcover type and age class were derived from direct field measures from the study area by developing detailed and comprehensive models of deciduous shrub and sapling density for the region (Routh and Nielsen 2021). Specifically, Routh and Nielsen (2021) investigated moose and white-tailed deer winter browse (i.e., deciduous shrub and sapling)



succession in the first 150 years post-wildfire in upland and lowlands forests of the boreal mixedwoods of northeastern Alberta, Canada. Stem densities of 27 shrub species and 7 sapling species were measured in the field from a total of 164 field plots in the summer of 2019. Based on prevalence of ungulate browsing recorded in the field, deciduous shrub and sapling species were classified into palatability categories (see Table 2.1 and 2.2 from Chapter 2), and later included in a three-way analysis of covariance (ANCOVA) using  $\log_{10}$  transformed deciduous shrub and sapling density as the response variable and stand age (as a continuous variable) and landcover type as fixed effects.

The ANCOVA model was used to predict deciduous shrub and sapling density as a function of landcover type, age class, and palatability category (i.e., preferred, high, medium and low). Four predicted values were used for each age class (e.g.: predicted values for the “<20” age class were at 1-, 7-, 14- and 20-years post-wildfire) for deciduous shrubs and saplings separately. To account for the higher nutritional values of preferred deciduous shrubs and saplings over lower palatability winter browse (i.e., high, medium and low browse species), predicted values of deciduous shrub and sapling density were multiplied by a constant. Specifically, predicted values were multiplied by 10, 5, 2 and 1 for preferred, high, medium, and low palatability, respectively. These four palatability weights (i.e., predicted values  $\times$  constant) were summed and averaged, thus creating a single unstandardized weighted coefficient for each landcover type and age class. These unstandardized weighted coefficients were then standardized to range from 0.01 to 1 using the following linear transformation equation:

$$\textit{Standardized Weight}_i = (0.99) \frac{\textit{Model Coefficient}_i - \textit{Model Coefficient}_{\textit{min}}}{\textit{Model Coefficient}_{\textit{max}} - \textit{Model Coefficient}_{\textit{min}}} + 0.01$$

Non-vegetated landcover types, such as anthropogenic disturbances (i.e., urban and agriculture areas) and lakes were masked by assigning a nutritional resource weight of 0. Additional details

on the decisions and assumptions used to prescribe an unstandardized weighted coefficient for each landcover type and age class for moose and white-tailed deer can be found in Appendix 3.1.

#### 3.4.1.2. Predation risk

Estimation of wolf predation risk for moose and white-tailed deer within each landcover type and age class were derived from empirical coefficients reported in RSF models of moose and white-tailed deer from previous studies. Specifically, coefficients for moose were from Osko et al. (2004) and Fisher et al. (2020) for white-tailed deer (Appendix 3.1). Both studies examined habitat selection within the study area (i.e., Boreal Plains ecoregion of Alberta), and do not represent direct mortality by wolves, the primary predator of both ungulates (Latham et al. 2011*b*). Thus, the distribution of wolves on the landscape was considered in this study to be more representative of the reality between predator-prey relationships. For example, moose are known to select mixedwood forests in early winter and progressively shift into coniferous forests as winter progresses and snow depth reaches critical levels (Timmermann and McNicol 1988, Bjørneraas et al. 2011); yet this spatial behaviour could be associated with thermoregulation or foraging opportunities rather than strategies for predator escape. By including wolf habitat selection in winter, landcover types that are more frequented by wolves, such as mixedwood forests (Latham 2009), would therefore have higher predation risk in comparison with other landcover types because ungulates are more likely to encounter a wolf. The inclusion of winter habitat selection of wolves was done by adjusting the coefficients from Osko et al. (2004) and Fisher et al. (2020) with those reported in Latham (2009).

However, RSF studies report unstandardized coefficients which ultimately differ between studies as a result of differences in the range or magnitude of measured data (e.g., stand age

measured on a categorical or continuous scale); therefore, coefficients were inversely standardized to weights ranging from 0.01 to 1 using the following linear transformation equation:

$$\text{Standardized Weight}_i = 1 - \left[ (0.99) \frac{\text{RSF Coefficient}_i - \text{RSF Coefficient}_{\min}}{\text{RSF Coefficient}_{\max} - \text{RSF Coefficient}_{\min}} \right]$$

Non-vegetated landcover types, such as anthropogenic disturbances (i.e., urban and agriculture areas) and lakes, were also masked by assigning a predation risk weight of 0. Additional details on the decisions and assumptions taken to prescribe an RSF coefficient for each landcover type and age class for both moose and white-tailed deer can be found in Appendix 3.1.

#### 3.4.1.3. Winter survival

Estimation of winter survival was derived from a winter severity index (WSI) combining daily snow-water equivalent (SWE; kg/m<sup>2</sup>) and minimum air temperature (TMIN; °C). SWE is the amount of water that would result from melting a quantity of snow, and is dependent on snow depth and snow density. Daily SWE and TMIN data were obtained from “Daymet” by the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC; Thornton et al. 2018), a data product which extrapolated daily meteorological observations since 1980 to produce daily estimates of weather parameters at 1 km × 1 km resolution (Thornton et al. 2018). Daily SWE and TMIN rasters from 1980 to 2000 were downloaded directly from the ORNL DAAC website available online (<https://daymet.ornl.gov/overview>). Only rasters from between 1 November and 30 April for each year were used in this study as they are biologically relevant to the research objectives (i.e., the snow period in northern Alberta), and were later clipped to the study area and resampled at a 500-m resolution.

Previous research has found that white-tailed deer movement is limited by snow depth over 38 cm and winter temperatures below -17.7 °C as it significantly reduces body condition (DelGiudice et al. 2002, Garroway and Broders 2005). In fact, snow depths greater than 45 cm

exclude this species from an environment (Gilbert et al. 1970, Telfer 1978, Parker et al. 1984). Likewise, moose are adapted to cold environments, with temperatures as low as -30 °C failing to stimulate metabolic rate (i.e., expend energy to maintain body heat) (Renecker and Hudson 1986a). Moose can tolerate snow depths up to 70 cm, but snow depths over 90 cm critically limit moose movements in winter (Peek 1997). A yearly WSI was calculated separately for moose and white-tailed deer. For each study area pixel for individual SWE and TMIN GeoTIFF rasters of a given year, one point was assigned to each day between 1 November and 30 April where SWE was  $\geq 175$  kg/m<sup>2</sup> (moose) or  $\geq 81$  kg/m<sup>2</sup> (white-tailed deer) and TMIN was  $\leq -30.0^\circ\text{C}$  (moose) or  $\leq -17.7^\circ\text{C}$  (white-tailed deer) for a total of 2 points per day. The SWE thresholds were determined based on the following linear regression equation of snow depth to SWE by Delgiudice et al. (2001):

$$SWE = -3.1449 + 0.29462 \times \text{snow depth}$$

Once each pixel was assigned a value between 0 and 2, these values were summed (i.e., each value from 1 November to 30 April) to create the yearly WSI. Yearly WSI from 1980 to 2000 were averaged for moose and white-tailed deer separately. An inverse normalization was applied to the average yearly WSI to normalize minimum and maximum WSI values to range from 0 to 1 to constitute the winter severity component of the winter habitat index.

### 3.4.2. Winter habitat index

Winter habitat for moose and white-tailed deer was calculated by summing the nutritional resources and predation risk habitat components  $HC$  by their corresponding weight of importance  $W$ , multiplied by the winter severity habitat component (representing a constraint on winter habitat):

$$WH = \left( (HC_{\text{nutrition}} \times W_{\text{nutrition}}) + (HC_{\text{predation}} \times W_{\text{predation}}) \right) \times HC_{\text{winter severity}}$$

Winter habitat was rescaled to values ranging from 0 to 1 to provide the same relative range of values as the habitat components. The nutritional resources and predation risk habitat components were assigned an overall importance weight representing their relative importance to the winter habitat of moose and white-tailed deer.

Barber et al. (2018) performed a sensitivity analysis on relative nutrition and predation risk weighting, but presented their results with a weight of 70% predation risk and 30% nutrition. This decision was based on the fact that woodland caribou populations in Alberta are primarily predation-limited rather than nutrition-limited (Stuart-Smith et al. 1997, Festa-Bianchet et al. 2011). Regardless, I used a range of winter habitat weights in this study, more specifically on relative predation risk contributing 100%, 80%, 75%, 70%, 60%, 50%, 25%, and 0% of the winter habitat. This provides a broader array of possibilities for moose and white-tailed deer winter habitat as the relative proportion of predation risk on both ungulate populations are currently not well known. Thus, winter habitat was calculated separately for moose and white-tailed using each of the different weighting scenarios.

### *3.4.3. Simulated landscape*

#### *3.4.3.1. Vegetation change scenarios*

I used landscape simulations from Stralberg et al. (2018), who parameterized future vegetation change and wildfire activity over the 21<sup>st</sup> century in northern Alberta's boreal forest. Specifically, simulations were conducted with the Burn-P3 model (Parisien et al. 2005) which uses inputs of fuel, topography, fire weather, and patterns of fire ignitions to spatially simulate ignition and growth of individual wildfire parameters using the Prometheus fire growth model (Tymstra et al. 2010). These individual wildfire perimeters are deterministically simulated for one year and repeated for a very large number of iterations to capture the stochastic variability of the model.

Stralberg et al. (2018) investigated three fuel scenarios (i.e., static, climate-driven and fire-mediated), and two fire regime scenarios (i.e., constrained and unconstrained). For static fuel scenarios, historical fuels were held constant. For climate-driven scenarios, fuels were based on climate-projected potential vegetation for three Global Climate Models (GCMs). For fire-mediated scenarios, climate-projected fuels were updated according to wildfire simulation outputs from the Burn-P3 model. For both fire regimes scenarios, future projected daily fire weather was added as an input to the Burn-P3 model based on Wang et al. (2017), who applied monthly change anomalies to daily baseline values of daily fire weather. In the unconstrained fire regime scenarios, Stralberg et al. (2018) assumed climate-related increases in fire regime parameters, particularly in the number of escaped fires and the duration of fire spread conditions (Wang et al. 2014). However, due to uncertainties about how these different fire regime parameters would interact under novel future fuel-climate combinations, these fire regime parameters were held constant in the constrained fire regime scenarios.

The authors found that fire-driven and climate-driven scenarios resulted in very different levels of future vegetation change in the boreal forest of northern Alberta. Given the complexity and uncertainty related to future fire regimes, I examined four scenarios, which allowed me to cover a wider range of potential future vegetation change than other studies (Whitman et al. 2017, Barber et al. 2018). More specifically, two fuel scenarios (i.e., static and fire-mediated) and two fire regime scenarios (i.e., constrained and unconstrained) were investigated.

#### 3.4.3.2. Vegetation model

Vegetation (i.e., ecosite type and phase) was modeled empirically using random forest classification models with geology, climate, terrain, and wetness classes as inputs (further details in Stralberg et al. 2018). Models were used to predict baseline (1981–2010) and projected future

(2011–2040, 2041–2070, and 2071–2100) ecosite types (500-m resolution) using changes in climate conditions. Current topo-edaphic characteristics (i.e., geology, topography, soil moisture, and nutrition conditions) were assumed to remain constant over the 21<sup>st</sup> century. Uplands were modelled and projected, while lowlands (i.e., peatlands and other wetlands) were assumed to remain static due to negative hydrologic feedbacks that retain water through drought stress and wildfire (Schneider et al. 2016).

Future climate projections were derived from representative concentration pathway (RCP) 8.5 as it captures the conditions that are expected without dramatic reductions in greenhouse gas emissions (Fuss et al. 2014). Specifically, three GCMs from the Coupled Model Intercomparison Project, Phase 5 (CMIP5, Taylor et al. 2012) were used by Stralberg et al. (2018) and subsequently this study: CanESM2 (Chylek et al. 2011), CSIRO-Mk3 (Gordon et al. 2002), and HadGEM2-ES (Jones et al. 2011).

The baseline and projected ecosite layers from Stralberg et al. (2018) included 50 vegetation types, ranging from poor-xeric jack pine to medium-mesic aspen to rich-hygic black spruce (see Stralberg et al. 2018 for the detailed list). For the purposes of this study, baseline and projected ecosite layers were clipped to the study area and reclassified into broader categories of landcover type: jack pine forests, black spruce forests, mixedwood forests, deciduous forests, grasslands, bogs, fens, swamps, and marshes. For static fuel scenarios, the baseline (1981–2010) ecosite layer from Stralberg et al. (2018) was used as the landcover layer for each projected time period (2011–2040, 2041–2070, and 2071–2100). For fire-mediated fuel scenarios, the corresponding projected ecosite landscape from Stralberg et al. (2018) was used in this study as the landcover layer for each time period (e.g.: the projected 2041–2070 ecosite layer was used for the 2041–2070 time period).

### 3.4.3.3. Time since wildfire

Wildfire perimeters for each scenario (i.e., baseline, static constrained, static unconstrained, fire-mediated constrained, and fire-mediated unconstrained), time period (i.e., 2011–2040, 2041–2070 and 2071–2100), and GCM (i.e., CanESM2, CSIRO and HadGEM2) were simulated with the Burn-P3 model across the boreal forest of Alberta by Stralberg et al. (2018). Only large wildfires ( $\geq 200$  ha) were simulated as they account for ~97% of the total area burned in Canada (Stocks et al. 2002). More details on wildfire simulation, including general information, fire weather, fire regime, and fuel parameters, can be found in Stralberg et al. (2018).

Thirty sets of 100 iterations of wildfire perimeters, each representing a simulated 100-year time period, were randomly chosen from the 3000 iterations for each scenario, time period, and GCM. Each of the thirty sets of 100 iterations were converted to a raster format using the ‘fasterize’ function in the “fasterize” package (Ross 2020), where the most recently burned pixel was assigned a stand age (e.g., a pixel that last burned in the 25<sup>th</sup> iteration was assigned a stand age of 25). Next, each thirty 100 iterations were added to their corresponding ecosite layers (i.e., time since wildfire + ecosite) to produce raster layers of time since wildfire (Erni et al. 2018). The time-since-wildfire rasters were later used to assign standardized weighted coefficients for each habitat component to create a winter habitat index for both moose and white-tailed deer.

## 3.5. Results

### 3.5.1. Habitat components

Median nutritional resources for moose and white-tailed deer under baseline conditions was 0.61 (Table 3.1). Median nutritional resources decreased slightly under the static fuel scenario and constrained fire regime in the 2050s and 2080s and further decreased under the static fuel scenario and unconstrained fire regime in the 2050s and 2080s, as well as under the fire-mediated



fuel scenario and constrained fire regime in the 2050s (Table 3.1; Figure 3.2; Appendix 3.4). The latter only decreased substantially in the 2080s where median nutritional resources reached 0.35, representing a 43% reduction from baseline conditions (Table 3.1; Appendix 3.4). However, the greatest decline was projected under the fire-mediated fuel scenario and unconstrained fire regime, where median nutritional resources dropped to 0.35 and 0.17 in the 2050s and 2080s, respectively, representing a 72% reduction in nutritional resources for moose and white-tailed deer by the end of the 21<sup>st</sup> century (Table 3.1; Figure 3.2; Appendix 3.4).

Median predation risk for moose and white-tailed deer under baseline conditions was 0.37 and 0.24, respectively (Table 3.1). Median predation risk decreased slightly under the static fuel scenario and constrained fire regime in the 2050s and 2080s (Table 3.1; Figure 3.2; Appendix 3.4). For both moose and white-tailed deer under the static fuel scenario and unconstrained fire regime, predation risk remained similar to the 2020s conditions in the 2050s, but further decreased in the 2080s at 0.32 and 0.18, respectively (Table 3.1; Figure 3.2; Appendix 3.4). However, median predation risk for moose increased to 0.50 under both fire-mediated fuel scenarios in the 2050s, and further increased to 0.76 and 0.84 in the 2080s for the constrained and unconstrained fire regime, respectively (Table 3.1; Figure 3.2; Appendix 3.4). The latter represented a 105% and 126% reduction in the probability of encountering a wolf. Finally, median predation risk for white-tailed deer under the fire-mediated fuel scenarios decreased to 0.16 and 0.14 in the 2050s for the constrained and unconstrained fire regime scenarios, respectively (Table 3.1; Figure 3.2). Median predation risk further decreased to 0.14 in the 2080s for the constrained fire regime, while it remained identical for the unconstrained fire regime (Table 3.1; Appendix 3.4); thus, representing a 40% and 43% increase in the probability of encountering a wolf by the end of the 21<sup>st</sup> century.

Additional information on habitat components, including the 1<sup>st</sup> quantile, median and 3<sup>rd</sup> quantile for each GCM within both fuel and fire regime scenarios, can be found in Appendix 3.4.

### 3.5.2. *Winter habitat index*

Relative predation risk contributing to 0% (WH<sub>0</sub>), 50% (WH<sub>50</sub>), and 100% (WH<sub>100</sub>) of the winter habitat for both moose and white-tailed deer remained similar to baseline conditions under the static fuel scenario and constrained fire regime (Table 3.1; Figure 3.3 and Figure 3.4; Appendix 3.5). Under the static fuel scenario and unconstrained fire regime, median winter habitat for both moose and white-tailed deer remained similar to the 2020s conditions in the 2050s, but decreased in the 2080s (Table 3.1; Figure 3.3 and Figure 3.4; Appendix 3.5). Generally, median winter habitat for both moose and white-tailed deer was higher in the WH<sub>0</sub> scenario and significantly lower in the WH<sub>100</sub> scenario (WH<sub>0</sub> > WH<sub>50</sub> > WH<sub>100</sub>; Table 3.1).

The greatest changes in winter habitat for moose and white-tailed deer occurred in the fire-mediated fuel scenarios. Under the constrained fire regime, median winter habitat for moose decreased from 0.34 (WH<sub>100</sub>) – 0.50 (WH<sub>0</sub>) under baseline conditions to 0.32 (WH<sub>100</sub>) – 0.43 (WH<sub>0</sub>) in the 2050s (Table 3.1; Figure 3.3). Median winter habitat for white-tailed deer decreased from 0.17 (WH<sub>100</sub>) – 0.40 (WH<sub>0</sub>) under baseline conditions to 0.12 (WH<sub>100</sub>) – 0.34 (WH<sub>0</sub>) in the 2050s (Table 3.1; Figure 3.4). In the 2080s, median winter habitat for white-tailed deer further decreased to 0.11 (WH<sub>100</sub>) – 0.18 (WH<sub>0</sub>), representing a 33% to 54% reduction in winter habitat for white-tailed deer by the end of the 21<sup>st</sup> century (Table 3.1; Appendix 3.5). On the other hand, median winter habitat for moose in the 2080s either decreased to 0.26 (WH<sub>0</sub>) or increased to 0.61 (WH<sub>100</sub>) (Table 3.1; Appendix 3.5). The latter ranged from a 47% reduction to a 77% increase in winter habitat for moose from baseline conditions by the end of the 21<sup>st</sup> century.

Under the unconstrained fire regime, median winter habitat for moose in the 2050s either decreased to 0.28 (WH<sub>0</sub>) or increased to 0.58 (WH<sub>100</sub>) from baseline conditions (Table 3.1; Figure 3.3). However, winter habitat for moose decreased in the 2080s from the 2050s conditions to 0.13 (WH<sub>0</sub>) – 0.48 (WH<sub>100</sub>) (Table 3.1; Appendix 3.5). Overall, this ranged from a 74% reduction to a 42% increase in winter habitat for moose from baseline conditions by the end of the 21<sup>st</sup> century. Median winter habitat for white-tailed deer decreased from baseline conditions to 0.10 (WH<sub>100</sub>) – 0.21 (WH<sub>0</sub>) in the 2050s and remained at 0.10 (WH<sub>0</sub> – WH<sub>100</sub>) in the 2080s (Table 3.1; Figure 3.4). The latter represented a 38% to 76% reduction in winter habitat for white-tailed deer by the end of the 21<sup>st</sup> century (Table 3.1; Appendix 3.5).

### **3.6. Discussion**

#### *3.6.1. Long-term winter habitat quality without changes in vegetation*

Simulation results suggested that winter habitat quality will remain similar to current conditions without vegetation change in the 21<sup>st</sup> century (regardless of changes in fire regime). Climate-induced wildfires will continue to provide high winter forage availability (i.e., nutritional resources) to moose and white-tailed deer in the boreal mixedwoods (Routh and Nielsen 2021). Greater forage availability from wildfires is directly linked with ungulate abundance (Peek 1974b, Schwartz and Franzmann 1989, Loranger et al. 1991); therefore, the persistence of mixedwood forests combined with increasing climate-induced wildfires in the 21<sup>st</sup> century would be sufficient to maintain high quality winter habitat for moose and white-tailed deer resulting in higher moose populations and continuous expansion of white-tailed deer populations in northern Alberta (Maier et al. 2005, Fisher et al. 2020a). Yet, it is unclear if climate-induced wildfires will increase predation risk for moose and white-tailed deer. Wolf abundance is predominantly determined by the biomass of ungulate prey (Hebblewhite et al. 2007), suggesting that higher ungulate

populations lead to higher wolf populations, and subsequently, greater hunting success on moose and white-tailed deer. While these two ungulates are more likely to be killed by wolves in mixedwood forests (Latham 2009, Neilson and Boutin 2017), shallower snow depth can lead to lower kill rates on moose and white-tailed deer (Fuller 1991, Post et al. 1999); thereby offsetting any advantages of greater prey availability.

### *3.6.2. Long-term winter habitat quality with changes in vegetation*

Perhaps of greater consequence for ungulates is substantial changes in vegetation, which, coupled with changes in fire regime, could compromise the long-term persistence of moose and white-tailed deer in the boreal forest of Alberta. As discussed in Stralberg et al. (2018), major changes in vegetation is projected to occur in Alberta throughout the 21<sup>st</sup> century. Within the boreal mixedwoods, the decline in coniferous and mixedwood forests is likely to result in the expansion of deciduous forests in the 2050s, but by the 2080s, deciduous and mixedwood forests could be replaced by grasslands as a result of a predicted 11- to 50-fold increase in burn probability. Widespread vegetation change reported in Stralberg et al. (2018), and subsequently in Barber et al. (2018) and this study, are in agreement with other studies investigating climate-driven vegetation change in the boreal forest (Schneider et al. 2016, Cadieux et al. 2020, Nenzén et al. 2020). By the 2080s, the boreal mixedwoods of northern Alberta are predicted to be dominated by climates currently associated with the fescue grassland and parkland natural subregions of Alberta (Schneider et al. 2016, Nenzén et al. 2020) as part of the Great Plains Grassland biome (Rehfeldt et al. 2012).

Bioclimatic models assume that vegetation will synchronously change with climate. Yet, in the absence of disturbance, vegetation change will likely lag behind changes in climate due to the climatic resilience of mature trees (Camill and Clark 2000, Schneider et al. 2016). By

considering wildfire as a catalyst for vegetation change, vegetation projections can be made more realistic. However, the Burn-P3 model that Stralberg et al. (2018) used to simulate wildfire did not consider stand age or legacy effects. Recently burned areas in the boreal forest generally resist reburning for upwards of 30 years post-wildfire (Erni et al. 2017, Parks et al. 2018), due to the lack of fuels needed for fire ignition and spread (Héon et al. 2014, Thompson et al. 2017). Thus, recently burned areas create a negative feedback where the rate of fire is reduced with a higher proportion of early seral successional forests on the landscape. Legacy effects, on the other hand, minimize altered vegetation change trajectories (e.g., mixedwood forests to deciduous forests) because pre-disturbance forested areas can persist following natural disturbances due to disturbance-response traits of species (i.e., information legacies) and the persistence of individuals, propagules, and other residuals following the disturbance (i.e., material legacies) (Johnstone et al. 2016). Furthermore, the Burn-P3 model could not consider various mechanisms that may promote the persistence of remnants of boreal mixedwood forests on the landscape in microrefugia (Stralberg et al. 2020), or “areas relatively buffered from contemporary climate change over time that enable persistence of valued physical, ecological and socio-cultural resources” (Morelli et al. 2016). Thus, the replacement of mixedwood forests by deciduous forests and grasslands in the boreal forest may take decades to centuries longer than what is modelled in Stralberg et al. (2018), and subsequently this study. As a result, the projections of moose and white-tailed deer winter habitat quality should be interpreted with caution.

The expansion of deciduous forests in the boreal mixedwoods of northern Alberta, especially in the constrained fire regime scenario, should lead to a negative feedback process by which wildfire activity will be subdued (Terrier et al. 2013, Wang et al. 2016). Even with increases in extreme fire weather conditions (Wang et al. 2015), deciduous forests have lower potential for

fire initiation and spread (Hély et al. 2000, Cumming 2001, Krawchuk et al. 2006). This is mainly due to their higher leaf moisture content, lower flammability (i.e., low biomass of mosses and surface organic matter), and lack of ladder fuels that carry fire to the canopy (Hély et al. 2000, Kasischke et al. 2010). In fact, deciduous forests are approximately 2.6 to 6.6 times less likely to burn in a stand-replacing wildfire than coniferous forests (Bernier et al. 2016). As a result, the expansion of deciduous forests in the boreal mixedwoods is still projected to slightly decrease moose and white-tailed deer winter habitat quality. In the winter, moose and white-tailed deer often select mixedwood or coniferous forests, where snow depth is shallower, to minimize predation risk, travel through deep snow, and thermoregulation (i.e., reduce wind velocity and subsequently heat loss) (Timmermann and McNicol 1988). In the absence of coniferous cover in deciduous forests, moose and white-tailed deer will be more susceptible to predation by wolves even if nutritional resources available in mixedwood and deciduous forests are both of high quantity and high quality winter forage.

The transition from deciduous and mixedwood forests to grasslands is projected to further reduce winter habitat quality for both moose and white-tailed deer. With a relative predation risk contribution of 50% (WH<sub>50</sub>), winter habitat quality was projected to decline by 3–38% for moose and 40–69% for white-tailed deer by the 2080s. The greatest decline in both moose and white-tailed deer winter habitat occurred under the unconstrained fire regime scenario, which projected that grassland-dominated habitats would cover 54% of the study area (96% of upland vegetation). With less than 1% of grassland cover currently present in the boreal mixedwoods, it is difficult to anticipate how moose and white-tailed deer would respond to the expansion of grasslands in the boreal forest. Moose winter diet in the boreal mixedwoods consists exclusively of woody browse (Peek 1974a, Nowlin 1978, Renecker and Schwartz 2007). While the proportion of woody browse

in the diet of expanding white-tailed deer is currently unknown, it likely ranges from 74 to 91% (Hewitt 2011). Grasses, sedges and forbs are not typically consumed by these ungulates in the winter because 1) snow fully covers herbaceous plants rendering them useless in winter; 2) moose and white-tailed deer did not evolve distinctive physiological characteristics (i.e., crescent-shaped hooves) to dig through snow to access ground vegetation like woodland caribou (Thomas and Gray 2002); and 3) digestibility is maximized for foraging in early spring to June (Crawford 1982, Renecker and Hudson 1988). Also, moose rely on energy from highly digestible forage that rapidly travels through the gastrointestinal tract (Renecker 1987). Grasses, sedges, and forbs require long retention time before the rumen can optimize digestibility (Renecker 1987). Therefore, moose are unable to exploit grasses, sedges, and forbs in high quantity (Van Dyne et al. 1980, Timmermann and McNicol 1988). While moose and white-tailed deer may take advantage of higher quantities of grasses, sedges, and forbs during spring green up, they are unlikely to be able to do so in the winter, when vegetation senesces.

