

Potential impacts of climate change on the habitat of boreal woodland caribou

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Abstract. Boreal woodland caribou (*Rangifer tarandus caribou*) are currently listed as threatened in Canada, with populations in the province of Alberta expected to decline as much as 50 percent over the next 8–15 yr. We assessed the future of caribou habitat across a region of northeast Alberta using a model of habitat-quality and projections of future climate from three general circulation models. We used mapped climatic and topo-edaphic properties to project future upland vegetation cover and a fire simulation model to project the frequency and extent of wildfires. Based on those projections, we quantified the future habitat of caribou according to estimates of nutritional resources and predation risk derived from vegetation cover type and stand age. Grassland vegetation covered up to half of the study area by the 2080s, expanding from <1% in the present and contributing to a significant contraction in mixedwood and coniferous forests. This change in vegetation would increase the risk of predation and disease, as habitat becomes more suitable for white-tailed deer (*Odocoileus virginianus*) and, consequently, gray wolves (*Canis lupus*). Borne out, these changes would severely compromise the long-term persistence of caribou in the boreal forest of Alberta.

Key words: climate change; disturbance modeling; predation risk; wildland fire; woodland caribou.

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INTRODUCTION

Wildlife species are undergoing range shifts and facing extirpation as climate change erodes historical habitat and simultaneously opens up new environments to migrant species (Parmesan and Yohe 2003, Colwell et al. 2008). Accelerating climate change (IPCC 2013) thus presents a

challenge for land managers seeking to conserve habitat, especially as climate change often acts in concert with anthropogenic modifications to land cover to reduce available habitat (Forister et al. 2010). Although the impacts of climate change are frequently assessed, the interaction between disturbance and climate change is rarely considered. This is particularly important in biomes

such as the boreal forest, where wildfires are strong determinants of landscape structure (Burton et al. 2009). As such, habitat models that incorporate climate change and disturbance can be a powerful tool for informing long-term conservation decisions (Cáceres et al. 2013).

The Canadian boreal forest (hereafter, the “boreal forest”) covers approximately 3.09 million km² and is characterized by recurrent large wildfires. Climate change is likely to raise the mean annual temperature of the boreal forest by at least 2°C by the 2050s and up to 5°C by 2100 (Price et al. 2013), particularly if greenhouse gas emissions approximate the relative concentration pathway (RCP) 8.5 emission scenario (IPCC 2013). Climate change in the boreal region will also lead to earlier snowmelt, moderate increases in summer precipitation, and greater drought frequency (especially in western regions; Lemke et al. 2007, Price et al. 2013). These changes will likely translate into widespread increases in fire frequency and annual area burned (Flannigan and Van Wagner 1991, Flannigan et al. 2013, Boulanger et al. 2014), which may lead to persistent changes in boreal forest ecosystems (Price et al. 2013, Johnstone et al. 2016). Wang et al. (2017) have projected increases between 50% and 100% in the incidence of days with fire-conducive weather in the western boreal forest, and up to 150% elsewhere in Canada.

The response of boreal forest ecosystems to climate change will be complex and likely lead to the emergence of novel ecosystems (Schneider et al. 2016). It is often assumed that vegetation types will track the movement of historical climatic niches, although this represents a long-term outcome that does not account for time lags in ecosystem transitions (Schneider et al. 2009). The boreal forest in Alberta, Canada, is comprised two dominant terrain types: uplands characterized by a mixture of aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana*), and lowlands characterized by extensive peatlands, tamarack larch (*Larix laricina*), and black spruce (*Picea mariana*). In upland areas, resistance to vegetation change is largely due to the resilience of mature trees to climatic variation. Therefore, vegetation change will occur primarily where disturbance events, including wildfire and insect outbreaks, cause widespread tree mortality (Johnstone et al. 2016,

Schneider et al. 2016, Hogg et al. 2017). This change may occur rapidly (Foster et al. 2006, Frelich and Reich 2010), and a shift from late-successional conifers to early-successional conifers and broadleaf species is already occurring in the wider Canadian boreal (Searle and Chen 2017).

