

Dynamic patterns in winter ungulate browse succession in the Boreal Plains of Alberta

Mélanie R. Routh^{*}, Scott E. Nielsen

Department of Renewable Resources, University of Alberta, 751 General Services Building, Edmonton, AB T6G 2H1, Canada

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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, we collected vegetation and ungulate browsing data from 164 upland and lowland forest sites in northeastern Alberta, Canada. We 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 35–65% 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.

1. Introduction

Over the last 90–125 million years, wildfires have played a major role in the life-history and reproduction 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 characterized by being stand self-replacing (Ilisson and Chen, 2009a). In both cases, stands are gradually replaced

^{*} Corresponding author.

E-mail address: routh@ualberta.ca (M.R. Routh).

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by coniferous species over time, including black spruce, white spruce, jack pine, and balsam fir (Bergeron et al., 2014; Johnstone et al., 2010).

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 (Joly et al., 2016; Loranger et al., 1991; Lord and Kielland, 2015; MacCracken and Viereck, 1990; Maier et al., 2005; Peek, 1974; Spencer and Hakala, 1964; Weixelman et al., 1998). 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 m 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, 1974; 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, 1974; 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 moose diet, particularly in the winter, but they are generally not preferred and will only be consumed when hardwood availability or quality is low (Newbury et al., 2007; Peek, 1974; Raymond et al., 1996).

White-tailed deer are classified as concentrate selectors (Hofmann, 1989) and browse plants under 1.5 m 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 (Korschgen et al., 1980; Nixon et al., 1970). 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. Specifically, we're 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.

We 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. We predicted that: (1) early seral successional stands (≤ 30 years post-wildfire) will have higher deciduous shrub and sapling richness and abundance than older successional stands (≥ 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 (≤ 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., 2010), 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 (Frelich et al., 2020; Johnstone et al., 2010; Stralberg et al., 2018; Wang et al., 2020). We 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. Materials and methods

2.1. Study site description

This research took place in the Lower Athabasca Region (LAR) south of Lake Athabasca in northeastern Alberta, Canada (Fig. 1). This area encompassed 81,162 km² 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 ranged from approximately 200 m along the Athabasca River to 868 m in the Birch Mountains (Natural Regions Committee, 2006). The LAR was