Alternatively, unfavourable upland conditions may lead moose and white-tailed deer to utilize lowlands for foraging purposes as Chapter 2 found that lowlands provide higher foraging abundance of woody browse than surrounding uplands throughout the boreal succession. Currently, moose and white-tailed deer are known to avoid lowlands in the boreal mixedwoods (James et al. 2004, DeMars et al. 2019) as lowlands provide high quantity of low quality winter forage (Routh and Nielsen 2021). However, lowlands will gradually provide higher quality forage than the surrounding upland grasslands throughout the 21<sup>st</sup> century because low palatable browse will become more nutritious and beneficial to moose and white-tailed deer than grasses, sedges, and forbs that are not digestible in the winter; therefore, moose and white-tailed deer could persist through novel winters by changing their habitat preferences to lowlands.

### 3.6.3. *Winter severity*

Future expected changes in winter severity and length of the growing season in Alberta may promote the persistence of white-tailed deer (Dawe 2011, Latham et al. 2011*b*). Decreasing winter severity, combined with a longer growing season, has already increased the distribution and abundance of white-tailed deer across northern Alberta over the last 50 years (Dawe and Boutin 2016). Indeed, a decrease of one standard deviation in winter severity increased the odds of white-tailed deer presence by 7.3-fold, while an increase of 5.2 days in the length of the growing season increased the odds of presence by 2.7-fold (Dawe et al. 2014). Given that winter severity is the most important predictor of white-tailed deer distribution and expansion in the western boreal forest (Dawe et al. 2014, Dawe and Boutin 2016, Kennedy-Slaney et al. 2018), it is likely that the projected winter habitat index developed for white-tailed deer is an underestimate because winter severity was not projected in this study. Moose, on the other hand, are adapted to extremely cold environments, living in areas with temperatures as low as -30 °C and snow depths up to 70 cm (Renecker and Hudson 1986*a*, Peek 1997). Although the projected winter habitat index for moose is representative of the climatic conditions expected in the 21<sup>st</sup> century, winter habitat quality may increase in areas with deep snow and cold temperatures that are currently limiting to moose, such as the Birch Mountains.

Winter severity (i.e., snow-water equivalent and minimum air temperature) was kept constant at baseline levels in future projections (2020s, 2050s, and 2080s), regardless of fuel and fire regime scenarios, due to the uncertainty related to future changes in snow-water equivalent. Coarse-resolution climate models project a decrease in snowfall and snow-water equivalent with increasing temperature and precipitation in the boreal forest (i.e., transition of solid-state precipitation to liquid-state precipitation) (Räisänen 2008, Shi and Wang 2015, Santolaria-Otín



and Zolina 2020). However, the response of snow depth and snow-water equivalent to increasing temperature and precipitation is quite complex and ultimately depends on regional differences in climate regimes (Brown and Mote 2009, Hernández-Henríquez et al. 2015). Current projections of snow depth and snow-water equivalent do not properly illustrate regional differences at finer scales needed in this study (i.e., 500-m resolution) as these studies commonly use  $1-2.5^\circ \times 1-2.5^\circ$  latitude-longitude grids (Räisänen 2008, Shi and Wang 2015, Santolaria-Otín and Zolina 2020). While future projections of temperature could be applied to the winter severity habitat component, projecting snow-water equivalent in the 21<sup>st</sup> century was beyond the scope of this study.

Deep snow and cold temperatures have been shown to negatively impact winter survival in northern ungulates, such as moose and white-tailed deer, by increasing energetic costs (Parker et al. 1984, DelGiudice et al. 2002, Dumont et al. 2005, Kautz et al. 2020). Northern ungulates undergo periods of negative energy balance in winter (Dumont et al. 2005) as they cannot meet their energy requirements from ingestion of woody browse (Ullrey et al. 1970, Mautz et al. 1976). In some cases, white-tailed deer can burn up to 30% of their body reserves over the winter (Mautz 1978, Huot 1982) because snow depth over 30 cm can render 97% of woody browse availability (Moen and Evans 1971). However, shorter winters (i.e., short period of snow cover) and reduced snow depth would allow moose and white-tailed deer to forage on woody browse for longer periods of time; therefore, climate change may aid both ungulates in accessing winter forage and minimizing the length of period in negative energy balance (Dumont et al. 2005, Visscher et al. 2006). Although not captured in my study, this phenomenon could significantly impact the energy expenditure of white-tailed deer, and to a lesser extent moose, leading to a higher winter survival.

### 3.7. Conclusion

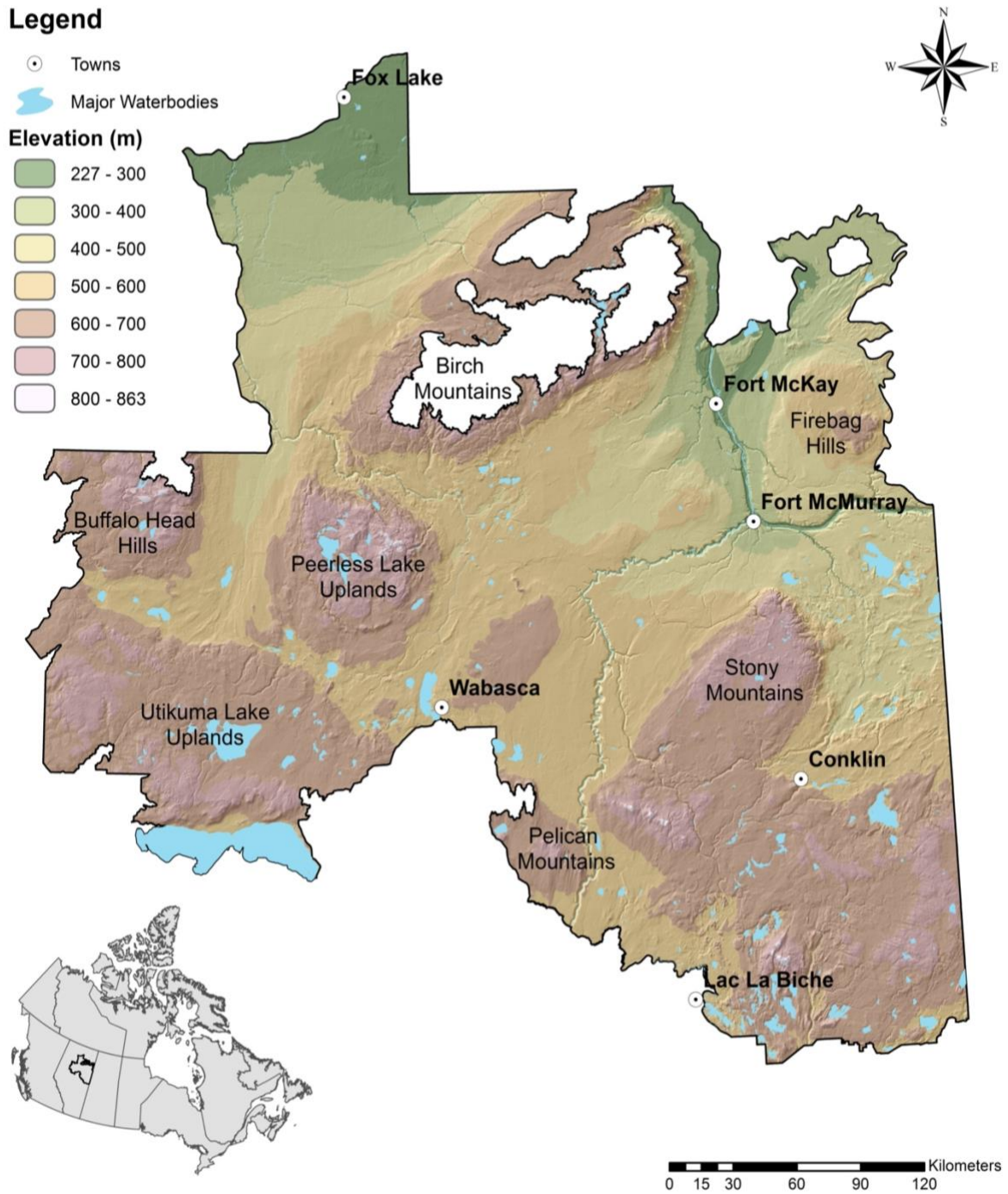
Understanding the effects of climate-induced changes in vegetation, wildfires, and winter severity on the distribution of species is fundamental for land use management and biodiversity conservation (Chen et al. 2011, Gilbert et al. 2020). There is a broad range of possible future outcomes for moose and white-tailed deer winter habitat quality, and these outcomes highlight the high levels of uncertainty associated with future fire regime and vegetation trajectories in the boreal mixedwoods of northern Alberta, Canada. Future research should focus on modelling more realistic and moderate scenarios of fire regime (Williams and Abatzoglou 2016), as well as including legacy effects or boreal microrefugia in vegetation simulations (Johnstone et al. 2020, Stralberg et al. 2020). If climate-related vegetation change is minimal, boreal mixedwood forests should continue to provide substantial winter nutritional resources to moose and white-tailed deer. However, wildfire-mediated vegetation change could compromise the long-term persistence of moose and white-tailed deer in the boreal forest of northern Alberta, particularly when mixedwood and deciduous forests transition to grassland-dominated habitats. Thus, the speed at which boreal mixedwoods will respond to climate-induced wildfires by the end of the 21<sup>st</sup> century will ultimately shape the distribution and persistence of moose and white-tailed deer, and without any doubt, many other wildlife species found in the boreal forest of Alberta. Lastly, these ecological impacts could further affect management decisions related to moose and white-tailed deer populations and demographics, but also severely impact the livelihood of recreational and non-recreational hunters, including Indigenous communities, who have already expressed their concerns over the effects of climate change on moose harvest opportunities in the boreal forest (Brinkman et al. 2016, Cold et al. 2020, Hasbrouck et al. 2020).

## Tables

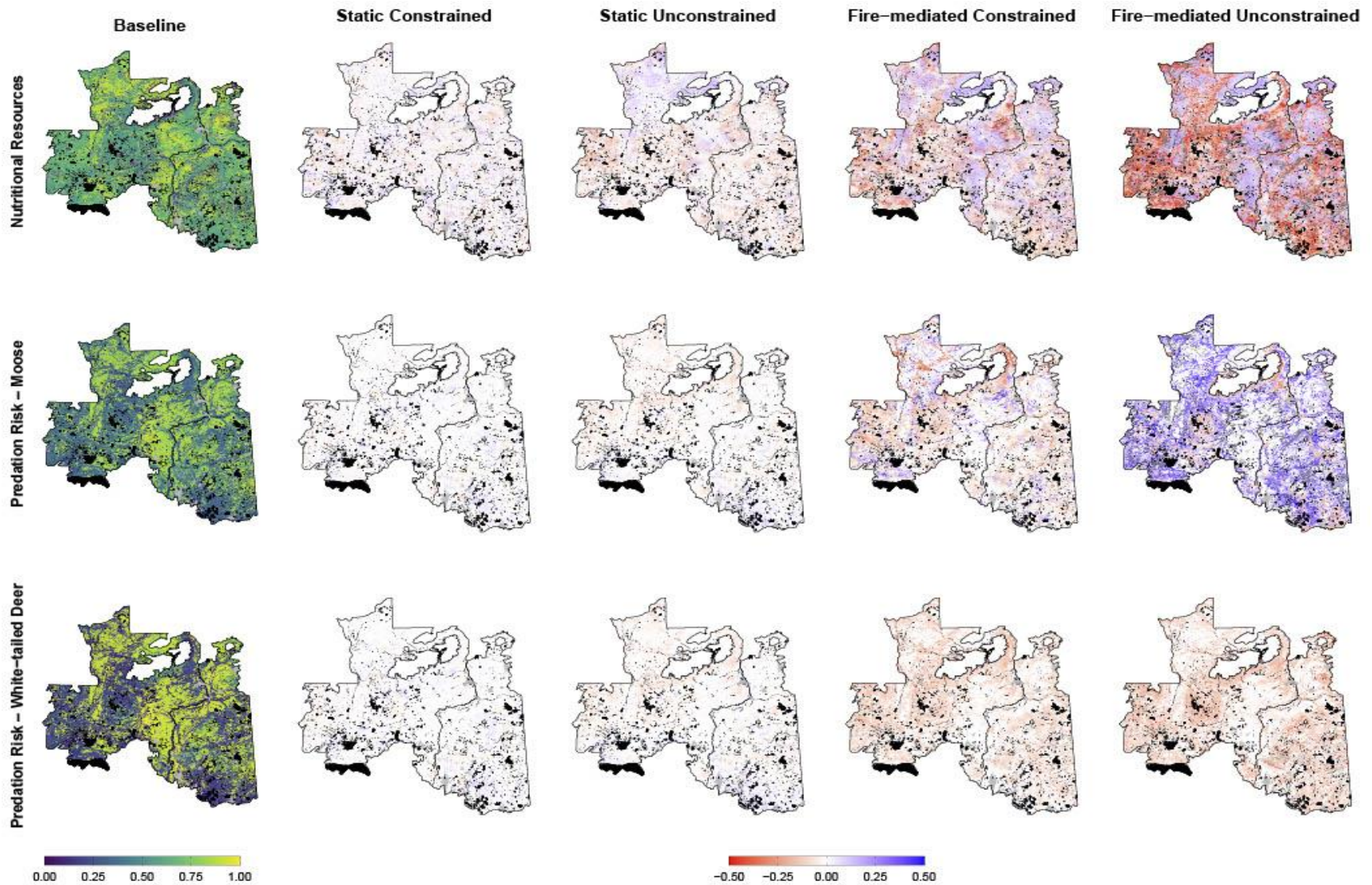
**Table 3.0.1.** Summary of median nutritional resources, predation risk and winter habitat (WH) for moose and white-tailed deer in each fuel scenario (static [S] and fire-mediated [FM]), fire regime scenario (constrained [C] and unconstrained [UC]), and time period (2011–2040, 2041–2070, and 2071–2100). Nutritional resources, predation risk, and winter habitat were averaged across three GCMs (CanESM2, CSIRO, and HadGEM2). WH is presented based on relative predation risk contributing to 0%, 50%, and 100% of the WH.

		Moose				White-tailed Deer			
		S C	S UC	FM C	FM UC	S C	S UC	FM C	FM UC
<b>Baseline</b>	Nutrition	0.609	—	—	—	0.609	—	—	—
	Predation risk	0.371	—	—	—	0.235	—	—	—
	WH <sub>0</sub>	0.499	—	—	—	0.397	—	—	—
	WH <sub>50</sub>	0.438	—	—	—	0.308	—	—	—
	WH <sub>100</sub>	0.341	—	—	—	0.165	—	—	—
<b>2011 – 2040</b>	Nutrition	0.601	0.589	0.600	0.588	0.601	0.589	0.600	0.588
	Predation risk	0.362	0.361	0.362	0.355	0.226	0.225	0.226	0.217
	WH <sub>0</sub>	0.496	0.489	0.496	0.486	0.392	0.386	0.391	0.384
	WH <sub>50</sub>	0.439	0.438	0.436	0.410	0.308	0.306	0.307	0.293
	WH <sub>100</sub>	0.341	0.344	0.339	0.323	0.168	0.171	0.167	0.159
<b>2041 – 2070</b>	Nutrition	0.605	0.562	0.521	0.354	0.605	0.562	0.521	0.354
	Predation risk	0.362	0.355	0.503	0.503	0.226	0.219	0.159	0.135
	WH <sub>0</sub>	0.501	0.468	0.428	0.280	0.395	0.376	0.340	0.205
	WH <sub>50</sub>	0.440	0.424	0.378	0.420	0.309	0.297	0.253	0.181
	WH <sub>100</sub>	0.339	0.340	0.319	0.582	0.165	0.170	0.122	0.097
<b>2071 – 2100</b>	Nutrition	0.605	0.530	0.349	0.169	0.605	0.530	0.349	0.169
	Predation risk	0.364	0.315	0.760	0.840	0.228	0.179	0.141	0.135
	WH <sub>0</sub>	0.499	0.460	0.263	0.129	0.395	0.378	0.182	0.096
	WH <sub>50</sub>	0.439	0.397	0.425	0.271	0.309	0.278	0.184	0.097
	WH <sub>100</sub>	0.339	0.302	0.605	0.483	0.165	0.140	0.111	0.103

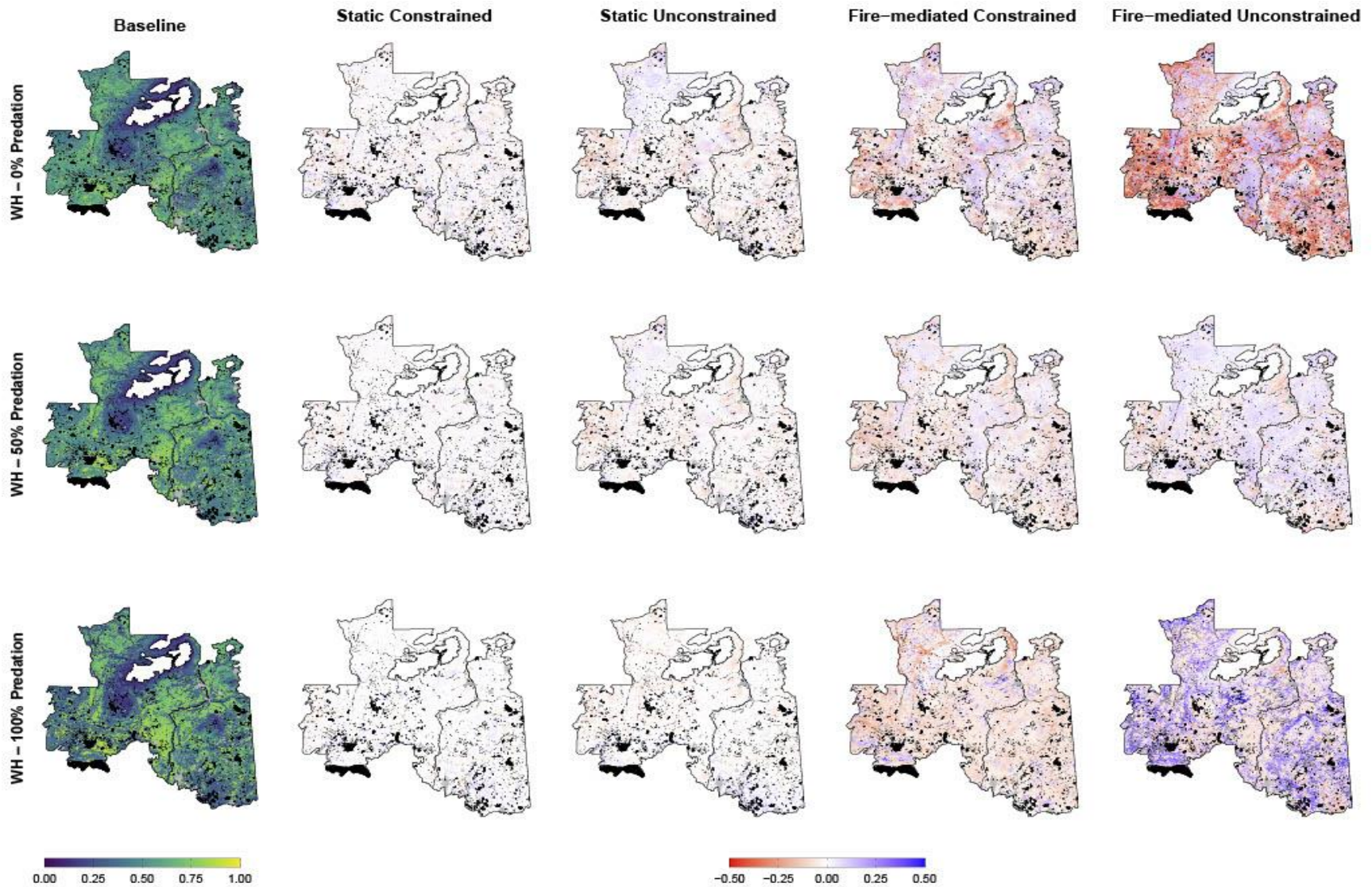
## Figures



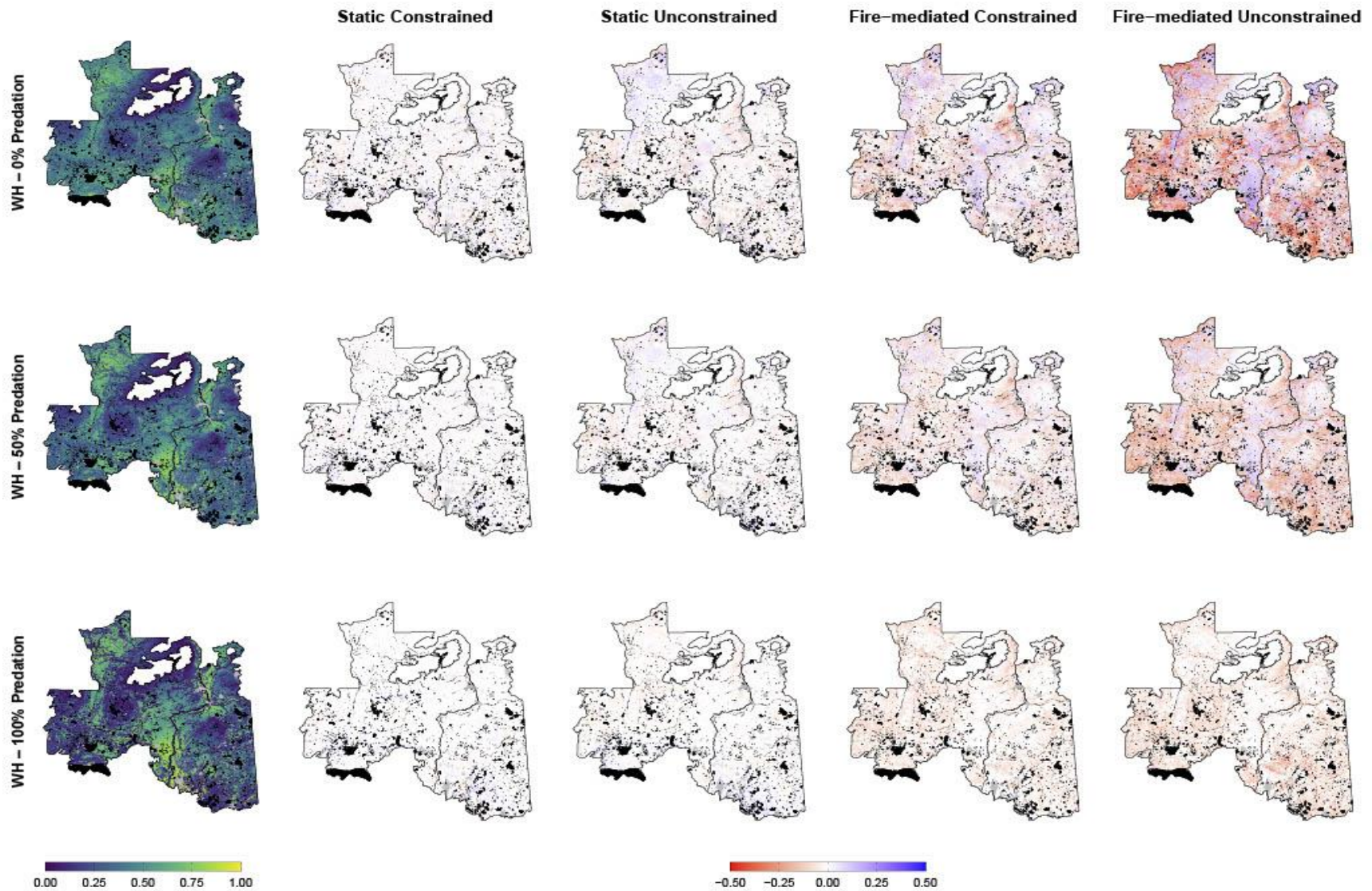
**Figure 3.0.1.** Study area found within the boreal mixedwood forests of northern Alberta, Canada. Inset map of Canada in the lower left with outline of study area.



**Figure 3.0.2.** Predicted proportional change in habitat components for current (baseline) and the 2050s (2041–2070) for moose and white-tailed deer in each fuel scenario (i.e., static and fire-mediated) and fire regime scenario (i.e., constrained and unconstrained). Nutritional resources and predation risk were averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Proportional change in red indicates worsening conditions while blue indicates improving conditions. Black areas represent waterbodies and light grey areas represent non-fuel types (i.e., urban and agriculture areas).



**Figure 3.0.3.** Predicted proportional change in moose winter habitat (WH) for current (baseline) and the 2050s (2041–2070) in each fuel scenario (i.e., static and fire-mediated) and fire regime scenario (i.e., constrained and unconstrained). WH is presented based on relative predation risk contributing to 0%, 50%, and 100% of the WH. WH was averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Proportional change in red indicates worsening conditions while blue indicates improving conditions. Black areas represent waterbodies and light grey areas represent non-fuel types (i.e., urban and agriculture areas).



**Figure 3.0.4.** Predicted proportional change in white-tailed deer winter habitat (WH) for current (baseline) and the 2050s (2041–2070) in each fuel scenario (i.e., static and fire-mediated) and fire regime scenario (i.e., constrained and unconstrained). WH is presented based on relative predation risk contributing to 0%, 50%, and 100% of the WH. WH was averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Proportional change in red indicates worsening conditions while blue indicates improving conditions. Black areas represent waterbodies and light grey areas represent non-fuel types (i.e., urban and agriculture areas).