Compared to uplands, peatlands are relatively resilient to climate fluctuations due to their ability to retain large volumes of water (Waddington et al. 2015). Negative feedbacks with peat decomposition, moss productivity, and moss surface resistance moderate water table decline in these systems (Waddington et al. 2015). The water table feedbacks inhibit vegetation change, which may allow peatlands to act as hydrologic refugia in spite of significant climatic warming (Price et al. 2013, Schneider et al. 2016). While peatland vegetation transition will undoubtedly occur in areas of shallow peatland depth (Ketrtridge et al. 2015), widespread vegetation regime change will likely take centuries (Schneider et al. 2016). This will be important for the Alberta boreal woodland caribou (*Rangifer tarandus caribou*), who depend on peatlands for foraging and predator avoidance (Bradshaw et al. 1995, Stuart-Smith et al. 1997, McLoughlin et al. 2003, James et al. 2004).

Boreal populations of woodland caribou are threatened throughout their Canadian range and protected under the federal Species at Risk Act (Festa-Bianchet et al. 2011, Government of Canada 2017). In Alberta, populations of boreal caribou are demonstrating relatively steep declines in abundance (Hervieux et al. 2013). Rapid and widespread industrial development, including oil-and-gas exploration and extraction, forestry, and mining, results in the displacement of caribou, a reduction in habitat, and an increase in the distribution and abundance of predators (McLoughlin et al. 2003, Latham et al. 2011b). Changes in the predator–prey dynamic are the result of apparent competition (Holt 1977) between caribou and other ungulates, where early-successional habitats resulting from industrial activities increase the distribution and abundance of white-tailed deer (*Odocoileus virginianus*) and moose (*Alces americanus*; Alberta Sustainable Resource Development and Alberta Conservation Association 2010, Festa-Bianchet et al. 2011). Greater numbers of deer and moose lead to an increase in wolf (*Canis lupus*) populations, the

primary predator of caribou (McLoughlin et al. 2003, Latham et al. 2011a). In addition to more wolves, industrial activity in the form of roads and seismic lines facilitates an increase in the distribution and movement of wolves, leading to incidental predation of caribou (Latham et al. 2013, DeMars and Boutin 2017, Dickie et al. 2017). Black bears (*Ursus americanus*), a secondary predator of caribou in western Canada, also benefit from early-successional plant communities and greater biomass of deer and moose (McLoughlin et al. 2003, Latham et al. 2011c). Caribou also encounter greater insect harassment in these early-successional forests (Raponi et al. 2018), and expansion of these habitats could have unpredictable consequences on caribou insect-avoidance behavior.

A warming climate has a number of potentially negative consequences for caribou, including loss of forest habitat (Schneider et al. 2009), increased predation (Bergerud and Luttich 2003, Latham et al. 2011b), and increased prevalence of diseases (Pickles et al. 2013). Whereas white-tailed deer were historically at the northern limit of their range in the study area, vegetation change in conjunction with decreasing winter severity and snow depth could greatly increase their distribution and population density (Dawe et al. 2014, Dawe and Boutin 2016). A greater number of white-tailed deer would likely increase the abundance and distribution of wolves. Furthermore, the northerly expansion of white-tailed deer has the potential to expose caribou to new pathogens, including meningeal worm (*Parelaphostrongylus tenuis*) and chronic wasting disease, both of which could greatly increase caribou mortality (Cumming 1992, Pickles et al. 2013).

Boreal caribou in Alberta and other areas of western Canada strongly select for peatland complexes, in particular fens and bogs (Bradshaw et al. 1995, Stuart-Smith et al. 1997, James et al. 2004, Mumma et al. 2017). This is likely a strategy to mitigate predation risk associated with the distribution of deer and moose (Stuart-Smith et al. 1997). Although caribou generally avoid uplands, caribou in Alberta are sometimes found in upland coniferous forests (Bradshaw et al. 1995, McLoughlin et al. 2005, Muhly et al. 2015). This may be a response to seasonal limitations in nutrition or an inability to assess increased predation

risk in those areas (McLoughlin et al. 2005, Denryter et al. 2017). Climate-induced changes in the distribution of wetland or upland communities could have implications for rates of predation and the availability of forage for boreal caribou.