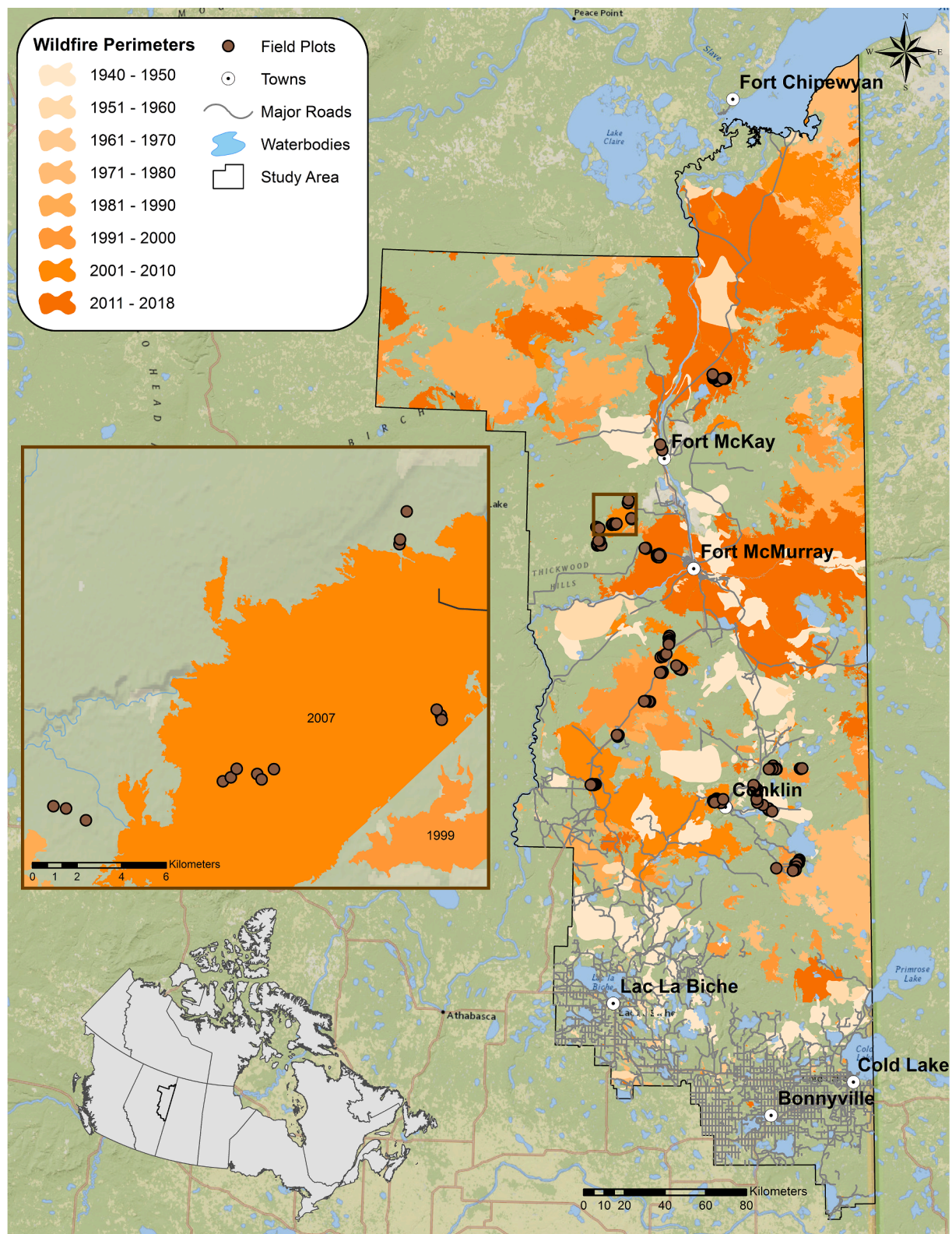


Fig. 1. Location of 164 field plots sampled in the summer of 2019 in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada (Fort McMurray is located at 56°43'N, 111°23'W). Inset map of Canada in the lower left with outline of study area.

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 (Guo et al., 2017;

Harper and Macdonald, 2001). 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 (Guo et al., 2017; Moss, 1983), 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, notably common blueberry, bearberry (*Arctostaphylos uva-ursi*), and woolly beach-heather (*Hudsonia tomentosa*) (Pinno and Errington, 2016).

The climate in the LAR was 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). Approximately 42,077 km² (51.84%) of the region has burned within the past 48 years (1970–2018), and the fire return interval is estimated between 59 and 180 years (De Groot et al., 2013; Larsen, 1997). 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 seismic lines (2–8 m wide clear-cut lines) and roads, make up 0.70% and 0.36% of the anthropogenic disturbances in the LAR, and reach densities of 1.49 km/km² and 0.5 km/km², respectively (Campos-Ruiz et al., 2018; Schneider et al., 2010). 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 occurred 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 km²; Fuller and Keith 1980), their population was recently estimated at 0.77–1.15 wolves/100 km² (Burgar et al., 2019; Latham et al., 2011). 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 (Burgar et al., 2019; Latham et al., 2011).

2.2. Study design

A total of 164 field plots were conducted between June 1 and August 19, 2019. Prior to field data collection, we 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. We 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. Field plots were at least 100 m from a road and 25 m 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 (Natural Regions Committee, 2006) 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).

2.3. Field data collection

Field plots consisted of 50 m belt transects (50 × 2 m; 100 m²) 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. Boring at a pre-determined 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):

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

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 upland forests (Brinkman and Roe, 1975; DeByle and Winokur, 1985); therefore, if the number of tree rings counted in the field ($Age_{measured \text{ at coring height}}$) 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 ≥30 cm in height (Fort McMurray average snow depth; Environment Canada 2019), as well as sapling stems ≥30 cm in height and <2 cm in diameter found within 1 m on the right side of the 50 m transect line (50 × 1 m; 50 m²) 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 m², respectively. Density of all species was later standardized to 100 m² for analysis. Estimates of 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 ratio of the number of browsed branches to the total

number of branches off the main stem. Estimates of 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. 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 plot based on active browse from the previous winter.