## CHAPTER 4 – GENERAL CONCLUSION

### 4.1. Summary

Understanding species' responses to wildfires and climate change are fundamental for land use management and biodiversity conservation (Chen et al. 2011, Gilbert et al. 2020). The overall goal of this thesis was to investigate the effects of wildfires and climate change on moose and white-tailed deer winter forage and habitat quality in the boreal mixedwoods of northeastern Alberta, Canada. Specifically, Chapter 2 examined the changes in winter browse richness, evenness, abundance, and community composition, as well as their use (browse levels) by moose and white-tailed deer, in post-wildfire upland and lowland forests over a 150-year post-wildfire period. I found that species richness and evenness peaked at both 10 – 25 years and ~90 years post-wildfire in mixedwood forests, as a result of fluctuations in preferred and highly palatable browse. Also, I found that deciduous shrub abundance in mixedwood forests remained constant over time. Numerous studies have documented an increase in deciduous shrub and sapling abundance, and subsequently moose and white-tailed deer habitat quality, between 11 and 30 years post-wildfire (LeResche and Bishop 1974, MacCracken and Viereck 1990, Weixelman et al. 1998, Maier et al. 2005, Lord and Kielland 2015, Joly et al. 2016). However, a second peak at older forest ages has not been found in previous studies, nor has it been detected in moose and white-tailed deer habitat selection studies. Although, it has been previously highlighted in the grey literature that moose and white-tailed deer selected winter habitat over 120 years post-wildfire in the boreal mixedwoods of Alberta (Stelfox et al. 1995). The double peak is attributed to the die-off of early successional species (i.e., trembling aspen and paper birch) occurring 75 – 125 years post-wildfire in boreal mixedwood forests (Harvey et al. 2002). This die-off of deciduous saplings allows more sunlight to reach the forest floor, allowing deciduous shrubs to outcompete and outgrow shade-tolerant coniferous saplings (Kneeshaw and Bergeron 1996, Chen and Popadiouk 2002).



In contrast to uplands, I found that black spruce and lowland forests had similar species richness, evenness, and abundance over the 150 year post-wildfire period examined. Also, I found that browse abundance in lowland forests was constantly higher than mixedwood forests, in exception to the first 10 years post-wildfire for sapling abundance, and mainly consisted of low palatable browse. This suggests that early seral lowland forests do not recruit winter browse species consumed by ungulates in the Boreal Plains of Alberta, as hypothesized by DeMars et al. (2019) and myself. Lowland forests provide ungulates with a high quantity of low quality forage, and while evidence of browsing was found in lowland forests (i.e. poor fens), the lack of significance suggests that ungulates select these habitats for other reasons than forage availability, such as vegetation cover for thermoregulation purposes, protection against deep snow or shelter from predators and hunters (Timmermann and McNicol 1988).

Chapter 3 assessed the long-term effects of climate-induced wildfires and vegetation change on the distribution and quality of moose and white-tailed deer winter habitat in the boreal mixedwoods. To address this question, I developed a winter habitat quality model for moose and white-tailed deer based on predicted changes in vegetation (i.e. static and fire-mediated) and fire regime (i.e. constrained and unconstrained) under an RCP 8.5 climate scenario in the 2020s, 2050s and 2080s. Regardless of changes in fire regime, I found that winter habitat quality for both moose and white-tailed deer will remain similar to current conditions if vegetation change does not occur in the 21<sup>st</sup> century. As a result, climate-induced wildfires will continue to provide high winter forage availability resulting in higher moose populations and continuous expansion of white-tailed deer populations in northeastern Alberta (Maier et al. 2005, Fisher et al. 2020a). It is unclear, however, if climate-induced wildfires will increase predation risk in mixedwood forests because shallower snow depth leads to lower ungulate kill rates (Fuller 1991, Post et al. 1999).

Alternatively, vegetation change coupled with changes in fire regime could compromise the long-term persistence of moose and white-tailed deer in the boreal mixedwoods of Alberta. I found that the expansion of deciduous forests in the boreal mixedwoods in the 2050s is projected to slightly decrease moose and white-tailed deer winter habitat quality. Although nutritional resources of forage in deciduous forests are of high quantity and quality like that of mixedwoods forests, the absence of coniferous cover in deciduous forests will result in higher predation risk for moose and white-tailed deer that often select coniferous cover from mixedwood or coniferous forests in the winter for predator avoidance, travel through deep snow, and thermoregulation (Timmermann and McNicol 1988).

Lastly, I found that the predicted transition between deciduous and mixedwood forests to grasslands in the 2080s is projected to significantly reduce winter habitat quality for both moose and white-tailed deer in the boreal mixedwoods of Alberta. While moose and white-tailed deer may take advantage of higher quantity of grasses, sedges, and forbs during spring green up, ultimately, there is high uncertainty about whether or not moose and white-tailed deer will have the capacity to modify their winter diet to incorporate more grasses, sedges, and forbs in the future. Unfavourable upland conditions may also lead moose and white-tailed deer to utilize lowlands for foraging purposes as I found in Chapter 2 that lowlands provide higher foraging abundance of woody browse than surrounding uplands throughout all stages of post-wildfire boreal succession.

#### **4.2. Management Implications**

Comprehensive and detailed data on moose and white-tailed deer foraging ecology and habitat quality throughout most of the boreal successional pathway are sparse, yet highly important to assess the feasibility of managing alternative prey population and expansion as a management tool. The latter is particularly important in winter, when moose and white-tailed deer undergo

periods of negative energy balance (Dumont et al. 2005), as they cannot meet their energy requirements from ingestion of woody browse (Ullrey et al. 1970, Mautz et al. 1976). Because of this limitation, winter strongly influences their life-history traits and population dynamics (Post and Stenseth 1998, Garroway and Broders 2005, Weiskopf et al. 2019).

My research suggests that wildfires can provide higher winter forage availability for ungulates residing in upland forests of the Boreal Plains of Alberta for longer periods of time than initially reported by the scientific community. The greater availability of high quality and quantity winter browse in uplands through wildfires could be an additional reason for higher numbers of moose populations and expanding populations of white-tailed deer in northeastern Alberta, aside from the known effects of anthropogenic disturbances and climate change (Latham et al. 2011*b*, 2013, Dawe et al. 2014, Fisher et al. 2020*a*). This trend is expected to continue with future climate-induced wildfires in the boreal mixedwoods of northeastern Alberta, especially if the boreal mixedwoods transition to deciduous forests. The latter has major management and conservation implications as intensive management efforts will be needed to maintain low enough densities to minimize apparent competition with woodland caribou (Serrouya et al. 2019), as well as fatal disease spread from white-tailed deer to other ungulates. Previous management actions to conserve woodland caribou in Alberta have mainly focused on reducing wolf numbers (i.e. top-down approach), either by wolf control (Hervieux et al. 2014) or through reductions in alternate prey populations from liberalized harvest regulations (Serrouya et al. 2015, 2017). However, these top-down management actions have been unsuccessful to stabilize or improve woodland caribou populations (McLoughlin et al. 2003, Hervieux et al. 2013).

Future management actions should start focusing on minimizing available forage or winter habitat for moose and white-tailed deer (i.e. bottom-up approach) in critical areas within woodland

caribou range to reduce the spatial overlap between these two ungulates and woodland caribou; thereby minimizing accidental predation from wolves on woodland caribou (Bergerud et al. 1984, James et al. 2004, McLoughlin et al. 2005). Land managers can use the nutritional resources habitat component or winter habitat index from Chapter 3 to spatially identify areas with either high quantity and quality winter browse or areas of high quality winter habitat for moose and white-tailed deer within six woodland caribou ranges (i.e., Red Earth, Richardson, West Side Athabasca, East Side Athabasca, Cold Lake, and Nipisi). Subsequently, land managers can implement specific bottom-up approaches to minimize the selection of these identified areas by moose and white-tailed deer. Examples of bottom-up approaches would be 1) restoration of seismic lines surrounding the identified areas by spreading logs, mounding, or planting undesirable deciduous shrubs (e.g., currants & gooseberries and honeysuckles) and coniferous saplings (Tattersall et al. 2020, Dickie et al. 2021), and 2) actively removing desirable deciduous shrubs (i.e., willows, beaked hazelnut, alders, and prickly wild rose) and deciduous saplings within the identified areas to reduce the overall quantity and quality of winter browse/winter habitat. Lastly, the implementation of two or more management actions (e.g., wolf reduction and maternity penning) has been shown to drastically increase woodland caribou populations (Serrouya et al. 2019); thus, it is time for managers to include both top-down and bottom-up management actions into woodland caribou conservation in Alberta.

#### **4.3. Future Research**

This study is the first to examine winter browse succession consumed by moose and white-tailed deer in both upland and lowland forests, but more importantly, throughout a chronosequence of 150 years post-wildfire. It is also one of the few studies to project moose and white-tailed deer winter habitat quality with future changes in vegetation and fire regime in the 21<sup>st</sup> century, while

accounting for winter severity. Consequently, this study is a major step forward in understanding ungulate foraging ecology in the Boreal Plains; however, like any other study, there is potential to build upon these results to provide additional information and recommendations on moose and white-tailed deer winter foraging and habitat quality in the Boreal Plains.

There are several methods to estimate ungulate diet composition, such as rumen content analysis (Rhude and Hall 1977, Korschgen et al. 1980), direct observation of bite counts from wild or tamed animals (Crawford 1982, Renecker and Hudson 1986*b*, Risenhoover 1989), browsing evidence surveys (MacCracken and Viereck 1990, Dumont et al. 2005, Newbury et al. 2007), and micro-histological analyses of feces (i.e. feces analysis) (MacCracken and Van Ballenberghe 1993, Bao et al. 2017). Browsing evidence is a good technique to estimate relative winter diet, but it is quite challenging to distinguish the bite of a moose versus another ungulate (i.e., woodland caribou and white-tailed deer) on woody browse in the field; therefore, it is not the most accurate method for estimating winter diet when multiple ungulate species are present on the landscape. Future research should examine ungulate winter diet at finer scales, particularly with feces analysis to fully separate the deciduous shrub and sapling species actively consumed by either moose or white-tailed deer and their relative frequency throughout the boreal succession. Although the bite-count technique is the most accurate method of estimating ungulate diet, it is extremely labour intensive and requires tamed animals; thus, feces analysis would be the most appropriate non-invasive method to estimate ungulate diet composition (Shrestha and Wegge 2006).

Additionally, “palatability” in this study represents an indirect measure of browse quality through evidence of browsing; thus, it assumes that deciduous shrub and sapling species with a higher percentage of browsed stems were more palatable, even though the nutritional value of these species (i.e., forage quality) was not measured. Winter browse species that are browsed

extensively by moose and white-tailed deer may not necessarily have the greatest nutritional value. For example, balsam fir constitutes 59 to 76% of white-tailed deer winter diet on Anticosti Island in eastern Canada (Lefort et al. 2007), but coniferous needles are very low in nutrients compared to most woody browse species, and their consumption in high levels lead to malnutrition, starvation, and death (Dahlberg and Guettinger 1956, Wetzel 1972). As a result, winter browse species identified as highly palatable in this study may not be beneficial to moose and white-tailed deer diet and overall health. Forage quality provides a more quantitative and robust representation of resource limitation, as well as browse selection or avoidance (Renecker and Hudson 1988). Therefore, future research should investigate the nutritional content (i.e., digestibility and chemical composition) of winter browse species consumed by moose and white-tailed deer in the boreal mixedwoods of Alberta.

In this study, winter severity was kept constant to baseline conditions in future projections (2020s, 2050s, and 2080s), regardless of fuel and fire regime scenarios, due to the uncertainty related to future changes in snow-water equivalent. The response of snow to increasing temperature and precipitation is quite complex and ultimately depends on regional differences in climate regimes (Brown and Mote 2009, Hernández-Henríquez et al. 2015). Recent projections of snow-water equivalent in the 21<sup>st</sup> century are modeled at a broad scale (e.g., Northern Hemisphere) (Maloney et al. 2014, Shi and Wang 2015, You et al. 2020), therefore it does not reflect the regional differences in climate regimes. Projecting snow-water equivalent is beyond the scope of this study, but I do urge other researchers to include future snow-water equivalent projections at a coarser scale into their winter habitat quality index once they are available; these projections would significantly improve the implications of future climate change on winter habitat quality for moose and white-tailed deer, but also any other wildlife species limited by winter severity.

Lastly, I would like to emphasize the importance of investigating white-tailed deer habitat selection, foraging ecology, and population demographics in northeastern Alberta as they have recently replaced moose as the primary prey species of wolves in the boreal forest (James et al. 2004, Latham et al. 2011*b*, 2013). Current research has focused on the mechanisms of white-tailed deer expansion, whether it is driven by anthropogenic disturbances (i.e. landscape alteration), climate change (i.e. reduction in winter severity), or both (Dawe et al. 2014, Dawe and Boutin 2016, Kennedy-Slaney et al. 2018, Fisher et al. 2020*a*); yet, very little is known about their habitat needs and diet in the boreal forest. White-tailed deer have a diverse and complex foraging ecology (Hewitt 2011), where findings from central Alberta (Rhude and Hall 1977), southwestern United States (Knipe 1977, Korschgen et al. 1980), midwestern United States (Nixon et al. 1970), or in the hemi-boreal region of the Northern Great Lakes in Minnesota (Rogers et al. 1981, Blouch 1984) would not apply to the expanding population of white-tailed deer in northeastern Alberta. Wildfire and land use managers should be cautious of using information from different regions of white-tailed deer range for management and conservation implications in northeastern Alberta; hence, the urgency to further understanding the ecology of white-tailed deer in the Boreal Plains.

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## APPENDICES

**Appendix 2.1.** Number of field plots surveyed in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada, in the summer of 2019 according to the factorial sampling design.

	<b>Young (0 – 30 years)</b>	<b>Intermediate (31 to 70 years)</b>	<b>Mature (71+ years)</b>
<b>Upland</b>			
Jack pine forest	21 plots	5 plots	5 plots
Black spruce forest	6 plots	8 plots	8 plots
Mixedwood forest	21 plots	9 plots	9 plots
<b>Lowland</b>			
Bog	15 plots	9 plots	9 plots
Poor fen	14 plots	4 plots	4 plots
Rich fen	10 plots	4 plots	3 plots
<b>Total</b>	<b>87 plots</b>	<b>39 plots</b>	<b>38 plots</b>

**Appendix 2.2.** Methodology used to standardize stand age from tree cores taken at a mean height of 55 cm for each field plot.

Estimating forest stand age is a key requirement for disturbance ecology research of the boreal forest, as it is severely altered naturally and anthropogenically (Wong & Lertzman, 2001). Ideally, boring a tree at the root-shoot boundary estimates the year of establishment non-destructively, but it is difficult, laborious and multiple problems can arise, such as coring fire scars, rot or flare beyond the length of the borer (Frelich & Reich, 1995; Stephenson & Demetry, 1995). Boring at a predetermined height above ground, typically at breast height (1.3–1.4 m) or 20–40 cm above ground, is preferred as it is less laborious and avoids the problems associated with boring at root-shoot boundary (e.g. Henry & Swan, 1974; Lorimer, 1980).

However, there are three possible sources of error associated with this method: 1) assigning years to tree rings, especially for species tending to have missing or false rings, 2) estimating the number of years to the pith of the core when the core misses or falls short of the pith, and 3) estimating the number of years to grow to the height of the core (Norton & Ogden, 1990). The first two sources of errors can be minimized by visual or computer-assisted cross dating (Yamaguchi, 1991) and modelling the number of missing years on cores that failed to hit the pith (Villalba & Veblen, 1997). The third source of error requires a “height correction ( $h_c$ )”, an estimate of the number of years for a tree to grow to coring height (Wong & Lertzman, 2001). Height corrections of increment cores sampled above ground follow this equation:

$$Age_{total} = Age_{measured\ at\ coring\ height} + h_c + e_{estimate\ of\ years\ to\ pith} + e_{estimate\ of\ missing/false\ rings}$$

In this study, the largest conifer stem or deciduous stem if no conifer species were big enough to be representative of the stand age was cored at an average core height of 55 cm. A total of 5 tree species were cored: black spruce (*Picea mariana*), white spruce (*Picea glauca*), tamarack (*Larix laricina*), jack pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*). Considering that all tree cores intersected the pith and stand age will be used as a relative value, the estimate of years to the pith, missing or false rings are not needed.

Species	Code	Years to core height ( $h_c$ )	Literature Review
Black Spruce ( <i>Picea mariana</i> )	Sb	Upland – 7	<p><u>Upland</u></p> <ul style="list-style-type: none"> <li>According to Fowells (1965), black spruce seedlings rarely grow more than 2.5 cm in their first growing season and are commonly between 8–13 cm after three growing seasons.</li> <li>Zasada et al. (1992) found that understory black spruce saplings can take 15 to 20 years to reach 150 cm in height, and it was common to see 40-year-old saplings under 150 cm.</li> <li>Based on data collected in the field, black spruce saplings were approximately 200 cm in height in the DL1009 Fire (1995), representing a constant growth rate of 8.33 cm/year.</li> </ul>
		Lowland – 14	



- This growth rate will be used to calculate the black spruce height correction as it varies greatly with site conditions and competition with other tree species. Thus, it takes on average seven years for black spruce saplings to reach the height of the core in a burned upland in the Lower Athabasca Region.

Lowland

- Lieffers (1986) found that black spruce saplings in north-central Alberta mostly established in peatlands four to seven years post-fire. Post-fire growth rates were nearly constant over time and 35-year-old black spruce stems were on average 200 cm in height.
- Assuming black spruce saplings established on average five years post-fire, their growth rate would be 6.67 cm/year (200 cm/30 years), suggesting it would take nine years for black spruce saplings to reach the height of the core in peatlands.
- Thus, it takes on average 14 years for black spruce saplings to reach the height of the core in a burned peatland in the Lower Athabasca Region.

White Spruce  
(*Picea glauca*)

Sw

13

- According to Abrahamson (2015), white spruce saplings do not emerge in the canopy until 60 years post-wildfire and do not dominate until 100–120 years post-wildfire. However, an older study found that white spruce saplings established 25 years post-wildfire (Youngblood, 1995).
- Based on data collected in the field, white spruce saplings were >30 cm in height in the MacKay River Wildfire (2007), but were on average 150 cm in the House River Wildfire (2002). Within five years, white spruce saplings in the Lower Athabasca Region grew approximately 120 cm, representing a constant growth rate of 24 cm/year.
- It would only take an additional year for the white spruce saplings to grow at the height of the core at the MacKay River Wildfire (2007), thus it takes on average 13 years for white spruce saplings to grow at the height of the core in a burned area in the Lower Athabasca Region.

Tamarack  
(*Larix laricina*)

Lt

7

- In full sunlight (which is expected after a wildfire), first-year seedlings are 18–23 cm in height and 46–51 cm after three growing seasons (Johnston, 1990). Based on Johnston (1990), it takes on average four years for tamarack saplings to reach the height of the core.
- Tamarack establish in burned areas within ten years post-fire and in some cases until 20 years post-fire (Parminter, 1983).

			<ul style="list-style-type: none"> <li>• Considering that tamarack are not present in the Horse River Wildfire (2016), but present in the McKay Fire (2011) as seedlings &gt;30 cm in height, suggesting that the saplings are second-year seedlings, tamarack seedlings established in the burned areas three years post-fire.</li> <li>• Thus, it takes on average seven years for tamarack saplings to reach the height of the core in a burned area in the Lower Athabasca Region.</li> </ul>
Jack Pine ( <i>Pinus banksiana</i> )	Pj	3	<ul style="list-style-type: none"> <li>• Chrosciewicz (1988) found that jack pine regeneration three years post-wildfire in central Saskatchewan was on average 47 cm in height with the tallest saplings being 71 cm, representing a growth rate of 12 cm/year and 24 cm/year, respectively.</li> <li>• Jack pine saplings in the Richardson Fire (2011) were approximately 150 cm in height, suggesting a growth rate of 19 cm/year.</li> <li>• If you extrapolate the growth rates obtained in Chrosciewicz (1988) to eight years post-fire, the average jack pine saplings would have been 96 cm in height, while the tallest saplings would have been 192 cm.</li> <li>• Due to variability in jack pine growth rates, possibly due to fire severity, the mean growth rate between the average and tallest jack pine saplings in Chrosciewicz (1988) is 18 cm/year.</li> <li>• Considering that the growth rate from the data collected in the field and Chrosciewicz (1988) are almost identical, it would take on average three years for jack pine saplings to grow at the height of the core in a burned area in the Lower Athabasca Region.</li> </ul>
Trembling Aspen ( <i>Populus tremuloides</i> )	Aw	2	<ul style="list-style-type: none"> <li>• DeByle &amp; Winokur (1985) found that first-year seedlings are 15–30 cm in height and take two to five years to reach 150 cm in height.</li> <li>• Brinkman &amp; Roe (1975) found that first-year seedlings are 15–61 cm in height.</li> <li>• Trembling aspen saplings in the Horse River Wildfire (2016) were over 55 cm in height, suggesting that it takes on average two years for trembling aspen saplings to reach the height of the core in the Lower Athabasca Region.</li> </ul>

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**Appendix 2.3.** Codes and visual assessment used to categorize ungulate browse severity by species in each field plot.

Code	Browse Severity	Visual Assessment	Example
0	None	No browsing occurred	
1	Low	Browsed branches with no dead wood and some healthy leader growth	

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2

Medium

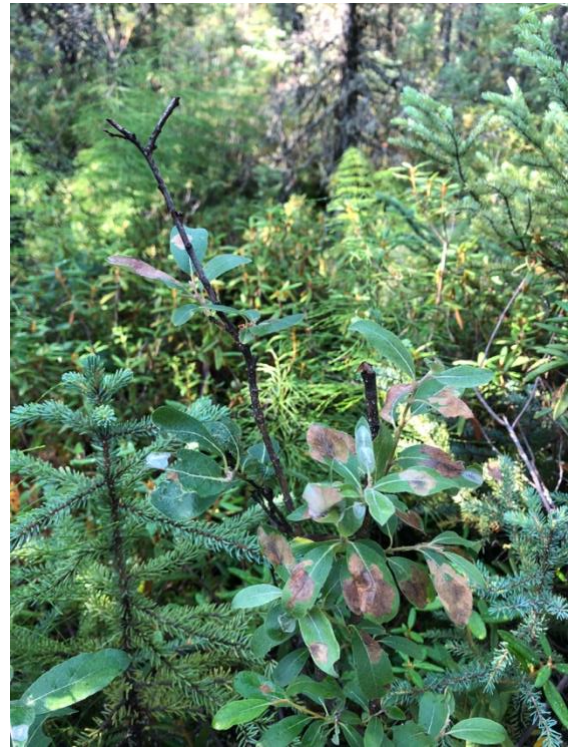
Browsed branches  
with moderate  
secondary growth  
(hedging) and dead  
wood



3

High

Browsed branches  
with substantial  
secondary growth  
(hedging) and  
excessive dead wood



---

4

Extreme

Stem or all branches  
browsed



**Appendix 2.4.** List of deciduous shrub and sapling species targeted for sampling in the summer of 2019 in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada. The list of species is ordered alphabetically by scientific name.