The purpose of our study was to assess the long-term effects of climate change and wildfire on the distribution and quality of caribou habitat. Specifically, we investigated the implications of upland vegetation change for caribou, under the assumption that peatland habitat remains intact. We used habitat suitability metrics to explore the effects of changing vegetation cover, mediated by future wildfire, on the availability of nutritional resources and the likelihood of predation or disease spread in a study area located in northern Alberta. This decompositional approach makes use of empirically-based but knowledge-driven relationships to assess separate components of habitat suitability, in the context of improved (fire-mediated) projections of vegetation change. However, the findings are exploratory, as there is considerable uncertainty in future vegetation projections and the possibility that current empirical relationships between caribou and their habitat may change in response to evolving environmental conditions. Our findings depend on an assumed relationship between white-tailed deer abundance and habitat suitability, which is uncertain primarily because white-tailed deer is currently at the northern limit of its historical range within the study area. Other factors, including snow, may limit the distribution or abundance of white-tailed deer (Beier and McCullough 1990). Despite these uncertainties, extrapolating these empirical relationships to future vegetation and climate conditions may give us critical insight into the future of endangered species' habitat.

METHODS

Study area

The study area encompasses approximately 63,700 km² across the Alberta-Pacific Forest Industries (Al-Pac) Forest Management Agreement in the Boreal Plains ecozone of northern Alberta, Canada (Ecological Stratification Working Group 1995). This area has relatively flat topography but includes several hill complexes, with elevations ranging from approximately 400 m in the northeast to 900 m in the southwest (Fig. 1). The

region receives an average of 450 mm of precipitation annually and is characterized by extensive mixedwood and coniferous forests, which are dominated by trembling aspen, white spruce, black spruce, and jack pine. Approximately 40% of the study area is lowland (Hird et al. 2017), much of which is currently caribou habitat for two caribou populations, the West Side Athabasca River (WSAR) population and the East Side Athabasca River (ESAR) population (Appendix S1: Fig. S1). Caribou habitat is fragmented by extensive oil-and-gas development (Muhly et al. 2015). Both caribou populations have an annual adult female survival rate of approximately 85% compared to the Alberta average of 91.8%; this is sufficiently low to place both populations at risk of rapid extirpation (Hervieux et al. 2013).

Model overview

We calculated caribou habitat-quality as an index, produced using the framework described by Whitman et al. (2017; Table 1), where habitat quality is defined as the union of several possible habitat components. We included nutritional resources and risk of predation and disease

(hereafter “habitat-quality modules”) as the two components of habitat-quality most important for caribou. Habitat-quality modules take the form of a series of matrices (e.g., Table 2) that estimate a habitat-quality index relative to the simulated vegetation type and age class at any point on the landscape. Reclassification weights for each season were derived from published studies that reported resource selection functions (Boyce et al. 2002), supplemented by expert-based inference where necessary (Muhly et al. 2015, Whitman et al. 2017). Our nutritional resources matrices were taken directly from Whitman et al. (2017), whereas our predation risk and disease matrices were based on Fisher et al. (2016) and Dawe et al. (2014). We used a simulated landscape and the Burn-P3 fire simulation model (Parisien et al. 2005) to model wildland fire for a baseline period, and for the 2050s and 2080s under simulated future conditions, as in Stralberg et al. (2018). Simulated vegetation cover and stand age, as modified by fire, were used to assign a value describing the nutrition and predation risk at each pixel. All analyses were conducted at a 500-m resolution. R code is provided in Appendix S2.