2.4. Winter browse species

A total of 32 deciduous shrub and 8 sapling species were considered and measured in the field (Appendix A). 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 (Appendix B). Browsing prevalence (in percentage) 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 1–20% browsing prevalence, medium palatable winter browse species had 21–50% browsing prevalence, highly palatable winter browse species had 51–90% browsing prevalence, and preferred winter browse species had 91–100% 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.

2.5. Statistical analyses

2.5.1. 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 m²), Hill's Shannon-Weaver Index (hereafter referred to as Hill's Index), and species abundance (stem density: number of stems/100 m²). 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 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 × landcover; stand age × palatability) and three-way interaction (stand age × landcover × 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 (≥ 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 m²) with a high number of zeros (Clarke, 1993).

2.5.2. 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 × 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).

3. Results

3.1. 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 1). 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 ($\beta_{\text{sapling}} = -0.087$, $SE = 0.026$, $p < 0.001$).

Deciduous shrub richness and Hill's Index in mixedwood forests peaked in the first 10 years post-wildfire at 10 species/100 m² and dropped to approximately 2.5 species/100 m² at 50–60 years post-wildfire, but increased with a second peak at 90 years post-wildfire (Fig. 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 m², decreased to 2 species/100 m² at 60–70 years post-wildfire, and increased slightly for a second peak of 3 species/100 m² at 80–90 years post-wildfire (Fig. 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 m² to 2 species/100 m², but remained constant in poor fens at approximately 5 species/100 m² (Fig. 2). Sapling richness and Hill's Index in poor fens, however, peaked in the first 20 years post-wildfire at 6 species/100 m², but dropped and remained constant at approximately 2.5 species/100 m² over time, while sapling richness and Hill's Index remained constant at approximately 1.5 species/100 m² in bogs (Fig. 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, in exception to sapling abundance in the first 10 years post-wildfire (Fig. 2). Deciduous shrub abundance in mixedwood forests remained constant at an average of 400 stems/100

m², while sapling abundance decreased exponentially from approximately 1,600 stems/100 m² to 25 stems/100 m² over this period (Fig. 2). Bogs showed similar trends to mixedwood forests with constant deciduous shrub abundance at an average of 785 stems/100 m² (Fig. 2). Poor fens, however, showed a linear decrease in deciduous shrub abundance from approximately 900 stems/100 m² to 400 stems/100 m² (Fig. 2). Sapling abundance in bogs increased to an average of 225 stems/100 m², whereas in poor fens, sapling abundance peaked at 400 stems/100 m² at 20 years post-wildfire and decreased to 25 stems/100 m² (Fig. 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 C.

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 (Fig. 3 and Appendix C, Fig. C7). In the first 10 years post-wildfire, deciduous shrub composition in all six landcover types were similar and overlapped (Fig. 3). Sapling composition in the first 10 years post-wildfire were already dissimilar between upland and lowland forests (Appendix C, Fig. C7). Segregation of deciduous shrub composition was evident between 11 and 30 years post-wildfire as lowland forests were further apart than uplands (Fig. 3). The segregation of deciduous shrub and sapling communities were evident for mature stands (≥ 71 years post-wildfire) as landcover types weren't overlapping, suggesting different community compositions (Fig. 3 and Appendix C, Fig. C7).

Successional trajectories of ungulate winter browse (deciduous shrubs and saplings) differed significantly by palatability (Table 2). 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). All palatability categories were

Table 1

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 m²) preferred by ungulates. Beta coefficients (β), 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		
	β	SE	p	β	SE	p
Species richness						
Intercept	3.256	0.426	<0.001	1.787	0.276	<0.001
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	<0.001	0.701	0.307	0.024
Poor fen	1.694	0.537	0.002	1.003	0.348	0.005
Rich fen	0.915	0.581	0.117	0.335	0.377	0.375
Hill's Index¹						
Intercept	0.470	0.029	<0.001	1.093	0.055	<0.001
Stand age	−0.0003	0.0002	0.169	−0.0002	0.0004	0.585
Bog	−0.080	0.033	0.018	0.025	0.062	0.687
Jack pine forest	−0.003	0.034	0.924	0.146	0.064	0.024
Mixedwood forest	0.156	0.032	<0.001	0.224	0.061	<0.001
Poor fen	0.078	0.037	0.037	0.268	0.069	<0.001
Rich fen	0.015	0.040	0.706	0.184	0.075	0.015
Abundance²						
Intercept	16.844	2.247	<0.001	13.744	1.956	<0.001
Stand age	−0.0005	0.018	0.980	−0.087	0.026	<0.001
Bog	10.688	2.552	<0.001	−5.772	2.396	0.017
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	<0.001	−4.354	2.562	0.091
Rich fen	12.686	3.069	<0.001	−4.994	2.834	0.080
Stand age × Bog	—	—	—	0.115	0.032	<0.001
Stand age × Jack pine	—	—	—	0.024	0.043	0.574
Stand age × Mixedwood	—	—	—	−0.038	0.037	0.301
Stand age × Poor fen	—	—	—	0.055	0.043	0.203
Stand age × Rich fen	—	—	—	0.077	0.048	0.107