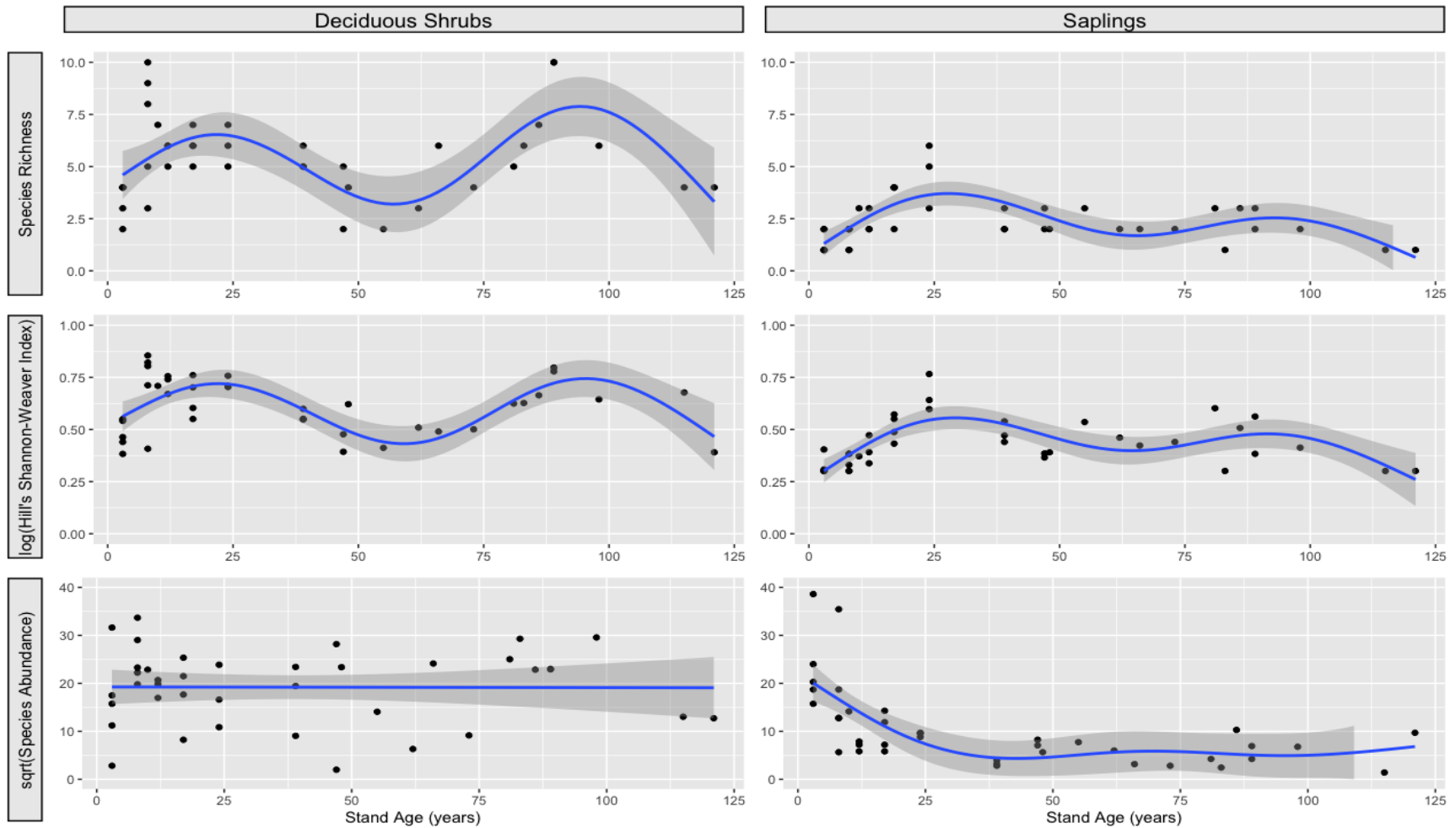
<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>	<b>Common Name</b>
AlnInc	<i>Alnus incana</i> subsp. <i>rugosa</i>	Betulaceae	Speckled Alder, River Alder
AlnVir	<i>Alnus viridis</i>	Betulaceae	Green Alder
AmeAln	<i>Amelanchier alnifolia</i>	Rosaceae	Saskatoon
BetGla	<i>Betula glandulosa</i>	Betulaceae	Dwarf Birch, Swamp Birch
BetPum	<i>Betula pumila</i> var. <i>glandulifera</i>	Betulaceae	Northern Bog Birch
CorCor	<i>Corylus cornuta</i>	Betulaceae	Beaked Hazelnut
CorSer	<i>Cornus sericea</i>	Cornaceae	Red-osier Dogwood
EndAln	<i>Endotropis alnifolia</i>	Rhamnaceae	Alder-leaved Buckthorn
LedGro	<i>Ledum groenlandicum</i>	Ericaceae	Labrador Tea
LonDio	<i>Lonicera dioica</i>	Caprifoliaceae	Twining Honeysuckle
LonInv	<i>Lonicera involucrata</i>	Caprifoliaceae	Bracted Honeysuckle
LonVil	<i>Lonicera villosa</i>	Caprifoliaceae	Mountain Fly Honeysuckle
PruPen	<i>Prunus pensylvanica</i>	Rosaceae	Pin Cherry
PruVir	<i>Prunus virginiana</i>	Rosaceae	Chokecherry
RosAci	<i>Rosa acicularis</i>	Rosaceae	Prickly Wild Rose
RosWoo	<i>Rosa woodsii</i>	Rosaceae	Common Wild Rose
RibAme	<i>Ribes americanum</i>	Grossulariaceae	American Black Currant
RibGla	<i>Ribes glandulosum</i>	Grossulariaceae	Skunk Currant
RibHir	<i>Ribes hirtellum</i>	Grossulariaceae	Swamp Gooseberry, American Gooseberry



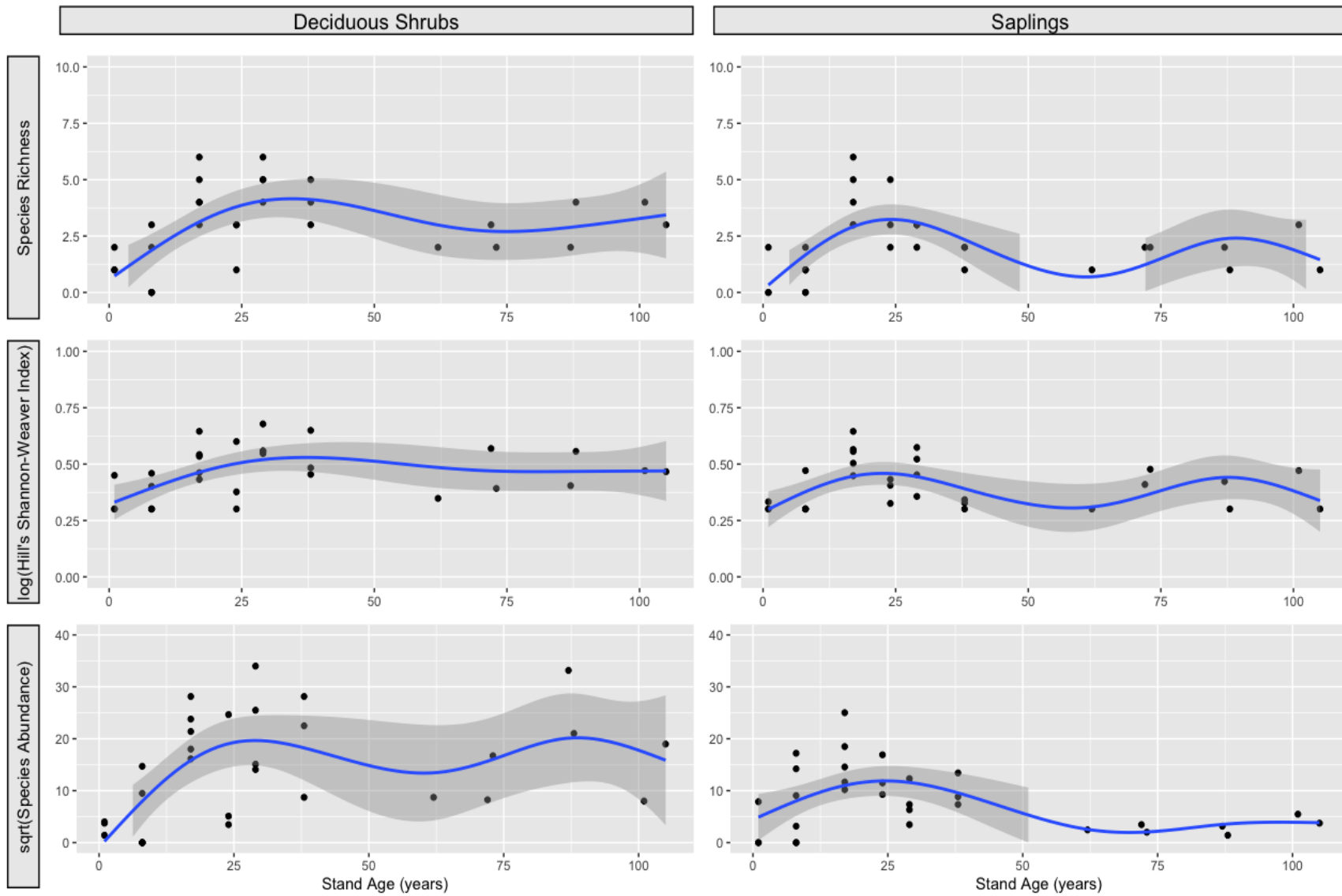
RibHud	<i>Ribes hudsonianum</i>	Grossulariaceae	Northern Black Currant
RibLac	<i>Ribes lacustre</i>	Grossulariaceae	Bristly Black Currant
RibOxy	<i>Ribes oxycanthoides</i>	Grossulariaceae	Canada Gooseberry, Wild Gooseberry
RibTri	<i>Ribes triste</i>	Grossulariaceae	Swamp Red Currant, Wild Red Currant
<hr/>			
RubIda	<i>Rubus idaeus</i>	Rosaceae	Wild Red Raspberry
Salix	<i>Salix</i> spp.	Salicaceae	Willow Shrubs/Trees
SheCan	<i>Shepherdia canadensis</i>	Elaeagnaceae	Soapberry, Canada Buffaloberry
SorSco	<i>Sorbus scopulina</i>	Rosaceae	Greene's Mountain-ash
<hr/>			
SymAlb	<i>Symphoricarpos albus</i>	Caprifoliaceae	Common Snowberry
SymOcc	<i>Symphoricarpos occidentalis</i>	Caprifoliaceae	Buckbrush
<hr/>			
VacCes	<i>Vaccinium cespitosum</i>	Ericaceae	Dwarf Blueberry
VacMyr	<i>Vaccinium myrtilloides</i>	Ericaceae	Common Blueberry
<hr/>			
VibEdu	<i>Viburnum edule</i>	Adoxaceae	Squashberry, Lowbush Cranberry
<hr/>			
Aw	<i>Populus tremuloides</i>	Salicaceae	Trembling Aspen
Ab	<i>Populus balsamifera</i>	Salicaceae	Balsam Poplar
Bw	<i>Betula papyrifera</i>	Betulaceae	Paper Birch, White Birch
Fb	<i>Abies balsamea</i>	Pinaceae	Balsam Fir
Lt	<i>Larix laricina</i>	Pinaceae	Tamarack, Larch
Pj	<i>Pinus banksiana</i>	Pinaceae	Jack Pine
Sb	<i>Picea mariana</i>	Pinaceae	Black Spruce
Sw	<i>Picea glauca</i>	Pinaceae	White Spruce

**Appendix 2.5.** Temporal changes (stand age) in deciduous shrub and sapling richness consumed by moose and white-tailed deer, Hill's Index, and abundance (number of stems/100 m<sup>2</sup>) in six landcover types in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.

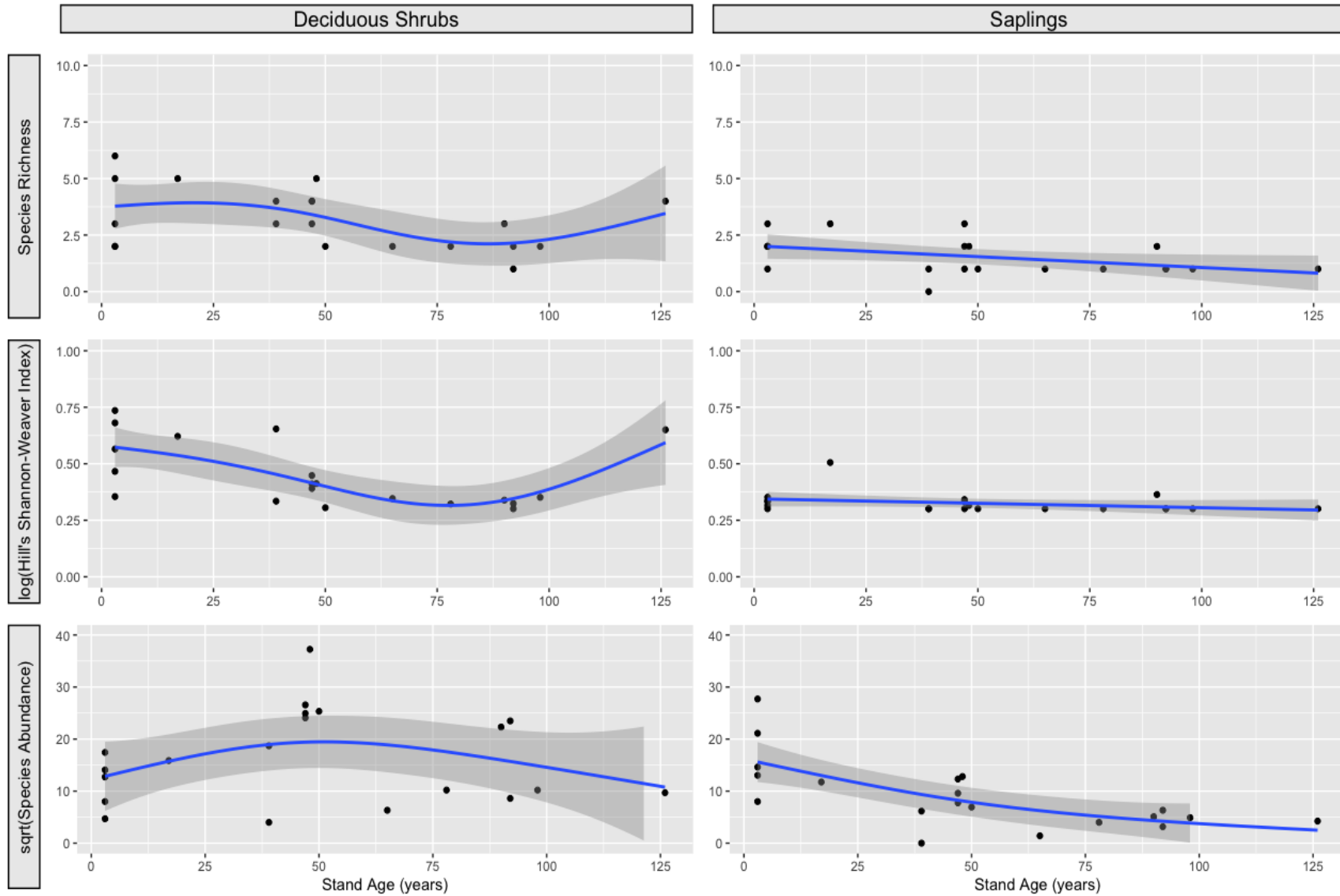
**Figure 2.5.1.** Temporal changes (stand age) in deciduous shrub and sapling richness consumed by moose and white-tailed deer, Hill's Index, and abundance (number of stems/100 m<sup>2</sup>) in mixedwood forests in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



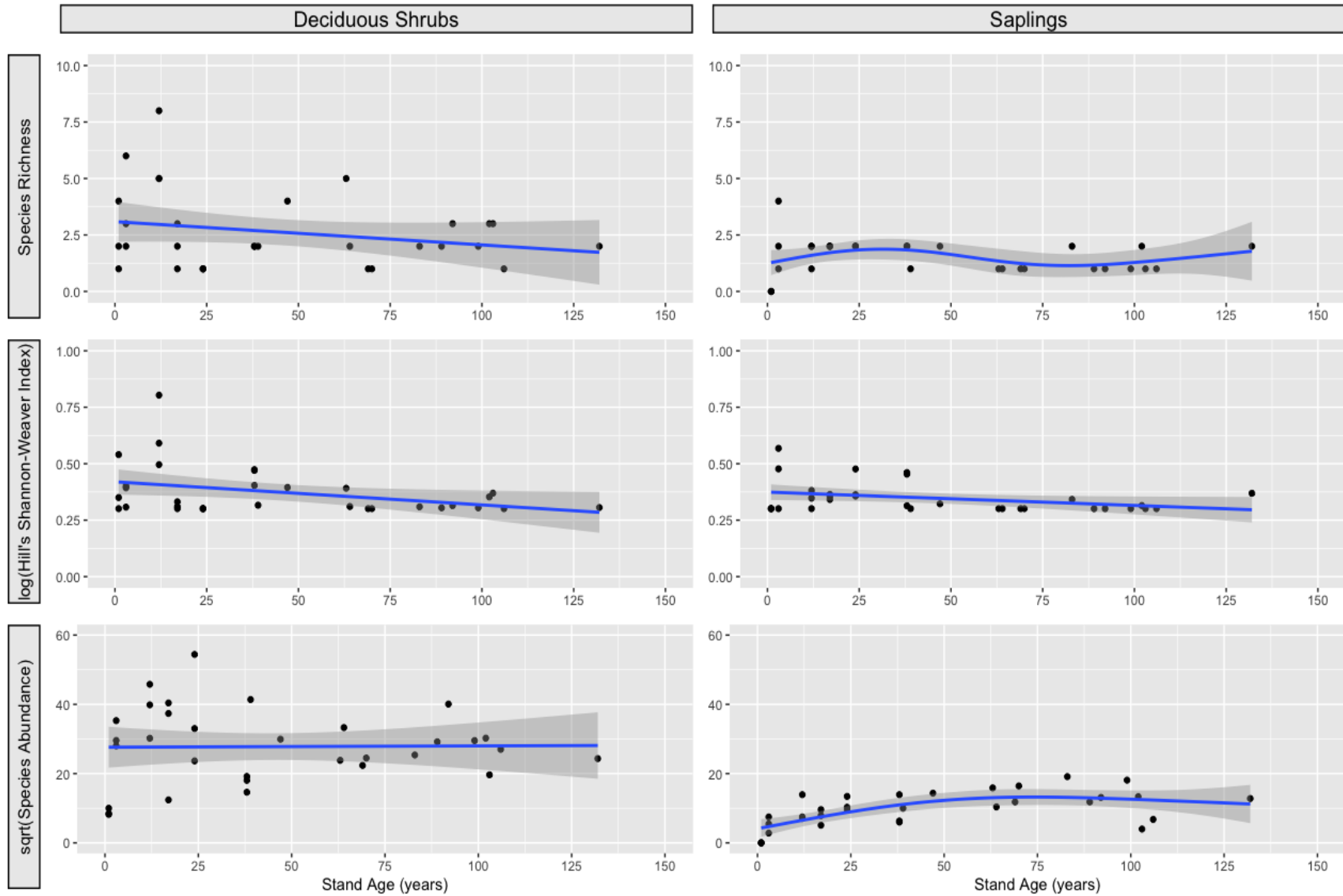
**Figure 2.5.2.** Temporal changes (stand age) in deciduous shrub and sapling richness consumed by moose and white-tailed deer, Hill's Index, and abundance (number of stems/100 m<sup>2</sup>) in jack pine forests in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



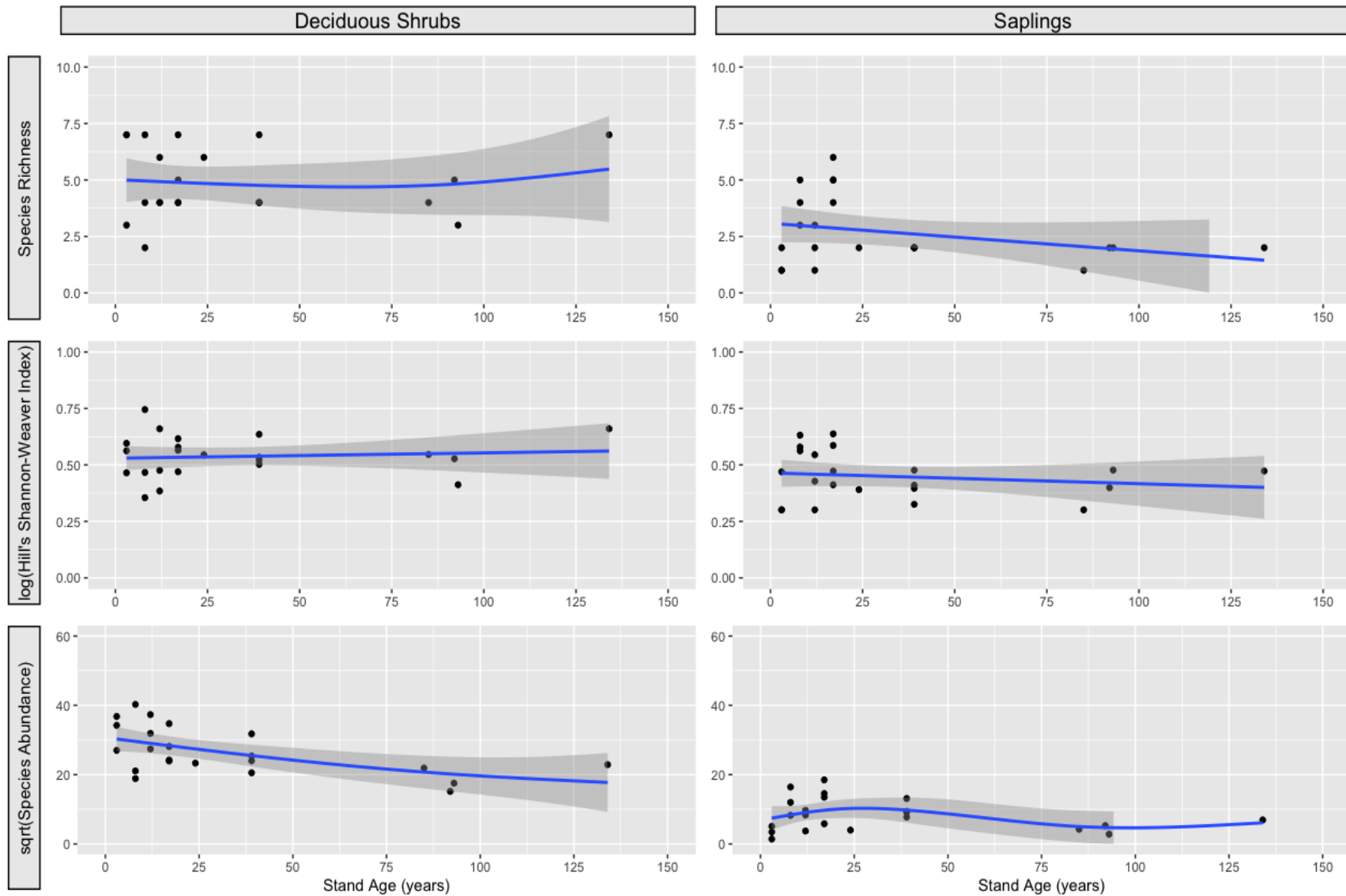
**Figure 2.5.3.** Temporal changes (stand age) in deciduous shrub and sapling richness consumed by moose and white-tailed deer, Hill's Index, and abundance (number of stems/100 m<sup>2</sup>) in black spruce forests in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



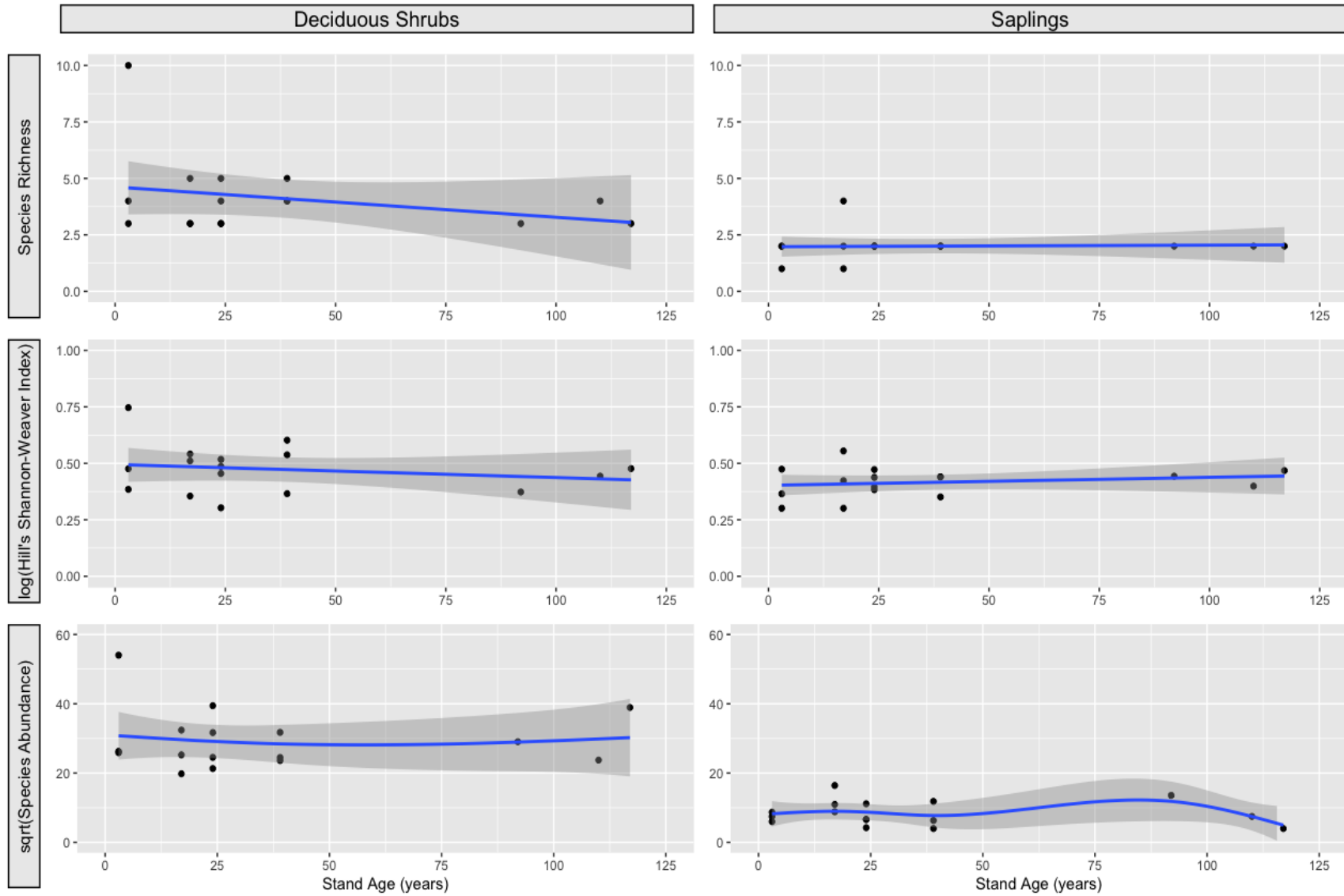
**Figure 2.5.4.** Temporal changes (stand age) in deciduous shrub and sapling richness consumed by moose and white-tailed deer, Hill's Index, and abundance (number of stems/100 m<sup>2</sup>) in bogs in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



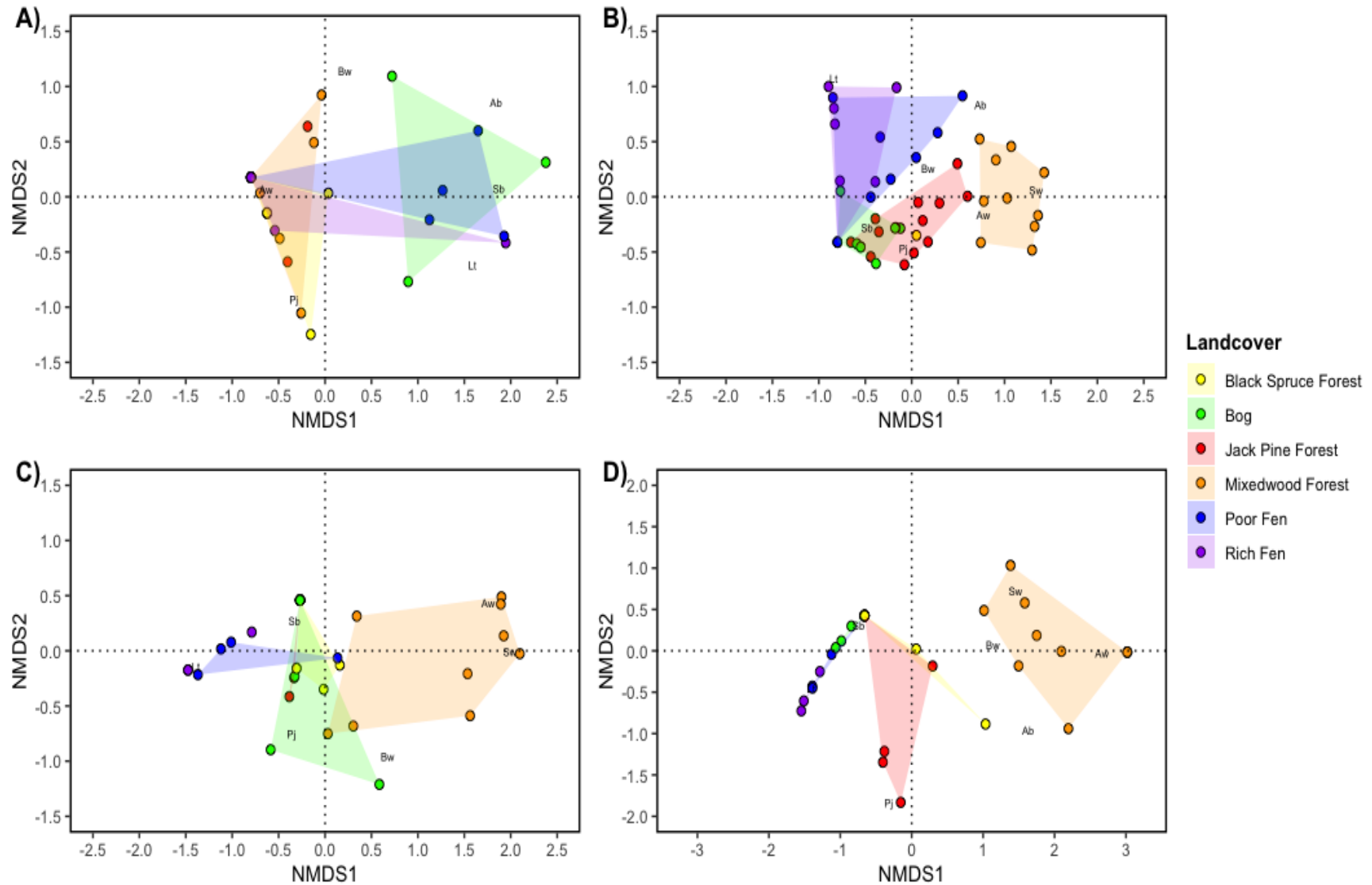
**Figure 2.5.5.** Temporal changes (stand age) in deciduous shrub and sapling richness consumed by moose and white-tailed deer, Hill's Index, and abundance (number of stems/100 m<sup>2</sup>) in poor fens in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



**Figure 2.5.6.** Temporal changes (stand age) in deciduous shrub and sapling richness consumed by moose and white-tailed deer, Hill's Index, and abundance (number of stems/100 m<sup>2</sup>) in rich fens in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.