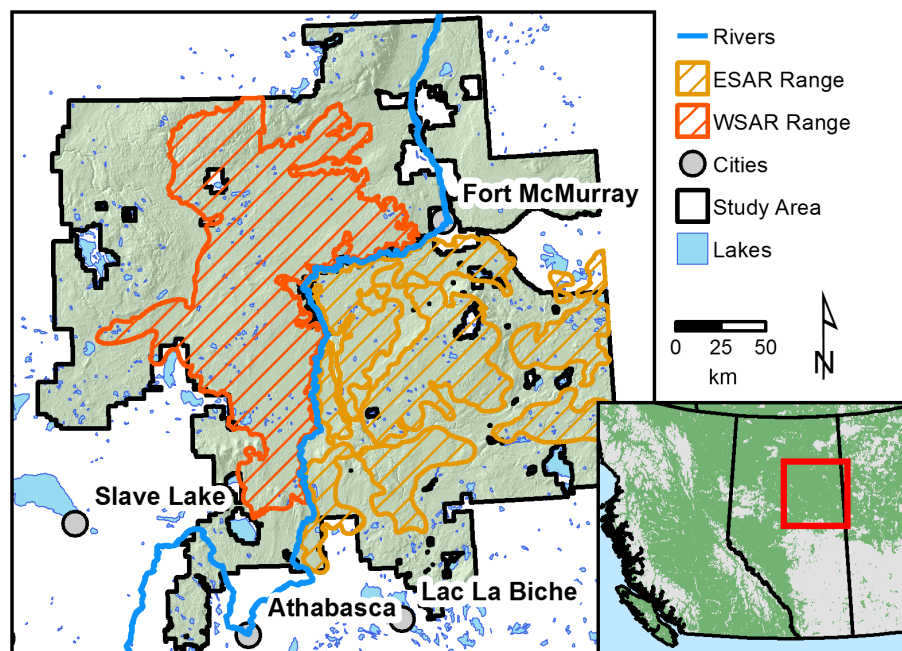


Fig. 1. Study area in Alberta, Canada, including the West Side Athabasca River (WSAR) and East Side Athabasca River (ESAR) caribou ranges. Green areas in the inset map represent tree-dominated vegetation cover.

Table 1. Data inputs and sources for deriving classes of vegetation cover, Burn-P3 input fire weather, and Burn-P3 input fuel layers.

Application	Dataset	Source
Caribou habitat-quality classes, Burn-P3 fuels	Modeled vegetation cover, baseline	Stralberg et al. (2018)
	Modeled vegetation cover, future projections	Stralberg et al. (2018)
Producing Alberta vegetation cover predictions/projections	Interpolated climate data (1961–1990 normal period, 2041–2070, 2071–2100)	Wang et al. (2012)
	Alberta Merged Wetland Inventory	Alberta Environment and Parks (2017)
	Surficial geology	Alberta Geological Survey
	Topographic indices	S. Nielsen, University of Alberta, species.abmi.ca
Burn-P3 input/calibration	Daily fire weather (i.e., temperature, relative humidity, wind speed, precipitation)	Canadian Forest Service historical observations
	Future daily fire weather	Wang et al. (2015)
	Historical fire point/shape data	Canadian National Fire Database, CFS (2015)

Table 2. Predation and disease risk associated with the distribution of white-tailed deer.

Vegetation cover	RSF coefficient	Weighting coefficient	Age class (years)					
			<20	21–30	31–50	51–70	71–90	>90
Fen	−0.243	0.051	0.051	0.051	0.051	0.051	0.051	0.051
Bog	−0.243	0.051	0.051	0.051	0.051	0.051	0.051	0.051
Other	0.812	1	0.935	0.935	0.935	0.935	0.935	0.935
Grass	0.812	1	1	1	1	1	1	1
Black spruce	−0.243	0.051	0.251	0.251	0.051	0.001	0.001	0.051
Pine	0.216	0.464	0.664	0.664	0.464	0.414	0.414	0.464
White spruce	0.216	0.464	0.664	0.664	0.464	0.414	0.414	0.464
Deciduous	0.569	0.781	0.981	0.981	0.781	0.731	0.731	0.781
Mixed coniferous and deciduous	0.393	0.623	0.823	0.823	0.623	0.573	0.573	0.623

Notes: Weights were derived from a reported resource selection function (RSF; Fisher et al. 2016), adjusted by expert knowledge for age class. For all other matrices, see Whitman et al. (2017).

Habitat-quality modules and inputs

Nutrition.—We mapped caribou nutritional resources by reclassifying vegetation cover and age into seasonal maps of forage availability in spring, summer/fall, and winter. The importance of each season's nutritional quality was not equal; winter nutritional resources were weighted at 0.5, spring nutritional resources were weighted at 0.25, and summer nutritional resources were weighted at 0.25. There is little empirical assessment of the relative value of seasonal forage for woodland caribou; thus, this weighting scheme is necessarily subjective. It should be noted that grasslands were classified as moderate-quality nutritional resources although their relative rarity in the current (i.e., baseline) landscape makes this a source of uncertainty in the future projections. Evidence from elsewhere in North America suggests that caribou are capable of foraging in

grasslands; mountain caribou in Alberta were found to consume 10–26% graminoids (Thomas et al. 1996). Alaskan caribou were found to have a summer diet of 50% graminoids (both alive and dead), 25% shrubs, and 14% forbs, with graminoids consumed throughout the year but in the highest proportions during the spring (Barten et al. 2001). Closer to our study site, Denryter et al. (2017) found that graminoids composed 1–16% of forage for tame caribou in northeastern British Columbia, when released in temporary pens in the wild. However, caribou diets vary greatly between herds and landscape types, so this is merely suggestive that Alberta caribou will take advantage of a novel grassland environment in the study area.