¹ β and SE are log transformed for deciduous shrub Hill's Index, but square root transformed for sapling Hill's Index.

² β and SE are square root transformed for both deciduous shrub and sapling abundance.

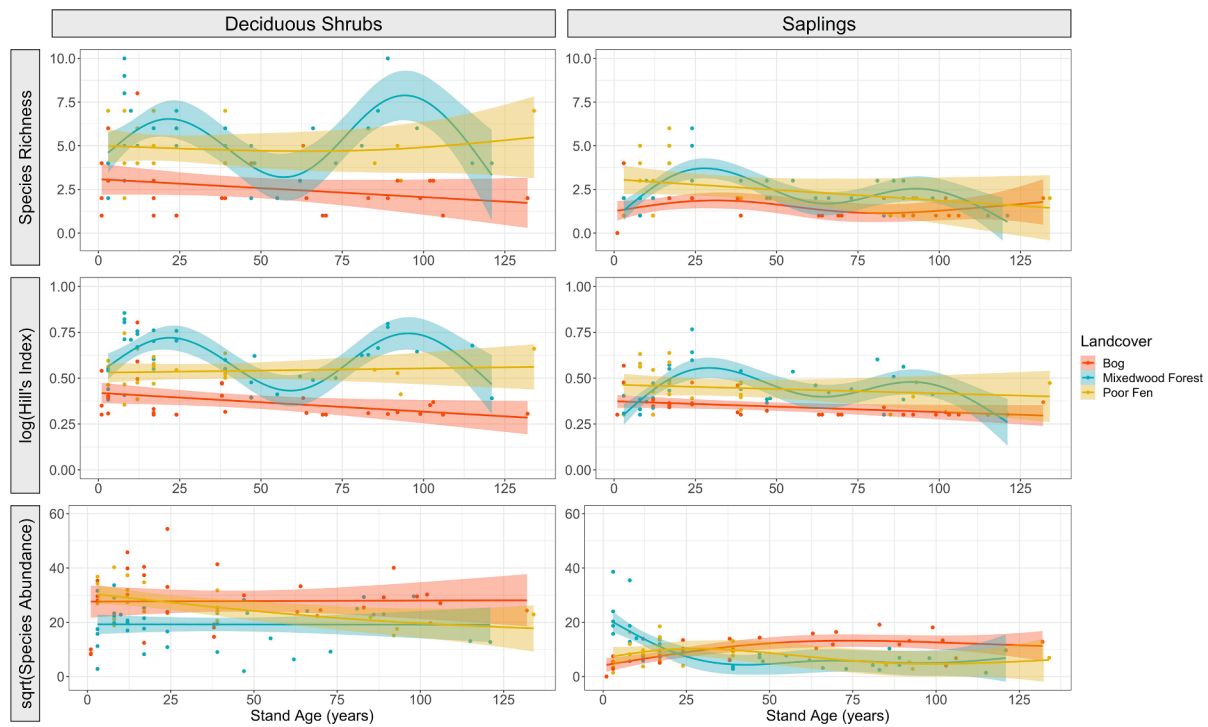


Fig. 2. Comparison of temporal changes (stand age) in deciduous shrub and sapling richness consumed by moose and white-tailed deer, Hill's Index, and abundance (number of stems/100 m²) in mixedwood forests, bogs and poor fens in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.