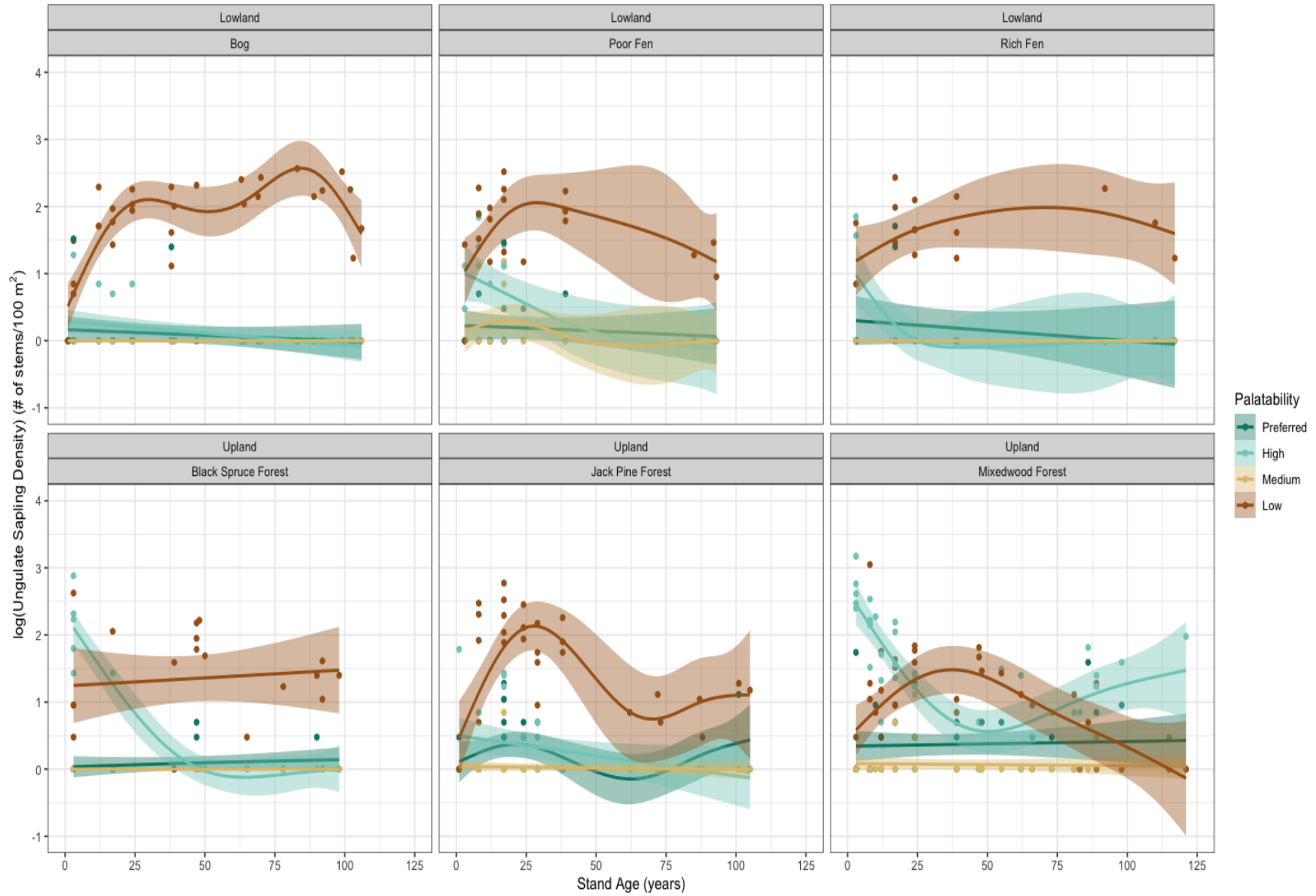


**Appendix 2.6.** Temporal changes (stand age) in sapling composition for species consumed by moose and white-tailed deer in A) 0 – 10 years post-wildfire (young forest), B) 11 – 30 years post-wildfire (young forest), C) 31 – 70 years post-wildfire (intermediate forest), and D)  $\geq 71$  years post-wildfire (mature forest) in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



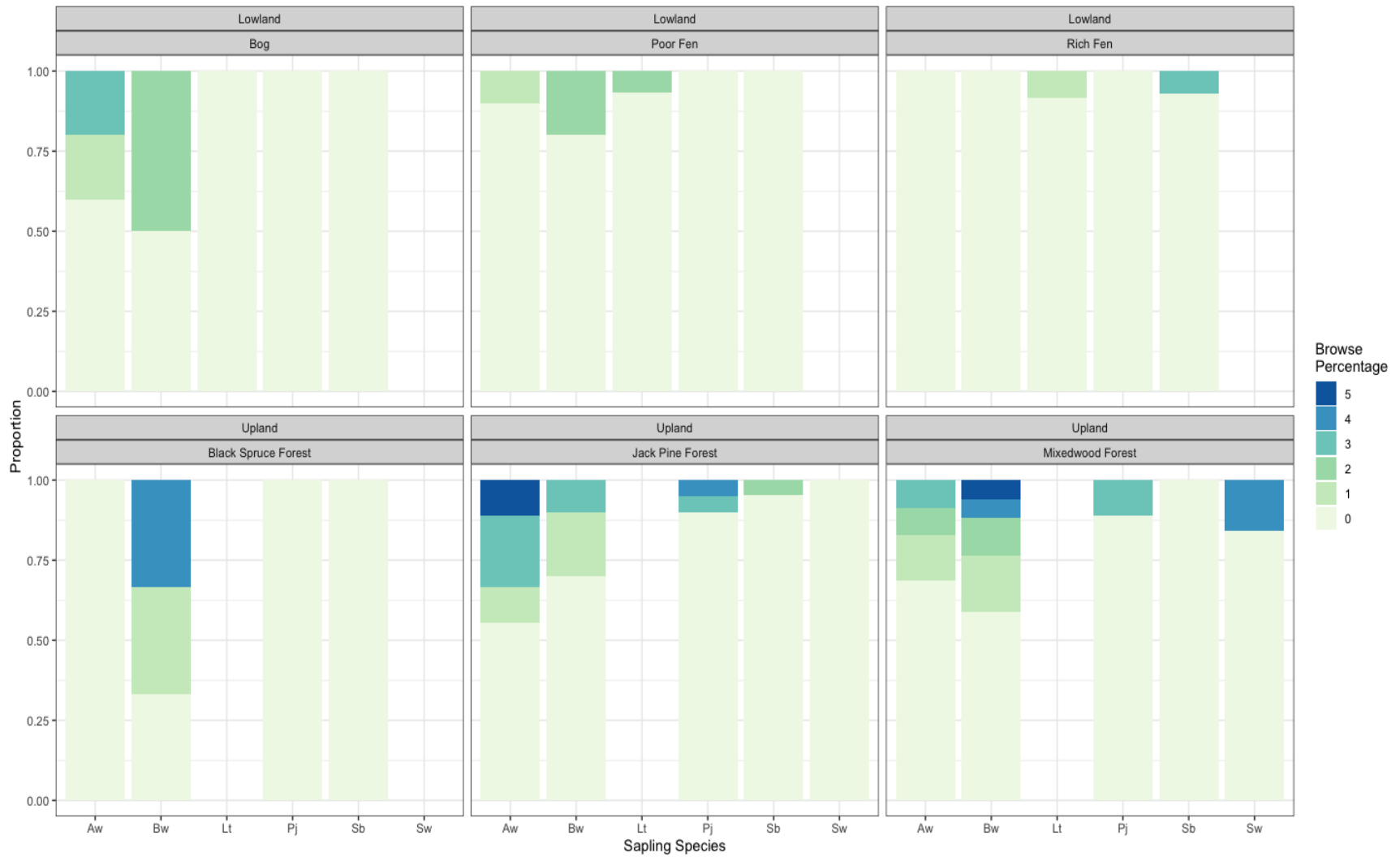


**Appendix 2.7.** Temporal changes (stand age) in sapling abundance (number of stems/100 m<sup>2</sup>) by palatability categories in six landcover types in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.

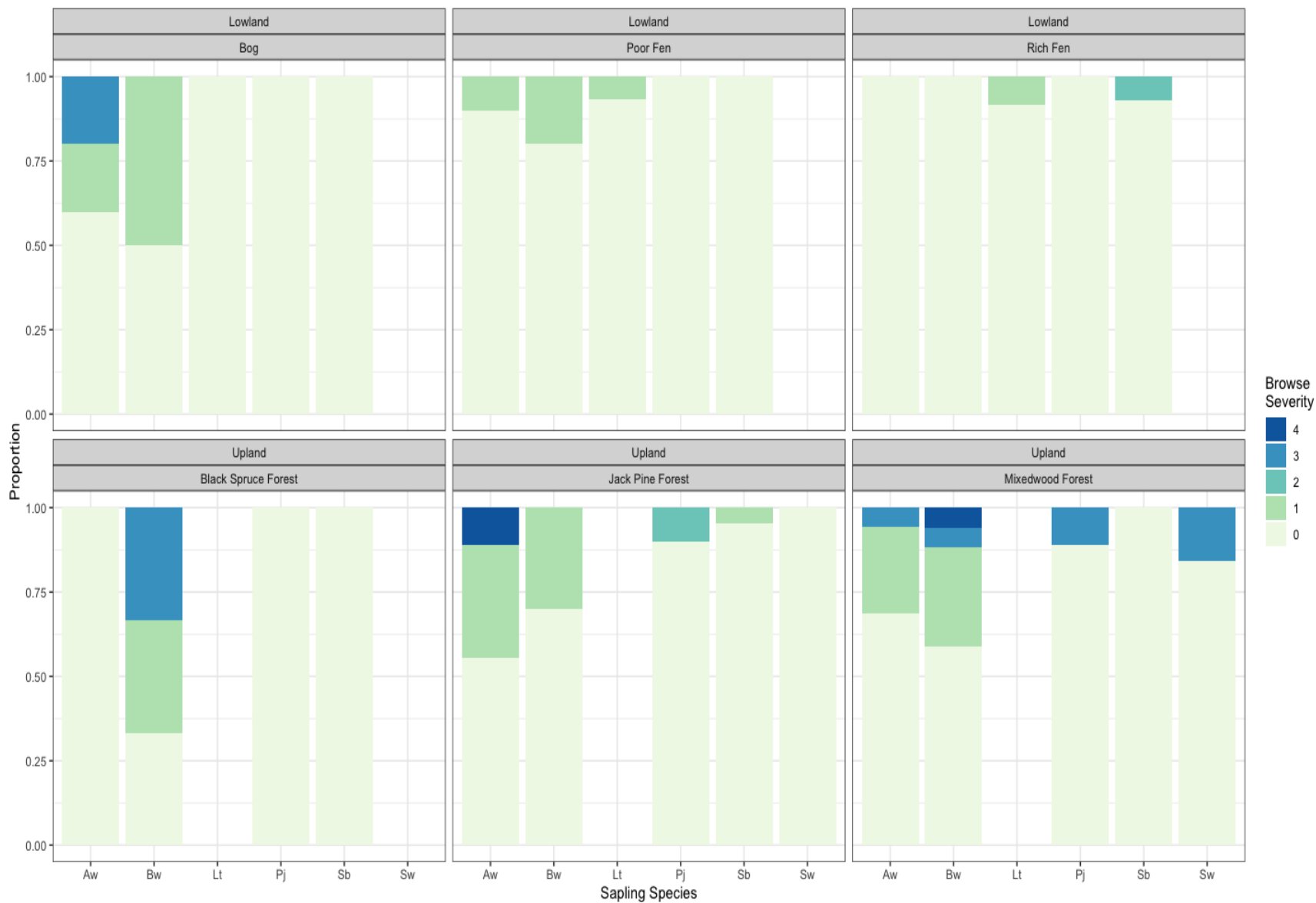


**Appendix 2.8.** Proportion of browse category for each sapling species consumed by moose and white-tailed deer in six landcover types in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.

**Figure 2.8.1.** Proportion of browse category (by percentage) for each sapling species consumed by moose and white-tailed deer in six landcover types in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



**Figure 2.8.2.** Proportion of browse category (by severity) for each sapling species consumed by moose and white-tailed deer in six landcover types in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.



**Appendix 3.1.** Decisions and assumptions taken to prescribe unstandardized weighted coefficients or RSF coefficients for the nutritional resources and predation risk habitat component matrices.

### **Nutritional resources**

The following are the decisions and assumptions taken to prescribe an unstandardized weighted coefficient for each landcover type and age class for both moose and white-tailed deer based on the final three-way ANCOVA model from Chapter 2:

- *Jack pine* was based on “Jack Pine Forest”, which was described as “open and closed canopy coniferous upland forests dominated by jack pine on dry sandy soils”.
- *Black spruce* was based on “Black Spruce Forest”, which was described as “open and closed canopy coniferous forests dominated by black spruce occurring on wet organic [woody or sphagnum peat] soils”.
- *Deciduous* and *Mixedwood* were based on “Mixedwood Forest”, which was described as “open and closed canopy upland forests with a minimum composition of 25% coniferous species [white spruce, black spruce, balsam fir, jack pine] and maximum composition of 75% hardwood species [trembling aspen, balsam poplar, white birch]”.
- Grasslands in the boreal forest are known to limit deciduous shrub and hardwood sapling establishment to mounds of exposed mineral soil due to intense competition with grasses and herbs (i.e. bluejoint reed grass (*Calamagrostis canadensis*)) (Collins and Schwartz 1998).
  - In fact, the carrying capacity of moose in deciduous and mixedwood forests can increase 20–40 fold (4–9 moose/km<sup>2</sup>) post-wildfire, whereas in grassland ecosystems, the carrying capacity does not exceed 0.2 moose/km<sup>2</sup>, similarly to the carrying capacity in mature upland forests (Collins and Schwartz 1998). Moose winter diet in northeastern Alberta consists exclusively of shrubs and regenerating trees (Nowlin 1978). That being said, *Grassland* was found to be the landcover type with the lowest nutritional resources (weight of 0.01) for moose.
  - In the hemi-boreal region of the Northern Great Lakes in Minnesota, white-tailed deer are known to consume grasses, sedges and evergreen forbs in the fall until these food sources are covered by snow, by which their winter diet is dominated by woody browse (Rogers et al. 1981). In fact, grasses constitute <2% of white-tailed deer winter diet from December to March, and between 11 and 14% in November and April (Rogers et al. 1981). That being said, *Grassland* was found to be the landcover type with the lowest nutritional resources (weight of 0.01) for white-tailed deer.
- *Bog* was based on “Bog”, which was described as “open canopy coniferous lowland forest dominated by black spruce occurring on wet thick organic [sphagnum peat] soils”.
- *Fen* was based on “Poor Fen”, which was described as “open canopy coniferous lowland forest dominated by black spruce and tamarack, shrubs and sedges/grasses occurring on wet organic [sphagnum peat] soils”.

- *Swamp* was based on “Black Spruce Forest”, which was described as “open and closed canopy coniferous forests dominated by black spruce or white spruce occurring on wet organic [woody or sphagnum peat] soils”.
- Marshes are mineral wetlands dominated by broad-leaved sedges, bluejoint grass, and emergent rushes (i.e. cattail and bulrush) (Ducks Unlimited Canada 2018). Deciduous shrubs and hardwood or coniferous saplings are not present in marshes (Ducks Unlimited Canada 2018).
  - Moose winter diet in northeastern Alberta consists exclusively of shrubs and regenerating trees (Nowlin 1978). That being said, *Marsh* was found to be the landcover type with the lowest nutritional resources (weight of 0.01) for moose.
  - In the hemi-boreal region of the Northern Great Lakes in Minnesota, white-tailed deer are known to consume grasses, sedges and evergreen forbs in the fall until these food sources are covered by snow, by which their winter diet is dominated by woody browse (Rogers et al. 1981). Regardless, white-tailed deer do not frequent marshes for nutritional purposes, but rather for predators escape and cover for thermoregulation (Compton et al. 1988, Olson 1992). That being said, *Marsh* was found to be the landcover type with the lowest nutritional resources (weight of 0.01) for white-tailed deer.

### **Predation Risk**

For the purpose of the predation risk matrices, three assumptions were made which were adapted from Whitman et al. (2017) and Barber et al. (2018):

- 1) The increase in favourable habitat for both moose and white-tailed deer will result in an increase in their respective populations, and through apparent competition, will increase wolf populations, therefore increasing predation risk for both ungulates;
- 2) The strength of selection (i.e. RSF coefficients) will remain constant as the relative proportion of landcover types change with future vegetation change and wildfire regimes.
- 3) RSF coefficient from previous studies often do not consider the changes in the strength of selection of species to specific landcover type over time (i.e. years post-wildfire); thus, RSF coefficients were used to represent mature landcover types (>70 years post-wildfire), unless otherwise stated by the study. Findings from Chapter 2 on the winter browse succession of moose and white-tailed deer in the boreal forest were then used to adjust weights associated with young (<20 and 21–30 years post-wildfire) and intermediate (31–50 and 51–70 years post-wildfire) landcover types.

### *Moose*

The predation risk for moose were taken directly from the RSF coefficients in “Zone T” defined as areas with more abundant uplands and merchantable timber, described in Osko et al. (2004). The following are the decisions and assumptions used to prescribe an RSF coefficient for each landcover type:

- *Jack pine* was based on “Conifer Upland”, which was described as “open and closed canopy coniferous forests (white spruce, balsam fir, jack pine)”.
- *Black spruce* was based on “Closed Conifer Wetland”, which was described as “coniferous closed canopy forests occurring on wet organic soils (black spruce, tamarack)”. Although Osko et al. (2004) did not describe a specific category for black spruce forests, the description provided is aligned with the definition from this study (i.e. closed canopy forest occurring on organic soil transitioning from lowlands).
- *Deciduous* was based on “Deciduous Upland”, which was described as “upland deciduous forests (aspen and balsam poplars, white birch)”.
- *Mixedwood* was based on “Mixedwood Upland”, which was described as “upland forests with mixtures of species in the 2 classes immediately above [white spruce, balsam fir, jack pine, aspen and balsam poplars, white birch]”.
- Upland conifer, mixedwood, and deciduous forests are predicted to be replaced by grasslands or novel grassland-dominated ecosystems that may include mosaics of shrubs and extant deciduous or mixedwood forests (Stralberg et al. 2018). Uncertainty around grasslands in the boreal forest is high as it is currently an unrepresented habitat class; grasslands cover less than 1% of the landscape (Barber et al. 2018). However, grasslands do not provide forage for moose as their carrying capacity in grassland ecosystems does not exceed 0.2 moose/km<sup>2</sup>, similarly to the carrying capacity in mature upland forests (Collins and Schwartz 1998). Based on these findings, *Grassland* was found to be the landcover type with the lowest predation risk (weight of 1) for moose.
- *Bog and Fen* were based on “Open Conifer Wetland”, which was described as “coniferous open canopy forests occurring on wet organic soils (black spruce, tamarack)”. Although Osko et al. (2004) did not describe a specific peatland category, the description provided suggests that it includes treed, shrubby and open bogs and fens.
- *Swamp* was based on “Closed Conifer Wetland”, which was described as “coniferous closed canopy forests occurring on wet organic soils (black spruce, tamarack)”. Although Osko et al. (2004) did not describe a specific category for swamps, the description provided is aligned with the definition from this study (i.e. closed canopy wetland occurring on mineral soil).
- *Marsh* was based on “Wet Meadows”, which was described as “meadow complexes of mosses and herbaceous flora, unforested”. Although Osko et al. (2004) did not describe a specific category for marshes, the description provided is aligned with the definition from this study (i.e. wetland characterized with emergent vegetation of reeds, rushes or sedges with an absence of woody vegetation).

#### *White-tailed deer*

The predation risk for white-tailed deer were taken directly from the RSF coefficients from Fisher et al. (2020). Detailed information of white-tailed deer habitat selection in northeastern Alberta are sparse. Although I acknowledge that the study did not categorize landcover types in

great detail, nor divide the analysis by season, Fisher et al. (2020) provides a good first quantification of white-tailed deer ecology at a regional and temporal scale, rather than landscape and local scales (Fisher et al. 2016, Darlington 2018, Fisher and Burton 2018).

The following are the decisions and assumptions used to prescribe an RSF coefficient for each landcover type:

- *Jack pine* and *Black spruce* were based on “conifer\_low”, which was described as “low density coniferous forest”. The latter was chosen instead of “conifer\_medhigh”, which corresponds to “medium-high density coniferous forest”, because mature coniferous forests have lower basal area than young and intermediate forests.
- *Deciduous* was based on “broadleaf\_medhigh”, which was described as “medium-high density broadleaf forest”. The latter was chosen instead of “broadleaf\_regen”, which corresponds to “regenerating broadleaf forest”, because mature deciduous forests have lower quality and quantity of early seral vegetation.
- *Mixedwood* was based on “mixedwood\_medhigh”, which was described as “medium-high density mixedwood forest”.
- *Grassland* was based on “grassland”.
- *Bog, Fen, Swamp* and *Marsh* were based on “wetland”. Although Fisher et al. (2020) did not describe a specific peatland category, it is unlikely a high predation risk category because it is assumed that white-tailed deer do not frequent peatlands comparable to moose who avoid these areas due to reduced quality and quantity of early-seral vegetation (Maier et al. 2005, DeMars et al. 2019).

## Tables

**Table 3.1.1.** Coefficients describing the nutritional resources’ matrix for moose and white-tailed deer in northeastern Alberta, Canada. Coefficients are weighted values derived from the final ANCOVA model reported in Chapter 2 and adjusted by palatability and age class.

Landcover	Unstandardized Model Coefficient						Standardized Weighted Coefficient					
	Age Class (years)						Age Class (years)					
	<20	21–30	31–50	51–70	71–90	>90	<20	21–30	31–50	51–70	71–90	>90
Jack pine	200.4	189.8	210	293.5	501.8	796.4	0.016	0.010	0.022	0.071	0.192	0.364
Black spruce	356.1	285.2	254.7	251	288.7	343.5	0.107	0.066	0.048	0.046	0.068	0.100
Deciduous	744.1	657.6	675.9	848.7	1292.0	1886.2	0.333	0.283	0.294	0.395	0.653	1.000
Mixedwood	744.1	657.6	675.9	848.7	1292.0	1886.2	0.333	0.283	0.294	0.395	0.653	1.000
Grassland	—	—	—	—	—	—	0.010	0.010	0.010	0.010	0.010	0.010
Bog	332.2	318.1	371.3	563.5	1005.8	1595.6	0.093	0.085	0.116	0.228	0.486	0.830
Fen	1257.5	1094.2	980.5	867.4	787.4	741.8	0.633	0.538	0.471	0.405	0.359	0.332
Swamp	356.1	285.2	254.7	251	288.7	343.5	0.107	0.066	0.048	0.046	0.068	0.100
Marsh	—	—	—	—	—	—	0.010	0.010	0.010	0.010	0.010	0.010

**Table 3.1.2.** Coefficients describing the predation risk matrix for moose in northeastern Alberta, Canada. Coefficients are weighted values derived using previously reported RSF coefficients from Osko et al. (2004) and adjusted according to expert opinion and Latham (2009).

Landcover	RSF Coefficient	Weighted Coefficient	Age Class (years)					
			<20	21–30	31–50	51–70	71–90	>90
Jack pine	0.066	0.933	0.633	0.633	0.783	0.783	0.833	0.833
Black spruce	0.107	0.628	0.528	0.528	0.578	0.578	0.628	0.628
Deciduous	0.190	0.010	0.010	0.010	0.050	0.050	0.100	0.100
Mixedwood	0.118	0.546	0.246	0.246	0.496	0.546	0.446	0.496
Grassland	—	—	1.000	1.000	1.000	1.000	1.000	1.000
Bog	0.065	0.940	0.940	0.940	0.940	0.940	0.940	0.940
Fen	0.065	0.940	0.840	0.840	0.840	0.840	0.840	0.840
Swamp	0.107	0.628	0.628	0.628	0.628	0.628	0.628	0.628
Marsh	0.057	1.000	1.000	1.000	1.000	1.000	1.000	1.000

*Note:* Jack pine, white spruce, mixedwood and fen coefficients were reduced by an additional 10% because these landcover types are frequently selected by wolves in winter (Latham 2009).

**Table 3.1.3.** Coefficients describing the predation risk matrix for white-tailed deer in northeastern Alberta, Canada. Coefficients are weighted values derived using previously reported RSF coefficients from Fisher et al. (2020) and adjusted according to expert opinion and Latham (2009).

Landcover	RSF Coefficient	Weighted Coefficient	Age Class (years)					
			<20	21–30	31–50	51–70	71–90	>90
Jack pine	-0.554	0.895	0.595	0.595	0.695	0.695	0.795	0.795
Black spruce	-0.554	0.895	0.595	0.595	0.695	0.695	0.795	0.795
Deciduous	0.204	0.010	0.010	0.010	0.050	0.050	0.100	0.100
Mixedwood	-0.139	0.410	0.110	0.110	0.360	0.410	0.310	0.360
Grassland	0.097	0.135	0.135	0.135	0.135	0.135	0.135	0.135
Bog	-0.644	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Fen	-0.644	1.000	0.900	0.900	0.900	0.900	0.900	0.900
Swamp	-0.644	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Marsh	-0.644	1.000	1.000	1.000	1.000	1.000	1.000	1.000

*Note:* Jack pine, white spruce, mixedwood and fen coefficients were reduced by an additional 10% because these landcover types are frequently selected by wolves in winter (Latham 2009).