Predation and disease.—We reclassified vegetation cover and patch age into two raster layers that accounted for the risk of predation by black bears,

and the risk of predation and disease associated with white-tailed deer. We adapted a resource selection function developed by Latham et al. (2011a) to quantify the risk of predation by black bears (details in Whitman et al. 2017). Wolves are the primary predator of caribou, and their diet and habitat associations are variable (Latham et al. 2011b) and difficult to predict in the context of a changing climate. In comparison, the effects of vegetation cover change on white-tailed deer are much more predictable. White-tailed deer, an important prey species for wolves (Latham et al. 2011b), are expected to increase in distribution and abundance as the climate warms (Dawe and Boutin 2016). Thus, we projected the future distribution of white-tailed deer habitat, a proxy for wolf predation and disease risk, based on relationships published in Fisher et al. (2016) and Dawe et al. (2014). Predation and disease risks associated with white-tailed deer were weighted at 0.7, and predation risk from black bears was weighted at 0.3, with high values indicating the least suitable caribou habitat. Because wolves and black bears cause unknown proportions of overall caribou mortality, weights are necessarily subjective, particularly for future predation risk. Our weights were chosen based on a qualitative interpretation of the literature to emphasize disease and wolf predation, as represented by the distribution of white-tailed deer. The majority of adult caribou mortality is attributable to wolves (McLoughlin et al. 2003), while black bears are thought to prey on calves (Latham et al. 2011a).

Habitat-quality.—We modeled overall habitat-quality by the additive combination of the nutrition and predation risk modules (see Whitman et al. 2017 for details on habitat-quality component combination schemes), and by scaling the result from 0 to 1. In comparison with a multiplicative approach, an additive combination makes no assumptions about the ecology of the species. This was necessary because while predation is the dominant cause of caribou decline (McLoughlin et al. 2003, Latham et al. 2011b, Hervieux et al. 2013), the interaction between predator avoidance and foraging is poorly understood even in the present, let alone under future conditions. For example, caribou sometimes use upland environments in spite of the increased predation risk (McLoughlin et al. 2005), perhaps to access specific forage resources

(Rettie and Messier 1998, Denryter et al. 2017), or simply as travel corridors.

We performed a sensitivity analysis on relative predation risk and nutrition weighting: equal predation risk/nutrition weighting (habitat-quality₅₀), and with predation risk contributing 60%, 70%, and 80% of the overall habitat-quality (habitat-quality₆₀, habitat-quality₇₀, and habitat-quality₈₀, respectively). We present habitat-quality₇₀ as the key result based on the knowledge that Alberta caribou are primarily predation-limited under current conditions, not nutrition-limited (Stuart-Smith et al. 1997, Festa-Bianchet et al. 2011). Habitat-quality was compared across scenarios using median landscape values and a visual assessment of change in habitat-quality components (Appendix S1: Fig. S2). Other data inputs included a 250-m digital elevation model (NASA JPL 2009) for modeling wildfire and a human footprint dataset (ABMI 2015) for defining built-up areas such as mine locations and urban areas.

Simulated landscape

Vegetation cover modeling.—We mapped vegetation cover using a two-stage nested model. We used mapped datasets of geology, climate, terrain, and wetland class, which were first used to build a random forest model (Breiman 2001) of present-day ecosite type (details in Stralberg et al. 2018); ecosite refers to specific site moisture and nutrient availability (Beckingham and Archibald 1996). Next, predicted ecosite was used as an input to a second model predicting present and future vegetation cover type, under the assumption that soil moisture and nutrients will remain relatively stable over the study period. The nested model was necessary because, while soil moisture and nutrients are critical determinants of vegetation type, high-resolution ecosite maps are not available. In order to avoid vegetation mapping errors, the models were parameterized using ground-based vegetation datasets rather than remotely sensed data. A total of 10,080 unique point locations were used for model building. Vegetation cover projections and ecosite projections were both based on 1961–1990 climate normals, downscaled to 500-m resolution using Climate WNA (Wang et al. 2012). Future climate projections were based on the RCP 8.5 scenario (IPCC 2013), using three general circulation models (GCMs): UKMO-HadGEM2, CSIRO-

Mk3, and CanESM2. These same projections were used for monthly fire weather projections, which were then temporally downscaled to daily fire weather projections for the wildfire model (Wang et al. 2017).