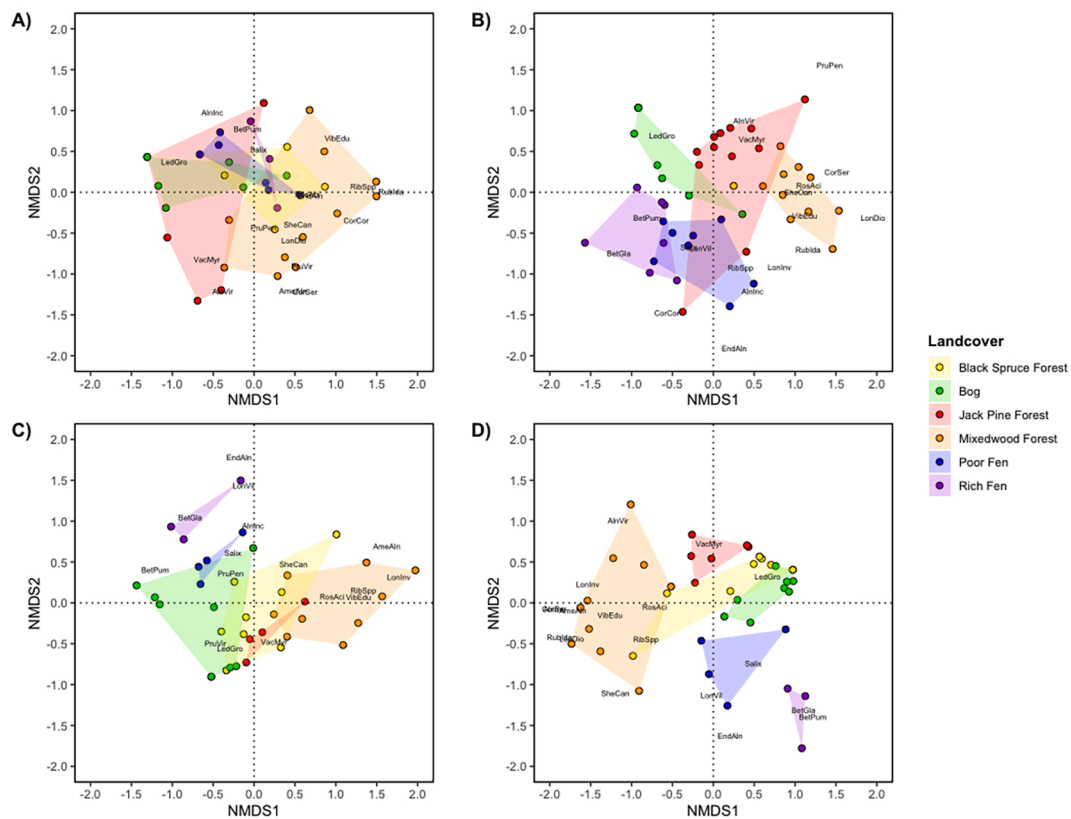


Fig. 3. Temporal changes (stand age) in deciduous shrub composition for species consumed by moose and white-tailed deer in A) 0–10 years post-wildfire (young forest), B) 11–30 years post-wildfire (young forest), C) 31–70 years post-wildfire (intermediate forest), and D) ≥71 years post-wildfire (mature forest) in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.

Table 2

Summary of three-way ANCOVA model testing the effects of stand age, landcover, and palatability categories on abundance of deciduous shrubs and saplings ($\log(\text{number of stems}/100 \text{ m}^2)$). Beta coefficients (β), 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		
	β	SE	p	β	SE	p
Intercept	1.194	0.176	<0.001	0.337	0.124	0.007
Stand age	-0.011	0.004	0.008	-0.003	0.003	0.265
Bog	0.065	0.190	0.732	-0.330	0.134	0.014
Jack pine forest	-0.416	0.187	0.027	-0.170	0.132	0.198
Mixedwood forest	0.411	0.182	0.024	0.098	0.128	0.444
Poor fen	0.708	0.197	<0.001	0.003	0.139	0.984
Rich fen	0.541	0.211	0.011	-0.203	0.148	0.172
High	-0.464	0.135	<0.001	0.747	0.095	<0.001
Moderate	-0.296	0.135	0.029	-0.174	0.095	0.067
Low	0.380	0.135	0.005	1.089	0.095	<0.001
Stand age \times High	0.006	0.005	0.228	-0.012	0.003	0.001
Stand age \times Moderate	-0.002	0.005	0.762	0.0009	0.003	0.803
Stand age \times Low	0.020	0.005	<0.001	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	0.024	0.002	0.004	0.612
Stand age \times Mixedwood \times High	0.019	0.005	<0.001	0.014	0.003	<0.001
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	0.030	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	0.049	0.001	0.004	0.828
Stand age \times Rich fen \times Moderate	0.029	0.006	<0.001	0.003	0.004	0.480
Stand age \times Bog \times Low	0.006	0.005	0.190	0.014	0.003	<0.001
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	0.011	-0.010	0.003	0.002
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	<0.001	0.007	0.004	0.088