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**Appendix 3.2.** Summary statistics and spatial distribution of burn probability for each fuel scenario (i.e., static and fire-mediated), fire regime scenario (i.e., constrained and unconstrained), time period (i.e., 2011–2040, 2041–2070, and 2071–2100) and GCM (i.e., CanESM2, CSIRO, and HadGEM2).

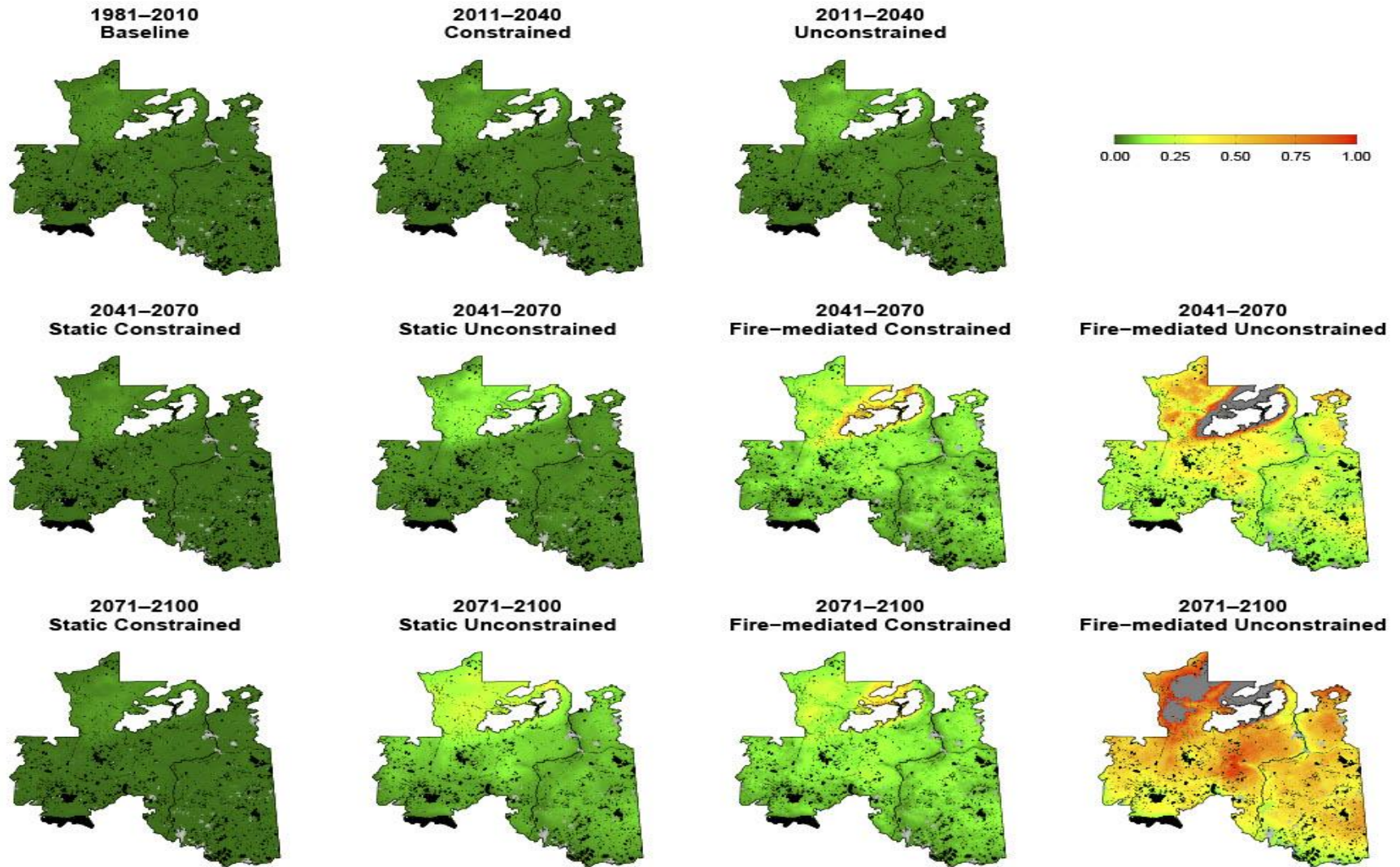
To assess changes in wildfire activity in the 21<sup>st</sup> century relative to the baseline period (1981–2010), burn probability (%) was calculated for each fuel scenario (i.e., static and fire-mediated), fire regime scenario (i.e., constrained and unconstrained), time period (i.e., 2011–2040, 2041–2070, and 2071–2100) and GCM (i.e., CanESM2, CSIRO, and HadGEM2). Burn probability corresponded to the proportion of individual Burn-P3 iterations for which a given pixel burned within a given scenario, time period and GCM.

Median burn probability under baseline conditions was 0.01% (Table 3.2.1; Figure 3.2.1). Under a static fuel scenario and constrained fire regime, median burn probability in the 2050s (2041–2070) and in the 2080s (2071–2100) was projected to remain similar to the baseline conditions (Table 3.2.1; Figure 3.2.1). Under a static fuel scenario and unconstrained fire regime, median burn probability was projected to slightly increase to 0.03% in the 2050s and 0.08% in the 2080s (Table 3.2.1; Figure 3.2.1). Under a fire-mediated fuel scenario, median burn probability was projected to increase to 0.10% (10-fold increase) and 0.25% (25-fold increase) in the 2050s and further increase to 0.11% (11-fold increase) and 0.50% (50-fold increase) in the 2080s for the constrained and unconstrained fire regime, respectively (Table 3.2.1; Figure 3.2.1). However, median burn probability reached a maximum of 0.72% (72-fold increase) and 2.16% (216-fold increase) in the 2050s, while it reached 0.65% (65-fold increase) and 2.10% (210-fold increase) in the 2080s for the constrained and unconstrained fire regime, respectively (Table 3.2.1; Figure 3.2.1).

**Table 3.2.1.** Summary of burn probability for each fuel scenario (i.e., static and fire-mediated), fire regime scenario (i.e., constrained and unconstrained), time period (i.e., 2011–2040, 2041–2070, and 2071–2100) and GCM (i.e., CanESM2, CSIRO, and HadGEM2).

		<b>1<sup>st</sup> Quantile</b>	<b>Median</b>	<b>3<sup>rd</sup> Quantile</b>	<b>Maximum</b>	<b>1<sup>st</sup> Quantile</b>	<b>Median</b>	<b>3<sup>rd</sup> Quantile</b>	<b>Maximum</b>
<b>2011 – 2040</b>	Baseline	0.008	0.011	0.015	0.066	—	—	—	—
	CanESM2	0.008	0.011	0.015	0.064	0.014	0.018	0.025	0.124
	CSIRO	0.017	0.023	0.032	0.134	0.017	0.023	0.032	0.134
	HadGEM2	0.008	0.010	0.014	0.068	0.020	0.026	0.035	0.149
	Mean	0.011	0.015	0.020	0.087	0.017	0.023	0.030	0.133
		<b>Static Constrained</b>				<b>Static Unconstrained</b>			
<b>2041 – 2070</b>	CanESM2	0.007	0.010	0.015	0.082	0.020	0.027	0.038	0.254
	CSIRO	0.008	0.011	0.015	0.072	0.025	0.033	0.041	0.107
	HadGEM2	0.008	0.010	0.014	0.070	0.028	0.039	0.051	0.303
	Mean	0.008	0.011	0.014	0.074	0.025	0.033	0.044	0.219
<b>2071 – 2100</b>	CanESM2	0.008	0.011	0.015	0.081	0.032	0.043	0.056	0.251
	CSIRO	0.009	0.012	0.016	0.068	0.009	0.012	0.016	0.068
	HadGEM2	—	—	—	—	0.096	0.124	0.178	0.691
	Mean	0.009	0.012	0.015	0.074	0.059	0.076	0.103	0.358
		<b>Fire-mediated Constrained</b>				<b>Fire-mediated Unconstrained</b>			
<b>2041 – 2070</b>	CanESM2	0.073	0.100	0.133	0.727	0.163	0.220	0.317	2.163
	CSIRO	0.077	0.107	0.140	0.800	0.173	0.250	0.333	1.463
	HadGEM2	0.063	0.090	0.130	0.783	0.173	0.243	0.377	3.280
	Mean	0.076	0.100	0.134	0.717	0.181	0.247	0.348	2.164
<b>2071 – 2100</b>	CanESM2	0.083	0.110	0.150	0.850	0.323	0.423	0.560	2.427
	CSIRO	0.083	0.107	0.137	0.780	0.303	0.437	0.540	1.497
	HadGEM2	0.077	0.103	0.137	0.703	0.420	0.597	0.870	3.083
	Mean	0.086	0.108	0.138	0.653	0.381	0.502	0.653	2.096

**Figure 3.2.1.** Mean burn probability (%) for each fuel scenario (i.e., static and fire-mediated), fire regime scenario (i.e., constrained and unconstrained) and time period (i.e., 2011–2040, 2041–2070, and 2071–2100). Burn probability was averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Black areas represent waterbodies and light grey areas represent non-fuel types (i.e., urban and agriculture areas).



**Appendix 3.3.** Summary statistics and spatial distribution of upland vegetation change for each fuel scenario (i.e., static and fire-mediated), fire regime scenario (i.e., constrained and unconstrained), time period (i.e., 2011–2040, 2041–2070, and 2071–2100) and GCM (i.e., CanESM2, CSIRO, and HadGEM2).

To assess changes in upland vegetation composition in the 21<sup>st</sup> century relative to the baseline period (1981–2010), upland vegetation composition (%) was calculated for each fire regime scenario (i.e., constrained and unconstrained), time period (i.e., 2011–2040, 2041–2070, and 2071–2100) and GCM (i.e., CanESM2, CSIRO, and HadGEM2). Upland vegetation composition was assessed by calculating the number of pixels of upland landcover types (i.e., jack pine, black spruce, mixedwood, deciduous, and grassland) and dividing by the total number of pixels in the study area.

Major upland vegetation changes in the 21<sup>st</sup> century was largely due to the replacement of boreal mixedwood forests by deciduous forests and grasslands (Table 3.3.1; Figure 3.3.1 and 3.3.2). Mixedwood forests covered 49.5% of the landscape (89.4% of upland vegetation) in baseline conditions (Table 3.3.1; Figure 3.3.1 and 3.3.2). By the 2080s, its distribution decreased to 19.0% and 1.5% under the constrained and unconstrained fire regime, respectively (Table 3.3.1; Figure 3.3.1 and 3.3.2). In contrast, grasslands covered 0.01% of the landscape under baseline conditions and increased to 31.0% (55.8% of upland vegetation) and 53.5% (95.5% of upland vegetation) in the 2080s under the constrained and unconstrained fire regime, respectively (Table 3.3.1; Figure 3.3.1 and 3.3.2). Deciduous forests covered 0.2% of the landscape in baseline conditions (Table 3.3.1; Figure 3.3.1 and 3.3.2), but peaked at 6.6% in the 2050s and 11.6% in the 2020s under the constrained and unconstrained fire regime, respectively, and decreased to 3.4% and 0.5% in the 2080s (Table 3.3.1; Figure 3.3.1 and 3.3.2). Jack pine and black spruce forests, which represented 1.5% and 4.2% of the total landscape in baseline conditions, declined to <1% in both the constrained and unconstrained fire regime in the 2080s (Table 3.3.1; Figure 3.3.1 and 3.3.2).

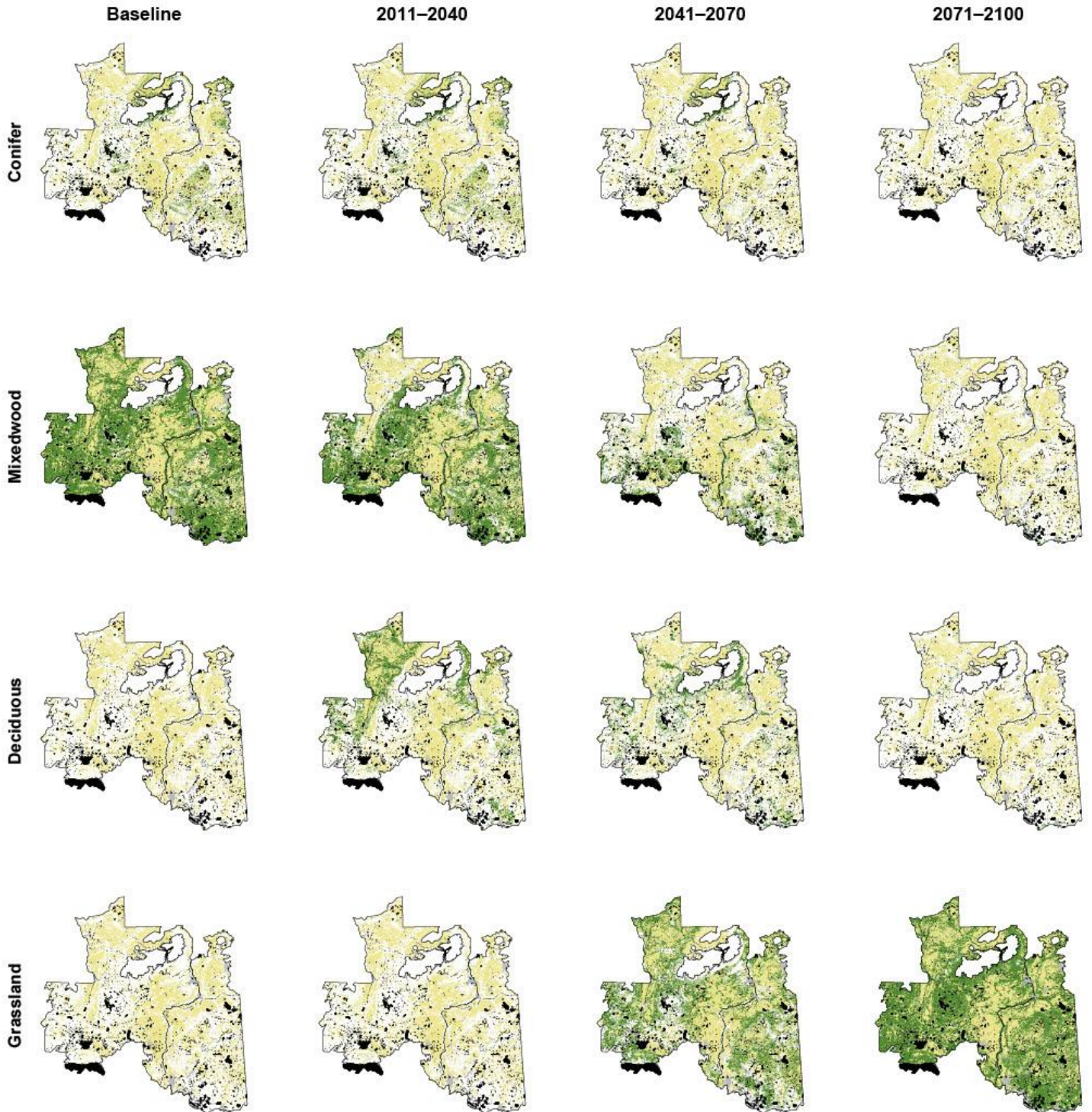
**Table 3.3.1.** Summary of upland vegetation change (in percentage) for each time period (i.e., 2011–2040, 2041–2070, and 2071–2100) and global climate model (GCM; CanESM2, CSIRO, and HadGEM2) based on a fire-mediated fuel scenario, including both constrained and unconstrained fire regime scenarios.

	Jack Pine (%)	Black Spruce (%)	Mixedwood (%)	Deciduous (%)	Grassland (%)	Jack Pine (%)	Black Spruce (%)	Mixedwood (%)	Deciduous (%)	Grassland (%)
Baseline	1.506	4.157	49.543	0.173	0.011	—	—	—	—	—
	Fire-mediated Constrained					Fire-mediated Unconstrained				
<b>2011 – 2040</b>										
CanESM2	1.322	4.304	45.014	4.665	0.082	1.106	4.492	41.079	8.315	0.398
CSIRO	1.365	4.265	44.051	5.693	0.006	1.113	4.429	37.382	12.434	0.004
HadGEM2	1.219	4.418	44.128	5.596	0.032	0.876	4.662	24.767	24.852	0.241
Mean	1.301	4.336	45.324	4.421	0.007	1.041	4.550	38.118	11.598	0.095
<b>2041 – 2070</b>										
CanESM2	0.915	4.150	38.557	5.091	6.624	0.438	2.644	20.806	2.604	28.894
CSIRO	0.883	4.528	37.816	9.504	2.597	0.495	3.673	16.122	17.362	17.721
HadGEM2	1.065	3.504	37.995	7.678	4.962	0.222	1.198	4.848	14.829	34.193
Mean	1.038	4.377	41.036	6.635	2.257	0.350	2.477	13.457	8.669	30.488
<b>2071 – 2100</b>										
CanESM2	0.152	0.641	4.150	0.889	49.761	0.087	0.388	1.495	0.149	53.889
CSIRO	0.663	2.393	25.958	7.982	18.487	0.091	0.428	1.319	2.478	51.780
HadGEM2	0.685	2.248	24.899	5.023	22.722	0.200	0.824	4.943	9.847	40.042
Mean	0.501	1.688	18.950	3.412	31.022	0.089	0.399	1.529	0.520	53.459

**Figure 3.3.1.** Modelled distribution of conifer, mixedwood, deciduous, and grassland vegetation types for current (baseline) and future time periods (i.e., 2011–2040, 2041–2070, and 2071–2100) under a fire-mediated fuel scenario and constrained fire regime. Distribution was averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Black areas represent waterbodies, light grey areas represent non-fuel types (i.e., urban and agriculture areas) and beige areas represent lowlands (i.e., wetlands and peatlands).



**Figure 3.3.2.** Modelled distribution of conifer, mixedwood, deciduous, and grassland vegetation types for current (baseline) and future time periods (i.e., 2011–2040, 2041–2070, and 2071–2100) under a fire-mediated fuel scenario and unconstrained fire regime. Distribution was averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Black areas represent waterbodies, light grey areas represent non-fuel types (i.e., urban and agriculture areas) and beige areas represent lowlands (i.e., wetlands and peatlands).





**Appendix 3.4.** Summary statistics and spatial distribution of habitat components for moose and white-tailed deer for each fuel scenario (i.e., static and fire-mediated), fire regime scenario (i.e., constrained and unconstrained), time period (i.e., 2011–2040, 2041–2070, and 2071–2100) and GCM (i.e., CanESM2, CSIRO, and HadGEM2).

**Table 3.4.1.** Summary statistics of nutritional resources for moose and white-tailed deer in each fuel scenario (i.e., static and fire-mediated), fire regime scenario (i.e., constrained and unconstrained), time period (i.e., 2011–2040, 2041–2070, and 2071–2100) and global climate model (GCM; CanESM2, CSIRO, and HadGEM2). First quantile (Q1), median, and third quantile (Q3) are presented.

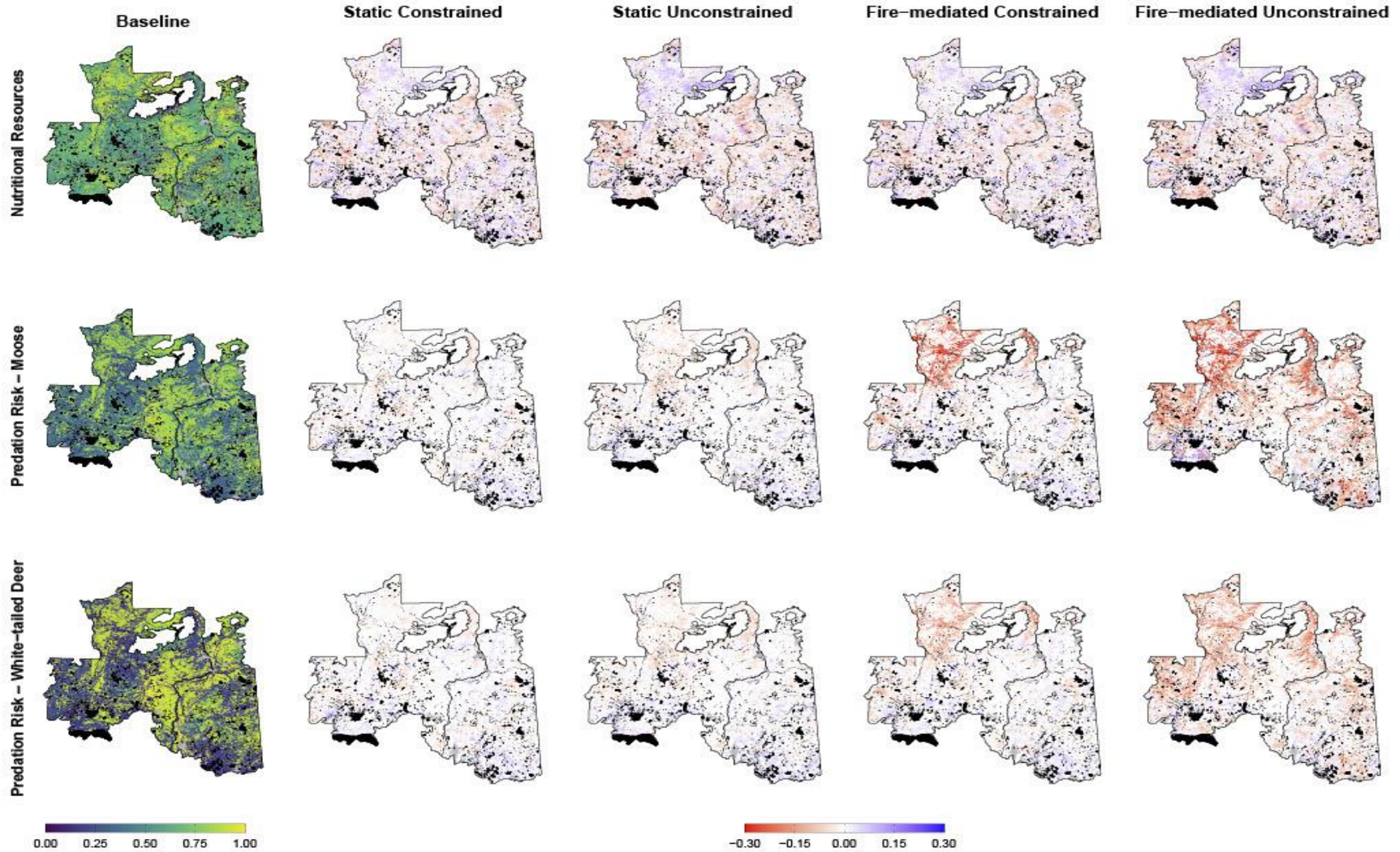
		Q1	Median	Q3	Q1	Median	Q3	Q1	Median	Q3	Q1	Median	Q3
Baseline		0.537	0.609	0.837	—	—	—	—	—	—	—	—	—
		Static Constrained			Static Unconstrained			Fire-mediated Constrained			Fire-mediated Unconstrained		
2011 – 2040	CanESM2	0.535	0.614	0.827	0.523	0.601	0.835	0.535	0.614	0.828	0.522	0.600	0.835
	CSIRO	0.519	0.585	0.837	0.519	0.585	0.837	0.519	0.585	0.837	0.520	0.586	0.837
	HadGEM2	0.535	0.606	0.832	0.517	0.577	0.842	0.535	0.606	0.832	0.517	0.577	0.842
	Mean	0.543	0.601	0.841	0.527	0.589	0.844	0.542	0.600	0.841	0.525	0.588	0.844
2041 – 2070	CanESM2	0.534	0.607	0.835	0.521	0.577	0.841	0.504	0.521	0.956	0.016	0.521	0.995
	CSIRO	0.537	0.607	0.833	0.514	0.561	0.853	0.511	0.523	0.963	0.147	0.526	0.995
	HadGEM2	0.534	0.606	0.831	0.513	0.548	0.860	0.507	0.522	0.952	0.016	0.518	1.000
	Mean	0.549	0.605	0.841	0.522	0.562	0.856	0.354	0.521	0.957	0.183	0.354	0.997
2071 – 2100	CanESM2	0.532	0.606	0.833	0.512	0.545	0.874	0.016	0.016	0.966	0.016	0.016	1.000
	CSIRO	0.534	0.606	0.838	0.508	0.523	0.906	0.140	0.519	0.968	0.016	0.016	1.000
	HadGEM2	—	—	—	0.516	0.523	0.974	0.016	0.517	0.964	0.016	0.147	1.000
	Mean	0.543	0.605	0.840	0.516	0.530	0.920	0.163	0.349	0.966	0.016	0.169	1.000

**Table 3.4.2.** Summary statistics of predation risk for moose and white-tailed deer in each fuel scenario (i.e., static and fire-mediated), fire regime scenario (i.e., constrained and unconstrained), time period (i.e., 2011–2040, 2041–2070, and 2071–2100) and global climate model (GCM; CanESM2, CSIRO, and HadGEM2). First quantile (Q1), median, and third quantile (Q3) are presented.