statistically significant for deciduous shrub and sapling abundance, except for moderate sapling palatability ($\beta_{\text{sapling}} = -0.174$, SE = 0.095, $p = 0.067$; Table 2). Regardless of landcover types, highly palatable sapling abundance decreased significantly over time, while low palatable deciduous shrub abundance increased significantly over time (Table 2).

However, three-way interactions between stand age, landcover type,

and palatability were significant demonstrating that successional trajectories for browse abundance differed between upland and lowland forests (Table 2, Fig. 4 and Appendix C, Fig. C8). Indeed, abundance of highly palatable deciduous shrubs differed significantly over time within jack pine forests, mixedwood forests, and rich fens (Table 2). 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). 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).

Changes in winter browse palatability were apparent within the first 150 years post-wildfire that were absent in the two-way ANCOVAs (Fig. 4 and Appendix C, Fig. C8). For example, abundance of deciduous shrubs in mixedwood forests remained constant at 400 stems/100 m² over time regardless of palatability categories (Fig. 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 (Fig. 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 C, Fig. C8). 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) (Fig. 4 and Appendix C, Fig. C8).

3.2. 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 3). Both browse percentage and browse severity on deciduous shrubs were statistically significant in jack pine forests, mixedwood forests, and poor fens (Table 3; Fig. 5 and Appendix C, Fig. C9). 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 3).

The presence of deciduous shrub species had significant effects on both browse percentage and browse severity (Table 3; Fig. 5 and Appendix C, Fig. C9). Twining honeysuckle, bracted honeysuckle, currants & gooseberries, wild red raspberry, and Canada buffaloberry were avoided by ungulates (Table 3; Fig. 5 and Appendix C, Fig. C9). 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 3), 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 3). 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 3; Fig. 5 and Appendix C, Fig. C9). These deciduous shrub species were browsed significantly with the exception of green alder, fly mountain honeysuckle, and pin cherry (Table 3). 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 3).

Stand age, landcover type, and the presence of sapling species consumed by ungulates failed to explain both browse percentage and