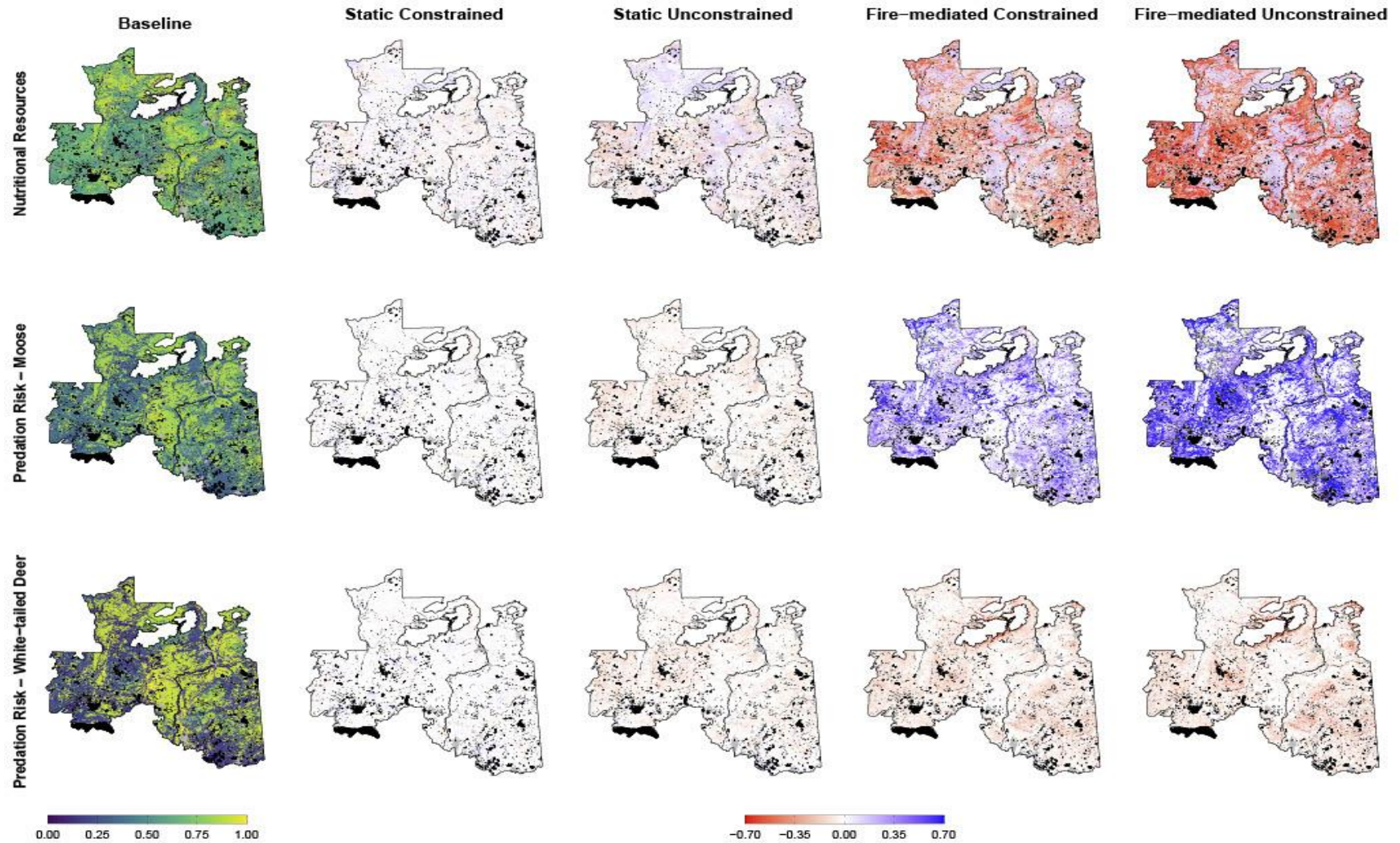
		<b>Moose</b>					<b>White-tailed Deer</b>						
		<b>Q1</b>	<b>Median</b>	<b>Q3</b>	<b>Q1</b>	<b>Median</b>	<b>Q3</b>	<b>Q1</b>	<b>Median</b>	<b>Q3</b>	<b>Q1</b>	<b>Median</b>	<b>Q3</b>
Baseline		0.328	0.371	0.840	—	—	—	0.192	0.235	0.900	—	—	—
		<b>Static Constrained</b>			<b>Static Unconstrained</b>			<b>Static Constrained</b>			<b>Static Unconstrained</b>		
<b>2011 – 2040</b>	CanESM2	0.333	0.378	0.840	0.333	0.374	0.840	0.197	0.242	0.900	0.197	0.238	0.900
	CSIRO	0.329	0.376	0.840	0.331	0.373	0.840	0.193	0.240	0.900	0.195	0.237	0.900
	HadGEM2	0.329	0.371	0.840	0.326	0.369	0.840	0.193	0.235	0.900	0.190	0.233	0.900
	Mean	0.335	0.362	0.840	0.335	0.361	0.840	0.199	0.226	0.900	0.199	0.225	0.900
<b>2041 – 2070</b>	CanESM2	0.329	0.374	0.840	0.326	0.371	0.840	0.193	0.238	0.900	0.190	0.233	0.900
	CSIRO	0.333	0.376	0.840	0.318	0.363	0.840	0.197	0.240	0.900	0.182	0.227	0.900
	HadGEM2	0.329	0.374	0.840	0.306	0.361	0.840	0.193	0.238	0.900	0.170	0.225	0.900
	Mean	0.335	0.362	0.840	0.322	0.355	0.840	0.199	0.226	0.900	0.186	0.219	0.900
<b>2071 – 2100</b>	CanESM2	0.331	0.374	0.840	0.299	0.354	0.840	0.195	0.238	0.900	0.163	0.218	0.900
	CSIRO	0.329	0.369	0.840	0.279	0.331	0.840	0.193	0.233	0.900	0.143	0.195	0.900
	HadGEM2	—	—	—	0.246	0.278	0.840	—	—	—	0.110	0.142	0.900
	Mean	0.334	0.364	0.840	0.278	0.315	0.840	0.198	0.228	0.900	0.142	0.179	0.900
		<b>Fire-mediated Constrained</b>			<b>Fire-mediated Unconstrained</b>			<b>Fire-mediated Constrained</b>			<b>Fire-mediated Unconstrained</b>		
<b>2011 – 2040</b>	CanESM2	0.331	0.376	0.840	0.326	0.373	0.840	0.193	0.240	0.900	0.190	0.237	0.900
	CSIRO	0.328	0.374	0.840	0.318	0.369	0.840	0.192	0.238	0.900	0.182	0.233	0.900
	HadGEM2	0.326	0.369	0.840	0.032	0.361	0.840	0.190	0.233	0.900	0.032	0.223	0.900
	Mean	0.331	0.362	0.840	0.237	0.355	0.840	0.195	0.226	0.900	0.144	0.217	0.900

<b>2041 – 2070</b>	CanESM2	0.254	0.528	0.840	0.254	0.840	1.000	0.118	0.160	0.900	0.118	0.135	0.900
	CSIRO	0.246	0.319	0.840	0.246	0.840	0.840	0.110	0.162	0.900	0.110	0.135	0.900
	HadGEM2	0.254	0.349	0.840	0.528	0.840	1.000	0.118	0.168	0.900	0.135	0.135	0.900
	Mean	0.260	0.503	0.840	0.260	0.503	0.840	0.118	0.159	0.900	0.093	0.135	0.900
<b>2071 – 2100</b>	CanESM2	0.840	0.940	1.000	0.840	1.000	1.000	0.135	0.135	0.900	0.135	0.135	0.900
	CSIRO	0.256	0.840	0.840	0.840	1.000	1.000	0.120	0.137	0.900	0.135	0.135	0.900
	HadGEM2	0.271	0.840	0.940	0.840	0.840	1.000	0.135	0.143	0.900	0.135	0.135	0.900
	Mean	0.521	0.760	0.840	0.840	0.840	1.000	0.127	0.141	0.900	0.135	0.135	0.900

**Figure 3.4.1.** Predicted proportional change in habitat components for current (baseline) and the 2020s (2011–2040) for moose and white-tailed deer in each fuel scenario (i.e., static and fire-mediated) and fire regime scenario (i.e., constrained and unconstrained). Nutritional resources and predation risk were averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Proportional change in red indicates worsening conditions while blue indicates improving conditions. Black areas represent waterbodies and light grey areas represent non-fuel types (i.e., urban and agriculture areas).



**Figure 3.4.2.** Predicted proportional change in habitat components for current (baseline) and the 2080s (2071–2100) for moose and white-tailed deer in each fuel scenario (i.e., static and fire-mediated) and fire regime scenario (i.e., constrained and unconstrained). Nutritional resources and predation risk were averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Proportional change in red indicates worsening conditions while blue indicates improving conditions. Black areas represent waterbodies and light grey areas represent non-fuel types (i.e., urban and agriculture areas).



**Appendix 3.5.** Summary statistics and spatial distribution of winter habitat for moose and white-tailed deer for each fuel scenario (i.e., static and fire-mediated), fire regime scenario (i.e., constrained and unconstrained), time period (i.e., 2011–2040, 2041–2070, and 2071–2100) and GCM (i.e., CanESM2, CSIRO, and HadGEM2).

**Table 3.5.1.** Summary statistics of winter habitat (WH) for moose in each fuel scenario (i.e., static and fire-mediated), fire regime scenario (i.e., constrained and unconstrained), time period (i.e., 2011–2040, 2041–2070, and 2071–2100) and global climate model (GCM; CanESM2, CSIRO, and HadGEM2). WH is presented based on relative predation risk contributing to 100%, 80%, 75%, 70%, 60%, 50%, 25%, and 0% of the WH. First quantile (Q1), median, and third quantile (Q3) are presented.

		Global Climate Model (GCM)											
		CanESM2			CSIRO			HadGEM2			Mean		
	WH	Q1	Median	Q3	Q1	Median	Q3	Q1	Median	Q3	Q1	Median	Q3
Baseline	WH <sub>0</sub>	—	—	—	—	—	—	—	—	—	0.344	0.499	0.642
	WH <sub>25</sub>	—	—	—	—	—	—	—	—	—	0.359	0.465	0.664
	WH <sub>50</sub>	—	—	—	—	—	—	—	—	—	0.354	0.438	0.691
	WH <sub>60</sub>	—	—	—	—	—	—	—	—	—	0.356	0.424	0.703
	WH <sub>70</sub>	—	—	—	—	—	—	—	—	—	0.350	0.413	0.720
	WH <sub>75</sub>	—	—	—	—	—	—	—	—	—	0.344	0.408	0.730
	WH <sub>80</sub>	—	—	—	—	—	—	—	—	—	0.337	0.402	0.741
	WH <sub>100</sub>	—	—	—	—	—	—	—	—	—	0.283	0.341	0.714
		Static Constrained											
2011 – 2040	WH <sub>0</sub>	0.345	0.501	0.638	0.335	0.482	0.646	0.341	0.497	0.635	0.341	0.496	0.640
	WH <sub>25</sub>	0.359	0.468	0.658	0.342	0.453	0.669	0.357	0.464	0.658	0.356	0.463	0.664
	WH <sub>50</sub>	0.355	0.443	0.687	0.338	0.435	0.696	0.353	0.439	0.686	0.350	0.439	0.690
	WH <sub>60</sub>	0.358	0.429	0.699	0.342	0.423	0.706	0.355	0.424	0.698	0.355	0.425	0.702
	WH <sub>70</sub>	0.353	0.418	0.718	0.337	0.415	0.722	0.349	0.414	0.716	0.351	0.415	0.719
	WH <sub>75</sub>	0.346	0.413	0.729	0.332	0.411	0.732	0.343	0.409	0.727	0.345	0.409	0.729
	WH <sub>80</sub>	0.340	0.406	0.741	0.327	0.405	0.742	0.337	0.402	0.740	0.339	0.402	0.741
	WH <sub>100</sub>	0.286	0.345	0.714	0.280	0.348	0.714	0.284	0.340	0.714	0.288	0.341	0.714

2041 – 2070	WH <sub>0</sub>	0.343	0.500	0.638	0.344	0.495	0.638	0.342	0.496	0.637	0.344	0.501	0.638
	WH <sub>25</sub>	0.358	0.467	0.661	0.358	0.463	0.661	0.356	0.463	0.659	0.360	0.467	0.662
	WH <sub>50</sub>	0.354	0.440	0.688	0.353	0.439	0.690	0.352	0.438	0.687	0.355	0.440	0.689
	WH <sub>60</sub>	0.355	0.426	0.700	0.356	0.425	0.702	0.355	0.424	0.699	0.357	0.425	0.701
	WH <sub>70</sub>	0.349	0.415	0.718	0.351	0.416	0.718	0.349	0.415	0.718	0.353	0.414	0.718
	WH <sub>75</sub>	0.343	0.410	0.729	0.344	0.412	0.728	0.343	0.410	0.729	0.347	0.408	0.728
	WH <sub>80</sub>	0.337	0.403	0.740	0.338	0.405	0.741	0.336	0.403	0.740	0.340	0.401	0.740
	WH <sub>100</sub>	0.284	0.342	0.714	0.285	0.344	0.714	0.282	0.343	0.714	0.288	0.339	0.714
2071 – 2100	WH <sub>0</sub>	0.343	0.497	0.637	0.347	0.495	0.642	—	—	—	0.346	0.499	0.640
	WH <sub>25</sub>	0.356	0.464	0.660	0.355	0.463	0.662	—	—	—	0.357	0.465	0.664
	WH <sub>50</sub>	0.352	0.438	0.689	0.351	0.439	0.689	—	—	—	0.353	0.439	0.691
	WH <sub>60</sub>	0.355	0.424	0.701	0.353	0.425	0.701	—	—	—	0.357	0.424	0.703
	WH <sub>70</sub>	0.351	0.414	0.718	0.348	0.415	0.718	—	—	—	0.353	0.414	0.719
	WH <sub>75</sub>	0.346	0.409	0.728	0.342	0.411	0.728	—	—	—	0.347	0.409	0.728
	WH <sub>80</sub>	0.339	0.402	0.739	0.335	0.404	0.740	—	—	—	0.341	0.402	0.739
	WH <sub>100</sub>	0.286	0.341	0.714	0.283	0.342	0.714	—	—	—	0.288	0.339	0.714
<b>Static Unconstrained</b>													
2011 – 2040	WH <sub>0</sub>	0.338	0.494	0.644	0.334	0.482	0.649	0.336	0.479	0.658	0.337	0.489	0.654
	WH <sub>25</sub>	0.351	0.463	0.666	0.343	0.453	0.672	0.341	0.450	0.681	0.347	0.459	0.676
	WH <sub>50</sub>	0.345	0.442	0.692	0.340	0.436	0.697	0.338	0.432	0.705	0.342	0.438	0.699
	WH <sub>60</sub>	0.350	0.428	0.703	0.343	0.424	0.708	0.339	0.420	0.713	0.346	0.425	0.709
	WH <sub>70</sub>	0.346	0.418	0.720	0.339	0.416	0.723	0.334	0.413	0.726	0.342	0.415	0.723
	WH <sub>75</sub>	0.341	0.414	0.731	0.334	0.412	0.732	0.329	0.409	0.735	0.337	0.411	0.733
	WH <sub>80</sub>	0.335	0.408	0.743	0.329	0.407	0.743	0.324	0.404	0.744	0.332	0.404	0.743
	WH <sub>100</sub>	0.284	0.347	0.714	0.281	0.349	0.714	0.276	0.347	0.714	0.284	0.344	0.714
2041 – 2070	WH <sub>0</sub>	0.339	0.481	0.666	0.330	0.462	0.661	0.329	0.454	0.677	0.333	0.468	0.674
	WH <sub>25</sub>	0.343	0.451	0.688	0.331	0.435	0.682	0.325	0.428	0.698	0.334	0.440	0.693
	WH <sub>50</sub>	0.336	0.433	0.710	0.336	0.420	0.704	0.324	0.415	0.718	0.333	0.424	0.713
	WH <sub>60</sub>	0.338	0.421	0.719	0.333	0.411	0.713	0.320	0.407	0.725	0.331	0.413	0.721

2071 – 2100	WH <sub>70</sub>	0.334	0.413	0.731	0.325	0.405	0.725	0.311	0.401	0.734	0.325	0.406	0.731
	WH <sub>75</sub>	0.329	0.410	0.740	0.319	0.402	0.734	0.306	0.398	0.741	0.319	0.403	0.738
	WH <sub>80</sub>	0.323	0.404	0.749	0.314	0.397	0.744	0.301	0.394	0.749	0.314	0.397	0.748
	WH <sub>100</sub>	0.276	0.346	0.714	0.266	0.342	0.714	0.255	0.340	0.714	0.267	0.340	0.714
	WH <sub>0</sub>	0.329	0.453	0.691	0.329	0.444	0.711	0.339	0.449	0.767	0.340	0.460	0.743
	WH <sub>25</sub>	0.323	0.425	0.708	0.319	0.412	0.722	0.319	0.410	0.769	0.326	0.423	0.746
	WH <sub>50</sub>	0.324	0.411	0.724	0.324	0.390	0.732	0.328	0.379	0.770	0.328	0.397	0.748
	WH <sub>60</sub>	0.318	0.402	0.729	0.316	0.383	0.735	0.313	0.366	0.770	0.317	0.387	0.749
	WH <sub>70</sub>	0.308	0.397	0.737	0.303	0.375	0.740	0.295	0.350	0.768	0.302	0.375	0.749
	WH <sub>75</sub>	0.303	0.394	0.743	0.295	0.370	0.746	0.285	0.341	0.769	0.294	0.368	0.753
WH <sub>80</sub>	0.296	0.389	0.751	0.288	0.363	0.753	0.275	0.330	0.772	0.286	0.360	0.759	
WH <sub>100</sub>	0.250	0.335	0.714	0.237	0.310	0.714	0.214	0.264	0.714	0.234	0.302	0.714	
<b>Fire-mediated Constrained</b>													
2011 – 2040	WH <sub>0</sub>	0.345	0.501	0.638	0.335	0.482	0.646	0.341	0.497	0.635	0.341	0.496	0.640
	WH <sub>25</sub>	0.336	0.467	0.658	0.318	0.451	0.669	0.338	0.462	0.658	0.336	0.461	0.664
	WH <sub>50</sub>	0.344	0.443	0.687	0.326	0.434	0.696	0.341	0.438	0.686	0.339	0.436	0.690
	WH <sub>60</sub>	0.353	0.428	0.700	0.332	0.422	0.707	0.348	0.423	0.698	0.344	0.422	0.702
	WH <sub>70</sub>	0.348	0.418	0.718	0.329	0.414	0.722	0.344	0.413	0.717	0.338	0.412	0.719
	WH <sub>75</sub>	0.343	0.413	0.729	0.324	0.410	0.732	0.338	0.408	0.728	0.332	0.407	0.729
	WH <sub>80</sub>	0.336	0.406	0.741	0.319	0.405	0.743	0.332	0.401	0.740	0.325	0.400	0.741
	WH <sub>100</sub>	0.264	0.321	0.667	0.273	0.347	0.714	0.262	0.318	0.670	0.276	0.339	0.714
2041 – 2070	WH <sub>0</sub>	0.207	0.431	0.732	0.281	0.433	0.737	0.248	0.433	0.734	0.259	0.428	0.736
	WH <sub>25</sub>	0.273	0.394	0.737	0.286	0.394	0.740	0.279	0.397	0.739	0.286	0.391	0.740
	WH <sub>50</sub>	0.315	0.379	0.742	0.296	0.376	0.744	0.309	0.383	0.743	0.306	0.378	0.743
	WH <sub>60</sub>	0.309	0.373	0.744	0.293	0.367	0.745	0.303	0.377	0.744	0.300	0.377	0.744
	WH <sub>70</sub>	0.297	0.368	0.749	0.280	0.359	0.747	0.290	0.372	0.747	0.287	0.376	0.746
	WH <sub>75</sub>	0.289	0.367	0.757	0.272	0.353	0.751	0.283	0.369	0.752	0.280	0.374	0.749
	WH <sub>80</sub>	0.280	0.363	0.763	0.264	0.346	0.760	0.275	0.364	0.759	0.273	0.373	0.755
	WH <sub>100</sub>	0.207	0.293	0.681	0.194	0.269	0.670	0.206	0.293	0.684	0.210	0.319	0.668



2071 – 2100	WH <sub>0</sub>	0.012	0.014	0.733	0.086	0.420	0.732	0.014	0.413	0.736	0.120	0.263	0.734
	WH <sub>25</sub>	0.210	0.242	0.737	0.227	0.378	0.737	0.221	0.371	0.740	0.231	0.313	0.738
	WH <sub>50</sub>	0.394	0.464	0.742	0.320	0.417	0.741	0.335	0.422	0.743	0.354	0.425	0.741
	WH <sub>60</sub>	0.454	0.557	0.743	0.318	0.446	0.743	0.329	0.498	0.745	0.387	0.477	0.743
	WH <sub>70</sub>	0.522	0.653	0.755	0.306	0.490	0.749	0.319	0.577	0.751	0.414	0.531	0.746
	WH <sub>75</sub>	0.555	0.701	0.774	0.297	0.516	0.760	0.312	0.613	0.763	0.426	0.561	0.755
	WH <sub>80</sub>	0.590	0.746	0.808	0.289	0.541	0.774	0.305	0.643	0.779	0.439	0.592	0.765
	WH <sub>100</sub>	0.594	0.718	0.815	0.215	0.541	0.725	0.230	0.617	0.741	0.419	0.605	0.703
<b>Fire-mediated Unconstrained</b>													
2011 – 2040	WH <sub>0</sub>	0.333	0.493	0.644	0.337	0.482	0.650	0.335	0.478	0.659	0.338	0.486	0.654
	WH <sub>25</sub>	0.320	0.457	0.666	0.315	0.442	0.672	0.311	0.416	0.682	0.323	0.439	0.676
	WH <sub>50</sub>	0.311	0.439	0.692	0.291	0.425	0.697	0.256	0.401	0.705	0.304	0.410	0.699
	WH <sub>60</sub>	0.321	0.426	0.703	0.271	0.415	0.708	0.219	0.398	0.714	0.291	0.397	0.709
	WH <sub>70</sub>	0.320	0.417	0.722	0.254	0.409	0.723	0.179	0.397	0.728	0.268	0.394	0.723
	WH <sub>75</sub>	0.317	0.412	0.734	0.252	0.406	0.732	0.157	0.394	0.737	0.255	0.390	0.733
	WH <sub>80</sub>	0.313	0.406	0.745	0.251	0.400	0.743	0.135	0.389	0.746	0.243	0.385	0.743
	WH <sub>100</sub>	0.247	0.317	0.656	0.206	0.316	0.657	0.027	0.307	0.660	0.189	0.323	0.702
2041 – 2070	WH <sub>0</sub>	0.013	0.401	0.748	0.076	0.414	0.760	0.013	0.239	0.756	0.132	0.280	0.761
	WH <sub>25</sub>	0.215	0.355	0.748	0.232	0.341	0.760	0.217	0.287	0.756	0.239	0.316	0.761
	WH <sub>50</sub>	0.346	0.427	0.749	0.258	0.428	0.761	0.298	0.451	0.756	0.340	0.420	0.761
	WH <sub>60</sub>	0.340	0.514	0.749	0.218	0.509	0.761	0.326	0.542	0.757	0.353	0.470	0.761
	WH <sub>70</sub>	0.328	0.604	0.755	0.185	0.585	0.764	0.330	0.633	0.763	0.365	0.525	0.762
	WH <sub>75</sub>	0.319	0.648	0.768	0.182	0.617	0.776	0.324	0.677	0.776	0.373	0.553	0.768
	WH <sub>80</sub>	0.309	0.690	0.790	0.181	0.639	0.793	0.315	0.720	0.804	0.294	0.433	0.763
	WH <sub>100</sub>	0.226	0.652	0.757	0.150	0.584	0.739	0.232	0.666	0.767	0.350	0.582	0.698
2071 – 2100	WH <sub>0</sub>	0.012	0.014	0.755	0.012	0.014	0.754	0.013	0.130	0.756	0.013	0.129	0.754
	WH <sub>25</sub>	0.071	0.094	0.755	0.069	0.091	0.754	0.214	0.267	0.756	0.122	0.173	0.754
	WH <sub>50</sub>	0.134	0.179	0.755	0.129	0.173	0.753	0.333	0.453	0.756	0.212	0.271	0.754
	WH <sub>60</sub>	0.160	0.215	0.755	0.154	0.204	0.749	0.354	0.545	0.756	0.241	0.324	0.754

WH <sub>70</sub>	0.188	0.251	0.755	0.177	0.232	0.736	0.363	0.637	0.762	0.268	0.377	0.755
WH <sub>75</sub>	0.201	0.270	0.757	0.187	0.245	0.731	0.382	0.682	0.776	0.281	0.404	0.757
WH <sub>80</sub>	0.214	0.286	0.757	0.198	0.258	0.730	0.403	0.725	0.806	0.381	0.581	0.775
WH <sub>100</sub>	0.250	0.335	0.714	0.237	0.310	0.714	0.407	0.679	0.775	0.305	0.483	0.704

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**Table 3.5.2.** Summary statistics of winter habitat (WH) for white-tailed deer in each fuel scenario (i.e., static and fire-mediated), fire regime scenario (i.e., constrained and unconstrained), time period (i.e., 2011–2040, 2041–2070 and 2071–2100) and global climate model (GCM; CanESM2, CSIRO, and HadGEM2). WH is presented based on relative predation risk contributing to 100%, 80%, 75%, 70%, 60%, 50%, 25%, and 0% of the WH. First quantile (Q1), median, and third quantile (Q3) are presented.