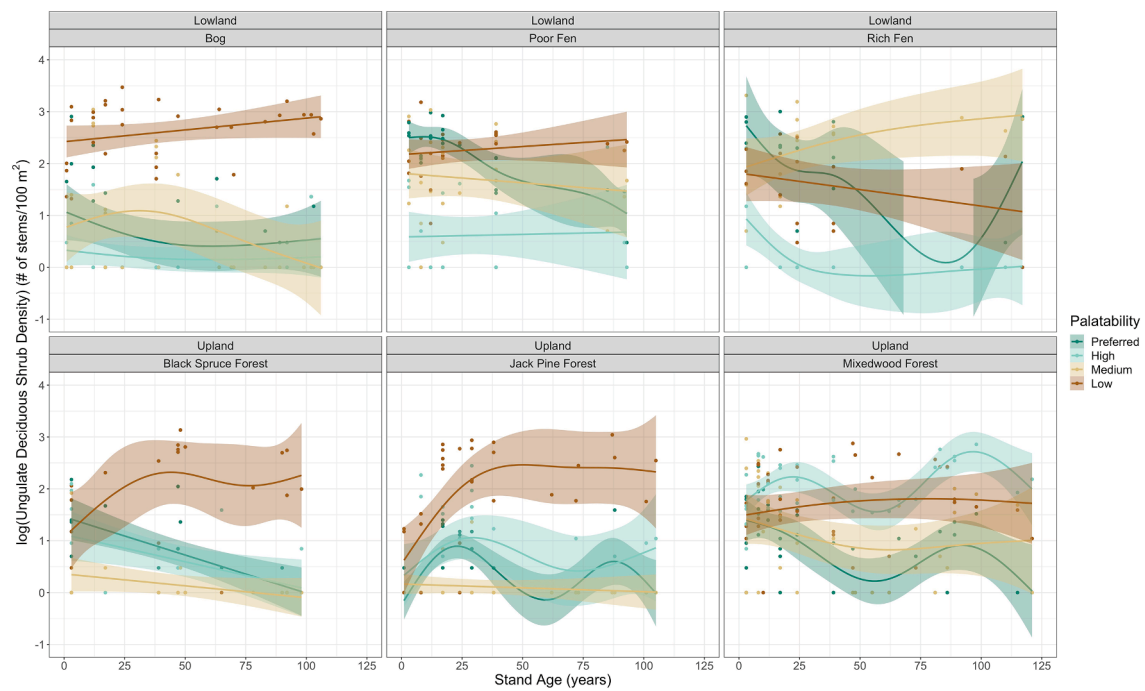


Fig. 4. Temporal changes (stand age) in deciduous shrub abundance (number of stems/100 m²) by palatability categories in six landcover types in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.

Table 3

Summary of the ordinal logistic regression models testing the effects of stand age, landcover, and presence of deciduous shrubs on browse percentage and browse severity. Odds ratios (OR), beta coefficients (β), 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 A.

	Browse Percentage				Browse Severity			
	OR	β	SE	p	OR	β	SE	p
Stand age	1.013	0.013	0.002	<0.001	1.014	0.014	0.002	<0.001
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	<0.001	2.567	0.943	0.310	0.002
Mixedwood forest	1.860	0.621	0.285	0.029	1.903	0.643	0.291	0.027
Poor fen	2.216	0.796	0.316	0.012	1.906	0.645	0.321	0.045
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	<0.001	13.440	2.598	0.576	<0.001
BetPum	2.748	1.011	0.484	0.037	3.310	1.197	0.493	0.015
LedGro	2.981	1.092	0.415	0.009	2.957	1.084	0.421	0.010
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	0.037	0.248	-1.391	0.672	0.039
RosAci	4.263	1.450	0.435	<0.001	4.220	1.440	0.439	0.001
RubIda	0.213	-1.548	0.857	0.071	0.194	-1.641	0.857	0.056
Salix	5.153	1.640	0.425	<0.001	4.918	1.593	0.429	<0.001
SheCan	0.622	-0.474	0.629	0.451	0.623	-0.474	0.634	0.455
VacMyr	4.151	1.423	0.431	<0.001	3.923	1.367	0.436	0.002
0 1	–	1.536	0.464	<0.001	–	1.531	0.469	0.001
1 2	–	2.248	0.469	<0.001	–	3.222	0.482	<0.001
2 3	–	2.972	0.475	<0.001	–	4.178	0.494	<0.001
3 4	–	4.000	0.486	<0.001	–	5.553	0.529	<0.001
4 5	–	5.614	0.525	<0.001	–	–	–	–

browse severity on saplings species, in exception to mixedwood forests ($\beta_{\text{severity}} = 0.800$, $SE = 0.821$, $p = 0.030$; Appendix C, Table. C1). 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 (Appendix C, Table. C1). 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 C, Fig. C10 and C11).

4. 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 (Chen et al.,

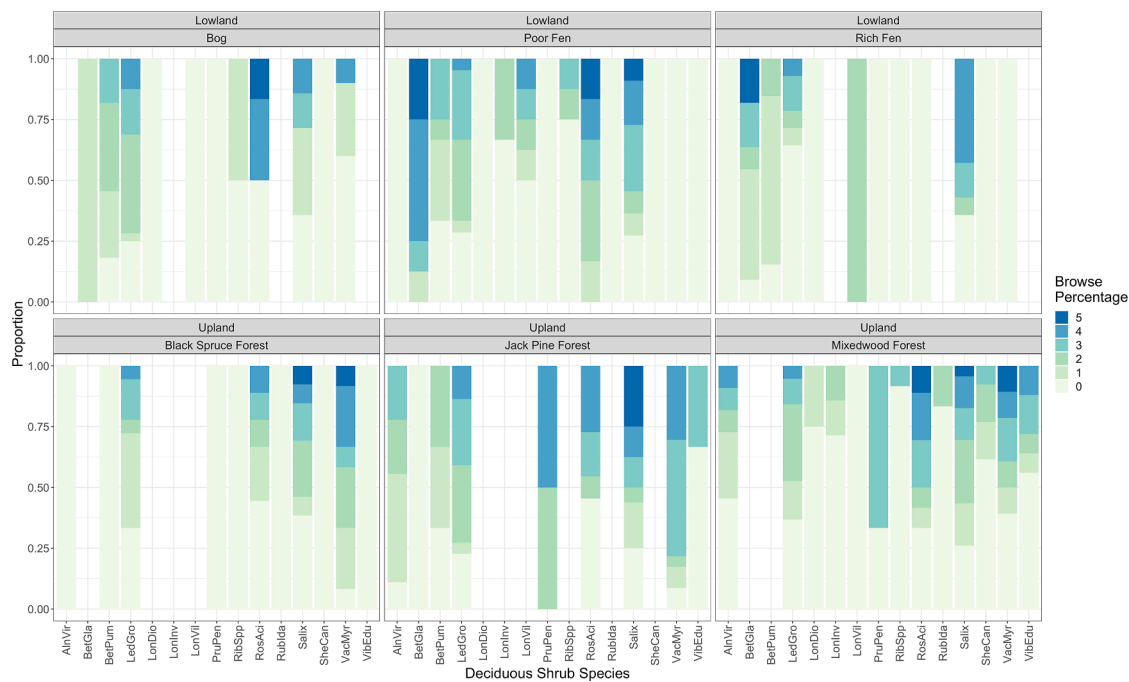


Fig. 5. Proportion of browse category (by percentage) for each deciduous shrub species consumed by moose and white-tailed deer in six landcover types in the Lower Athabasca Region south of Lake Athabasca in northeastern Alberta, Canada.

2009; Gutsell and Johnson, 2002; Ilisson and Chen, 2009b). 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 (Chapin et al., 2006; Spencer and Hakala, 1964; Weixelman et al., 1998). 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 m²) 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 (Benscoter et al., 2011; Zoltai et al., 1998). 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 (Auger et al., 2004; Bergeron, 2000), 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 (Aubin et al., 2000; Chen and Popadiouk, 2002; Kneeshaw and Bergeron, 1996; Waldron, 1959), 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 (Bjørneraas et al., 2011; Timmermann and McNicol, 1988). 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 (Joly et al., 2016; Maier et al., 2005). 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. 11–30 years post-wildfire) (MacCracken and Viereck, 1990; Maier et al., 2005; Weixelman et al., 1998), 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 (Joly et al., 2016; Loranger et al., 1991; Lord and Kielland, 2015; MacCracken and Viereck, 1990; Maier et al., 2005; Peek, 1974; Spencer and Hakala, 1964; Weixelman et al., 1998), 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) (Brown et al., 2018). Indeed, mean willow abundance was greater in poor and rich fens (270 ± 256 stems/100 m² and 302 ± 331 stems/100 m², 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 ± 658 stems/100 m²; poor fens: 851 ± 395 stems/100 m²; rich fens: 1024 ± 612 stems/100 m²) and constantly higher abundance of low palatable browse throughout the boreal lowland forest succession. Similarly, Mallon et al. (2016) found greater understory biomass and productivity in boreal lowlands in northern Ontario across all stand age classes, including shrub biomass, 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, in exception to 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 (Newbury et al., 2007; Regelin et al., 1987; Renecker and Schwartz, 2007; Risenhoover, 1989; Weixelman et al., 1998), 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 (Newbury et al., 2007; Peek, 1974; Raymond et al., 1996). 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, 1989; Crête and Courtois, 1997; Crête and Jordan, 1982). 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 (Crête, 1989; Crête and Jordan, 1982; Dumont et al., 2005; Ullrey et al., 1968).

5. 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 (Veitch, 2001; Webb, 1967). 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 prefers habitats with diverse food items (Maier et al., 2005). The latter suggests that wildfires can provide higher foraging 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 (Dawe et al., 2014; Fisher et al., 2020; Latham et al., 2013, 2011).

This study is also the first to test the paradigm prediction that moose avoid lowland forests presumably because they do not provide enough forage. 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 should be cautious in their wording of

the use of lowland forests by moose and white-tailed deer. 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 should 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., 2013, 2011). 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 should 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.

CRedit authorship contribution statement

Mélanie R. Routh: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Funding acquisition. **Scott E. Nielsen:** Conceptualization, Methodology, Resources, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119242>.

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