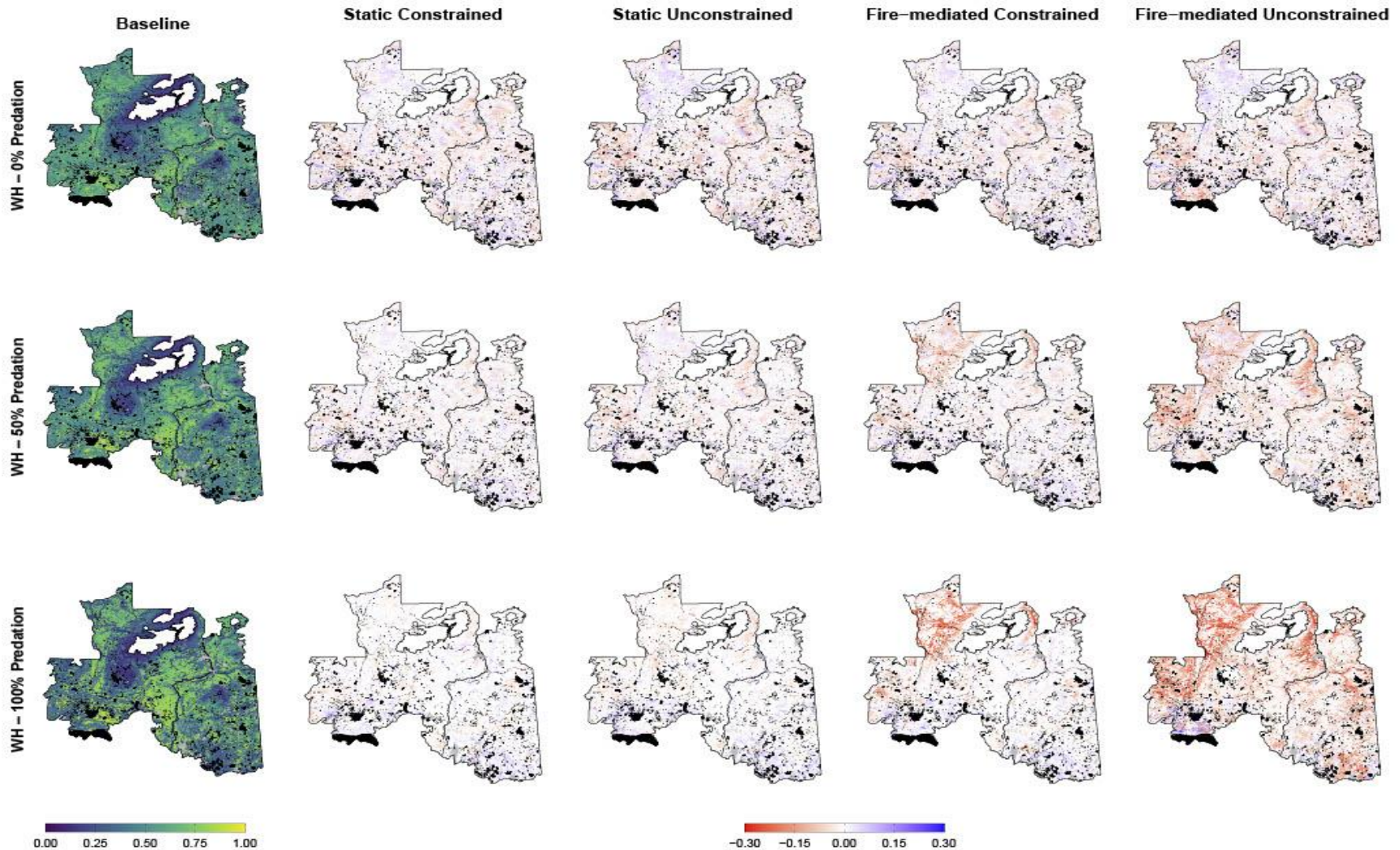
		Global Climate Model (GCM)											
		CanESM2			CSIRO			HadGEM2			Mean		
	WH	Q1	Median	Q3	Q1	Median	Q3	Q1	Median	Q3	Q1	Median	Q3
Baseline	WH <sub>0</sub>	—	—	—	—	—	—	—	—	—	0.236	0.397	0.510
	WH <sub>25</sub>	—	—	—	—	—	—	—	—	—	0.248	0.349	0.477
	WH <sub>50</sub>	—	—	—	—	—	—	—	—	—	0.230	0.308	0.496
	WH <sub>60</sub>	—	—	—	—	—	—	—	—	—	0.215	0.287	0.524
	WH <sub>70</sub>	—	—	—	—	—	—	—	—	—	0.197	0.262	0.557
	WH <sub>75</sub>	—	—	—	—	—	—	—	—	—	0.187	0.249	0.573
	WH <sub>80</sub>	—	—	—	—	—	—	—	—	—	0.176	0.236	0.586
	WH <sub>100</sub>	—	—	—	—	—	—	—	—	—	0.121	0.165	0.577
		Static Constrained											
2011 – 2040	WH <sub>0</sub>	0.239	0.394	0.515	0.230	0.381	0.512	0.235	0.395	0.510	0.235	0.392	0.512
	WH <sub>25</sub>	0.250	0.348	0.476	0.237	0.335	0.479	0.246	0.347	0.474	0.246	0.344	0.470
	WH <sub>50</sub>	0.231	0.310	0.494	0.219	0.305	0.496	0.228	0.310	0.496	0.227	0.308	0.495
	WH <sub>60</sub>	0.215	0.290	0.520	0.204	0.289	0.521	0.213	0.291	0.522	0.212	0.290	0.522
	WH <sub>70</sub>	0.195	0.265	0.551	0.185	0.266	0.553	0.194	0.266	0.556	0.196	0.265	0.555
	WH <sub>75</sub>	0.185	0.252	0.565	0.175	0.254	0.570	0.184	0.252	0.571	0.184	0.252	0.571
	WH <sub>80</sub>	0.174	0.238	0.578	0.165	0.242	0.585	0.173	0.237	0.582	0.173	0.239	0.585
	WH <sub>100</sub>	0.121	0.170	0.577	0.115	0.175	0.577	0.120	0.168	0.577	0.121	0.168	0.577
2041 – 2070	WH <sub>0</sub>	0.235	0.393	0.512	0.238	0.390	0.512	0.235	0.392	0.511	0.236	0.395	0.510
	WH <sub>25</sub>	0.248	0.348	0.473	0.248	0.345	0.473	0.247	0.345	0.475	0.249	0.347	0.468
	WH <sub>50</sub>	0.228	0.308	0.493	0.230	0.310	0.494	0.229	0.307	0.495	0.230	0.309	0.495
	WH <sub>60</sub>	0.212	0.287	0.518	0.215	0.291	0.521	0.214	0.288	0.523	0.216	0.289	0.522

2071 – 2100	WH <sub>70</sub>	0.194	0.262	0.549	0.196	0.266	0.554	0.195	0.264	0.555	0.197	0.264	0.555
	WH <sub>75</sub>	0.183	0.248	0.564	0.186	0.253	0.571	0.185	0.251	0.571	0.187	0.251	0.571
	WH <sub>80</sub>	0.173	0.235	0.577	0.176	0.240	0.585	0.174	0.237	0.582	0.177	0.237	0.585
	WH <sub>100</sub>	0.121	0.167	0.577	0.122	0.170	0.577	0.120	0.169	0.577	0.124	0.165	0.577
	WH <sub>0</sub>	0.235	0.394	0.512	0.236	0.393	0.515	—	—	—	0.235	0.395	0.512
	WH <sub>25</sub>	0.247	0.347	0.474	0.246	0.346	0.478	—	—	—	0.248	0.348	0.472
	WH <sub>50</sub>	0.228	0.308	0.496	0.228	0.309	0.496	—	—	—	0.228	0.309	0.496
	WH <sub>60</sub>	0.214	0.288	0.523	0.213	0.290	0.524	—	—	—	0.214	0.289	0.523
	WH <sub>70</sub>	0.195	0.263	0.556	0.194	0.265	0.555	—	—	—	0.195	0.264	0.556
	WH <sub>75</sub>	0.185	0.250	0.571	0.184	0.251	0.569	—	—	—	0.185	0.250	0.570
WH <sub>80</sub>	0.175	0.236	0.583	0.173	0.237	0.582	—	—	—	0.174	0.236	0.582	
WH <sub>100</sub>	0.121	0.166	0.577	0.121	0.168	0.577	—	—	—	0.123	0.168	0.577	
<b>Static Unconstrained</b>													
2011 – 2040	WH <sub>0</sub>	0.233	0.389	0.515	0.231	0.381	0.513	0.228	0.381	0.513	0.231	0.386	0.513
	WH <sub>25</sub>	0.244	0.343	0.480	0.239	0.336	0.480	0.237	0.333	0.481	0.241	0.338	0.476
	WH <sub>50</sub>	0.226	0.308	0.495	0.220	0.305	0.496	0.219	0.303	0.498	0.223	0.306	0.496
	WH <sub>60</sub>	0.211	0.290	0.522	0.205	0.289	0.522	0.204	0.287	0.523	0.208	0.289	0.522
	WH <sub>70</sub>	0.191	0.265	0.552	0.186	0.267	0.553	0.185	0.265	0.554	0.189	0.266	0.554
	WH <sub>75</sub>	0.181	0.252	0.567	0.176	0.255	0.570	0.175	0.253	0.571	0.179	0.254	0.571
	WH <sub>80</sub>	0.170	0.238	0.580	0.167	0.243	0.585	0.165	0.241	0.586	0.169	0.241	0.585
	WH <sub>100</sub>	0.120	0.171	0.577	0.116	0.175	0.577	0.114	0.174	0.578	0.118	0.171	0.577
2041 – 2070	WH <sub>0</sub>	0.231	0.382	0.518	0.224	0.373	0.513	0.223	0.368	0.511	0.226	0.376	0.513
	WH <sub>25</sub>	0.238	0.333	0.486	0.232	0.326	0.483	0.228	0.319	0.486	0.234	0.327	0.482
	WH <sub>50</sub>	0.218	0.303	0.501	0.214	0.295	0.501	0.208	0.291	0.505	0.214	0.297	0.503
	WH <sub>60</sub>	0.202	0.286	0.526	0.198	0.279	0.524	0.192	0.276	0.528	0.198	0.281	0.527
	WH <sub>70</sub>	0.182	0.264	0.556	0.178	0.256	0.551	0.172	0.255	0.556	0.179	0.259	0.556
	WH <sub>75</sub>	0.172	0.253	0.572	0.168	0.245	0.567	0.161	0.244	0.570	0.169	0.248	0.572
	WH <sub>80</sub>	0.161	0.241	0.587	0.158	0.233	0.580	0.150	0.233	0.584	0.158	0.235	0.585
	WH <sub>100</sub>	0.111	0.174	0.577	0.109	0.170	0.577	0.098	0.170	0.577	0.107	0.170	0.577

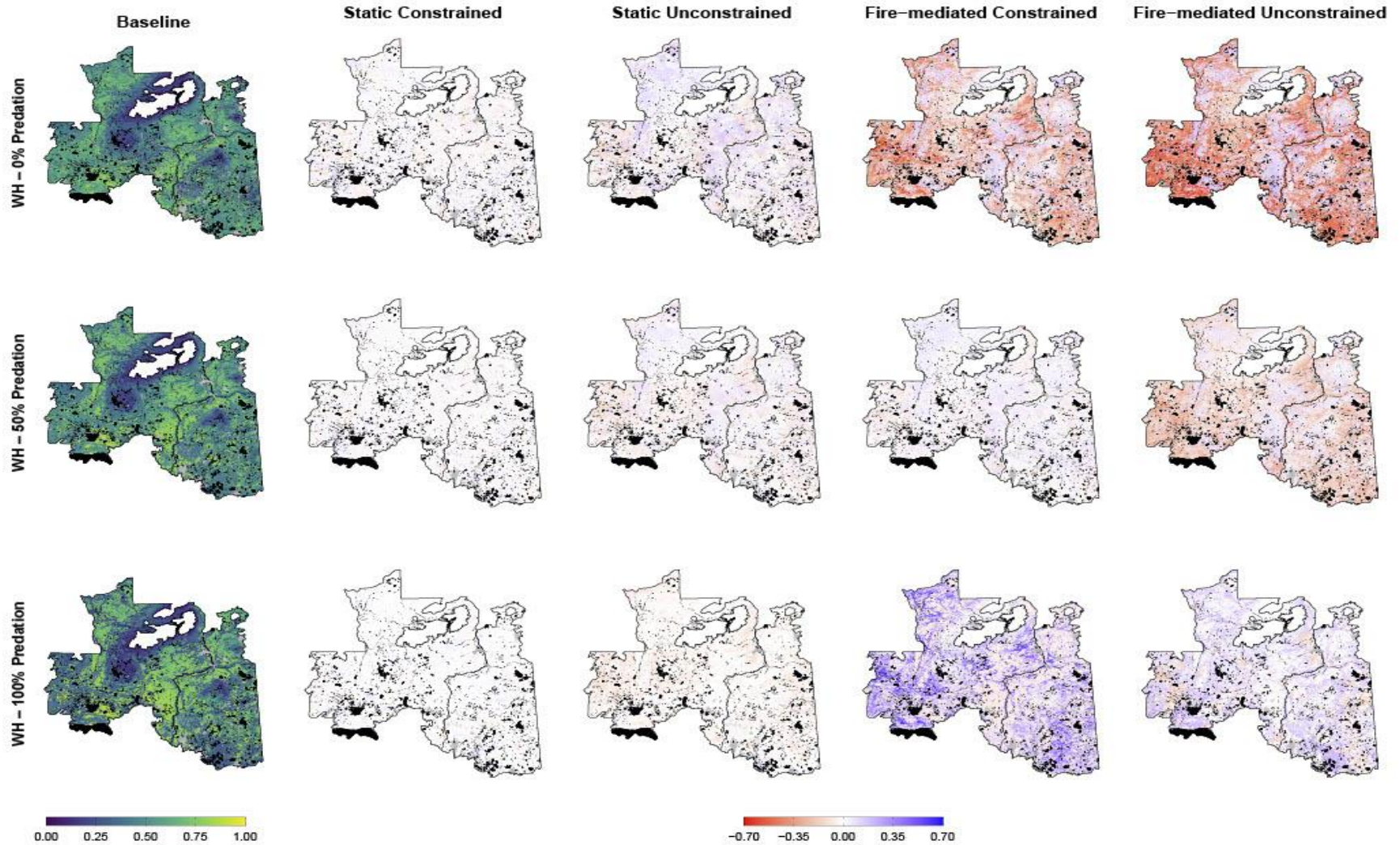
2071 – 2100	WH <sub>0</sub>	0.223	0.367	0.512	0.222	0.364	0.514	0.236	0.384	0.549	0.231	0.378	0.529
	WH <sub>25</sub>	0.226	0.317	0.489	0.224	0.311	0.495	0.233	0.321	0.536	0.230	0.320	0.508
	WH <sub>50</sub>	0.205	0.288	0.505	0.201	0.273	0.513	0.198	0.263	0.536	0.204	0.278	0.523
	WH <sub>60</sub>	0.188	0.272	0.527	0.183	0.254	0.532	0.176	0.235	0.549	0.185	0.257	0.541
	WH <sub>70</sub>	0.169	0.251	0.555	0.163	0.233	0.560	0.153	0.206	0.568	0.164	0.232	0.567
	WH <sub>75</sub>	0.159	0.240	0.572	0.153	0.221	0.575	0.141	0.191	0.580	0.153	0.220	0.582
	WH <sub>80</sub>	0.148	0.229	0.587	0.143	0.209	0.590	0.129	0.176	0.592	0.142	0.206	0.596
	WH <sub>100</sub>	0.095	0.165	0.577	0.089	0.147	0.577	0.072	0.110	0.577	0.086	0.140	0.577
<b>Fire-mediated Constrained</b>													
2011 – 2040	WH <sub>0</sub>	0.239	0.394	0.515	0.230	0.381	0.512	0.235	0.395	0.510	0.235	0.391	0.511
	WH <sub>25</sub>	0.247	0.346	0.476	0.235	0.332	0.479	0.243	0.346	0.473	0.243	0.342	0.470
	WH <sub>50</sub>	0.219	0.310	0.494	0.208	0.304	0.496	0.219	0.309	0.496	0.218	0.307	0.495
	WH <sub>60</sub>	0.202	0.290	0.520	0.189	0.288	0.522	0.203	0.290	0.522	0.201	0.288	0.522
	WH <sub>70</sub>	0.184	0.265	0.551	0.172	0.266	0.553	0.185	0.265	0.556	0.182	0.264	0.555
	WH <sub>75</sub>	0.175	0.251	0.565	0.164	0.254	0.570	0.175	0.251	0.571	0.172	0.251	0.571
	WH <sub>80</sub>	0.165	0.238	0.578	0.156	0.242	0.585	0.165	0.237	0.582	0.162	0.238	0.585
	WH <sub>100</sub>	0.117	0.170	0.577	0.110	0.175	0.577	0.115	0.167	0.577	0.112	0.167	0.577
2041 – 2070	WH <sub>0</sub>	0.134	0.350	0.511	0.191	0.355	0.517	0.169	0.353	0.512	0.180	0.340	0.511
	WH <sub>25</sub>	0.196	0.295	0.502	0.208	0.297	0.507	0.203	0.299	0.501	0.196	0.289	0.502
	WH <sub>50</sub>	0.170	0.254	0.516	0.174	0.256	0.520	0.173	0.258	0.515	0.167	0.253	0.517
	WH <sub>60</sub>	0.151	0.231	0.535	0.152	0.235	0.538	0.154	0.237	0.535	0.150	0.231	0.535
	WH <sub>70</sub>	0.129	0.206	0.560	0.128	0.212	0.561	0.132	0.214	0.560	0.131	0.208	0.560
	WH <sub>75</sub>	0.117	0.193	0.575	0.115	0.199	0.576	0.120	0.201	0.575	0.121	0.196	0.575
	WH <sub>80</sub>	0.108	0.180	0.590	0.105	0.185	0.591	0.111	0.189	0.590	0.112	0.183	0.590
	WH <sub>100</sub>	0.073	0.119	0.577	0.066	0.123	0.577	0.072	0.127	0.577	0.066	0.122	0.576
2071 – 2100	WH <sub>0</sub>	0.009	0.013	0.508	0.052	0.324	0.512	0.012	0.304	0.511	0.091	0.182	0.508
	WH <sub>25</sub>	0.028	0.037	0.503	0.096	0.278	0.505	0.035	0.270	0.503	0.097	0.206	0.502
	WH <sub>50</sub>	0.048	0.063	0.517	0.094	0.245	0.518	0.059	0.245	0.517	0.092	0.184	0.518
	WH <sub>60</sub>	0.056	0.073	0.535	0.083	0.222	0.534	0.069	0.223	0.535	0.088	0.171	0.536

	WH <sub>70</sub>	0.063	0.084	0.559	0.082	0.195	0.556	0.077	0.198	0.559	0.083	0.160	0.560
	WH <sub>75</sub>	0.067	0.089	0.574	0.083	0.182	0.570	0.080	0.184	0.574	0.084	0.153	0.574
	WH <sub>80</sub>	0.072	0.095	0.589	0.083	0.168	0.584	0.082	0.171	0.590	0.084	0.145	0.589
	WH <sub>100</sub>	0.080	0.106	0.575	0.070	0.109	0.576	0.075	0.110	0.575	0.071	0.111	0.574
<b>Fire-mediated Unconstrained</b>													
2011 – 2040	WH <sub>0</sub>	0.230	0.388	0.515	0.232	0.382	0.513	0.227	0.380	0.513	0.232	0.384	0.512
	WH <sub>25</sub>	0.239	0.337	0.479	0.235	0.328	0.478	0.226	0.320	0.480	0.238	0.334	0.475
	WH <sub>50</sub>	0.208	0.305	0.495	0.203	0.297	0.497	0.186	0.282	0.499	0.204	0.293	0.496
	WH <sub>60</sub>	0.185	0.288	0.522	0.178	0.280	0.522	0.160	0.266	0.523	0.180	0.273	0.522
	WH <sub>70</sub>	0.164	0.263	0.552	0.153	0.259	0.554	0.131	0.248	0.554	0.157	0.249	0.554
	WH <sub>75</sub>	0.155	0.250	0.567	0.142	0.248	0.570	0.115	0.238	0.571	0.146	0.237	0.570
	WH <sub>80</sub>	0.147	0.237	0.580	0.130	0.236	0.585	0.099	0.228	0.586	0.134	0.225	0.585
	WH <sub>100</sub>	0.108	0.169	0.577	0.087	0.170	0.577	0.022	0.163	0.577	0.079	0.159	0.577
2041 – 2070	WH <sub>0</sub>	0.011	0.262	0.513	0.046	0.328	0.530	0.011	0.165	0.520	0.101	0.205	0.530
	WH <sub>25</sub>	0.033	0.257	0.510	0.078	0.280	0.527	0.032	0.225	0.517	0.105	0.216	0.526
	WH <sub>50</sub>	0.055	0.231	0.522	0.080	0.233	0.535	0.054	0.185	0.526	0.094	0.181	0.531
	WH <sub>60</sub>	0.064	0.207	0.539	0.078	0.204	0.552	0.062	0.154	0.540	0.089	0.163	0.544
	WH <sub>70</sub>	0.073	0.180	0.562	0.080	0.175	0.571	0.069	0.121	0.561	0.083	0.146	0.564
	WH <sub>75</sub>	0.077	0.166	0.576	0.080	0.162	0.583	0.072	0.104	0.574	0.082	0.137	0.576
	WH <sub>80</sub>	0.080	0.151	0.589	0.079	0.148	0.595	0.072	0.096	0.588	0.081	0.128	0.589
	WH <sub>100</sub>	0.075	0.103	0.576	0.052	0.100	0.577	0.058	0.102	0.575	0.060	0.097	0.575
2071 – 2100	WH <sub>0</sub>	0.009	0.012	0.508	0.009	0.012	0.500	0.010	0.102	0.499	0.010	0.096	0.499
	WH <sub>25</sub>	0.027	0.036	0.504	0.028	0.036	0.497	0.029	0.198	0.497	0.030	0.107	0.496
	WH <sub>50</sub>	0.046	0.061	0.516	0.047	0.061	0.510	0.049	0.169	0.510	0.050	0.097	0.510
	WH <sub>60</sub>	0.054	0.071	0.531	0.055	0.072	0.526	0.057	0.142	0.527	0.058	0.092	0.525
	WH <sub>70</sub>	0.062	0.081	0.552	0.063	0.081	0.548	0.066	0.113	0.549	0.065	0.090	0.547
	WH <sub>75</sub>	0.066	0.086	0.566	0.066	0.086	0.562	0.069	0.099	0.563	0.068	0.092	0.561
	WH <sub>80</sub>	0.070	0.091	0.580	0.069	0.091	0.576	0.070	0.094	0.578	0.070	0.093	0.575
	WH <sub>100</sub>	0.080	0.105	0.572	0.078	0.105	0.571	0.064	0.101	0.573	0.070	0.103	0.570

**Figure 3.5.1.** Predicted proportional change in moose winter habitat (WH) for current (baseline) and the 2020s (2011–2040) in each fuel scenario (i.e., static and fire-mediated) and fire regime scenario (i.e., constrained and unconstrained). WH is presented based on relative predation risk contributing to 0%, 50%, and 100% of the WH. WH was averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Proportional change in red indicates worsening conditions while blue indicates improving conditions. Black areas represent waterbodies and light grey areas represent non-fuel types (i.e., urban and agriculture areas).

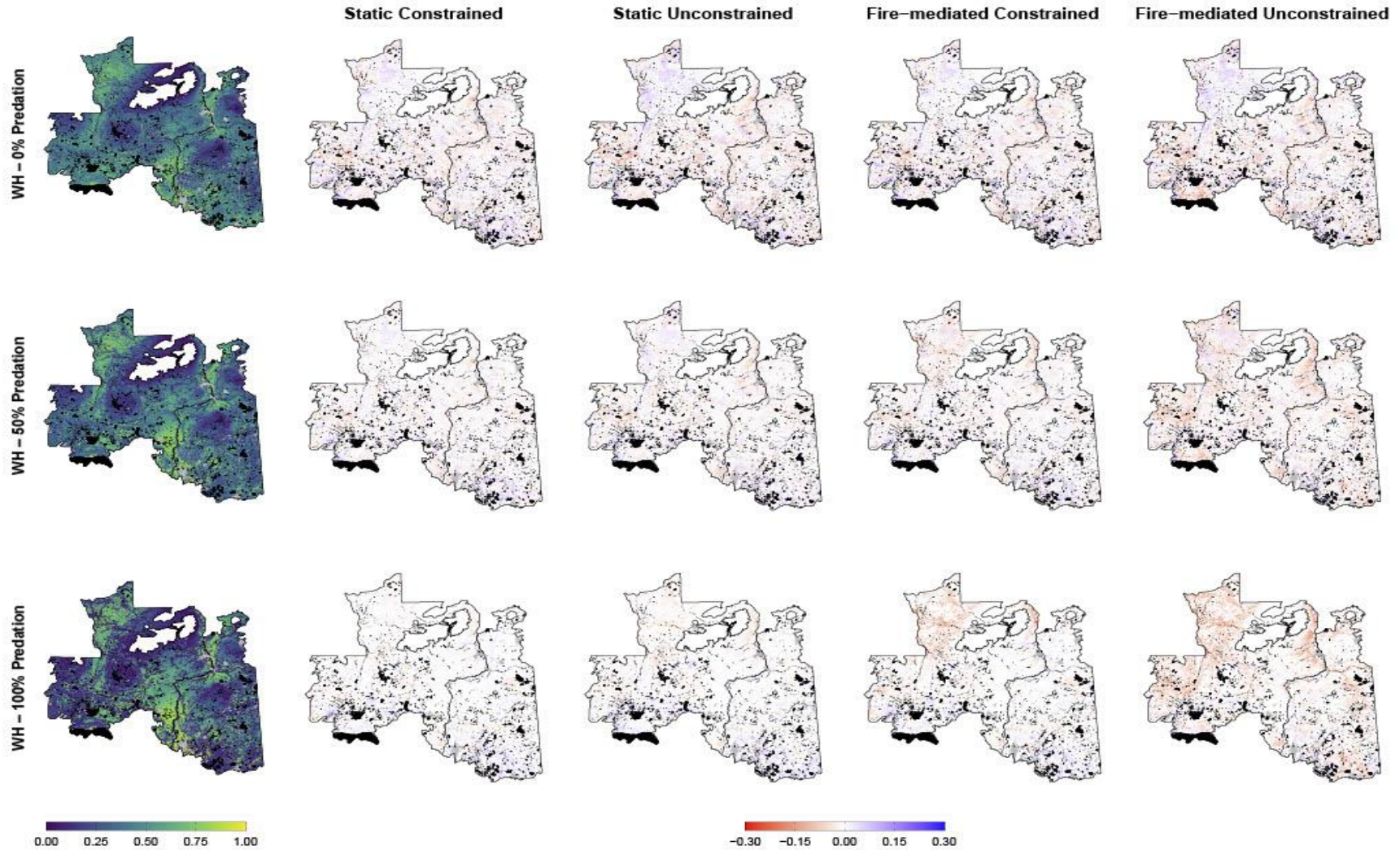


**Figure 3.5.2.** Predicted proportional change in moose winter habitat (WH) for current (baseline) and the 2080s (2071–2100) in each fuel scenario (i.e., static and fire-mediated) and fire regime scenario (i.e., constrained and unconstrained). WH is presented based on relative predation risk contributing to 0%, 50%, and 100% of the WH. WH was averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Proportional change in red indicates worsening conditions while blue indicates improving conditions. Black areas represent waterbodies and light grey areas represent non-fuel types (i.e., urban and agriculture areas).





**Figure 3.5.3.** Predicted proportional change in white-tailed deer winter habitat (WH) for current (baseline) and the 2020s (2011–2040) in each fuel scenario (i.e., static and fire-mediated) and fire regime scenario (i.e., constrained and unconstrained). WH is presented based on relative predation risk contributing to 0%, 50%, and 100% of the WH. WH was averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Proportional change in red indicates worsening conditions while blue indicates improving conditions. Black areas represent waterbodies and light grey areas represent non-fuel types (i.e., urban and agriculture areas).



**Figure 3.5.4.** Predicted proportional change in white-tailed deer winter habitat (WH) for current (baseline) and the 2080s (2071–2100) in each fuel scenario (i.e., static and fire-mediated) and fire regime scenario (i.e., constrained and unconstrained). WH is presented based on relative predation risk contributing to 0%, 50%, and 100% of the WH. WH was averaged across three global climate models (GCMs; CanESM2, CSIRO, and HadGEM2). Proportional change in red indicates worsening conditions while blue indicates improving conditions. Black areas represent waterbodies and light grey areas represent non-fuel types (i.e., urban and agriculture areas).