Projected vegetation cover was based on geology, terrain, wetland class, and future climate projections for the 2050s (2041–2070) and 2080s (2071–2100; details in Stralberg et al. 2018). In order to account for the tendency of vegetation cover to lag behind optimal climate until disturbance facilitates changes, vegetation changes were only permitted within simulated fire perimeters (Stralberg et al. 2018). For example, the 2041–2070 fire perimeters were applied to the 2050s vegetation layer, thereby producing the 2080s vegetation layer. This was done by randomly selecting 30 yr of simulated fire perimeters and updating the vegetation layer within those perimeters to match the projected climate conditions. We summarized projected vegetation as a change in generalized cover type, considering the grassland, deciduous, mixedwood, and coniferous types. For each time period and GCM, this process was repeated 10 times and averaged to capture the variability generated by multiple Burn-P3 simulations (Parisien et al. 2005).

We assumed that peatlands in our study area will remain intact through the current century due to the negative hydrologic feedbacks that prevent vegetation cover change. Consequently, vegetation transition was modeled in the uplands only, while holding constant vegetation on wetland sites (i.e., hydric and hygric moisture classes). It should be noted, however, that wetlands were still eligible as fuel in Burn-P3, and as a result, their age (i.e., time since fire) changed from the baseline scenario to future scenarios.

Burn-P3 fire modeling.—We modeled fires using the Burn-P3 model (Parisien et al. 2005), which uses the Prometheus fire growth engine to simulate ignition and spread of fires across a gridded landscape (Tymstra et al. 2010). Fires were modeled across all of Alberta as part of research by Stralberg et al. (2018), which we have subset to the study area. We used 3000 replicates of a fire season in which wildfires were simulated for a historical baseline (1961–1990), the 2050s, and the 2080s, resulting in a total of 9000 simulated years for each of the three climate scenarios. Fires larger than 200 ha account for approximately 97%

of the total area burned in Canada (Stocks et al. 2002), and consequently, we did not model fires smaller than 200 ha. We used historical fire data from 1981 to 2010 (Canadian Forest Service 2015) to calibrate baseline simulations.

Projected vegetation cover types were converted to Canadian Forest Fire Behavior Prediction (FBP) System fuel types (Forestry Canada 1992) for use in Burn-P3. We used historical weather station records of fire weather (i.e., daily noon temperature, relative humidity, wind speed, and 24-h precipitation) from 1981 to 2010 (Wang et al. 2015), with associated Canadian Fire Weather Index (FWI) System variables (Van Wagner 1974), to grow fires within Burn-P3. Future fire scenarios were modeled using future fire weather developed by Wang et al. (2015), who applied monthly change anomalies from our three selected GCMs to baseline daily weather records, thereby producing future daily fire weather for the 2050s and 2080s and RCP 8.5 emission scenario. We assessed seasonal fire behavior using burn probability, defined as the chance that any pixel will burn during a single fire season.

Stralberg et al. (2018) evaluated several alternative approaches to parameterizing future fire regimes in Burn-P3. They found that empirically-based extrapolations of fire regime parameters (specifically, the number of fires and fire duration) led to extremely high rates of fire, resulting in vegetation changes approaching the expected climate-driven equilibrium. Given the complexity and uncertainty of anticipating future fire regime parameters, we opted for a more conservative estimate of future fire. We held current fire regime parameters (i.e., number of fires, spread days) constant, but used future simulated fire weather inputs, resulting in a modest increase in burn probability over time. Although this scenario may be conservative in terms of future fire regimes, it nevertheless resulted in significant upland vegetation change stemming from the large magnitude of projected temperature change and accompanying reductions in moisture availability. Reserving judgment on which scenario may be more realistic, we used the one that resulted in a more gradual rate of change, assuming greater transferability of our habitat suitability model based on current conditions. Also, we were interested in future fire as a catalyst for vegetation change, not as a direct influence on caribou habitat suitability.

Burn-P3 produces simulated fire perimeters, which we converted to raster format to produce raster layers of time since fire (in years). This was done by dividing Burn-P3 outputs into thirty 100-iteration parcels, each representing a simulated 100-yr time period, and averaging the stand age of any pixel across all 100-yr parcels. We used these time-since-fire rasters to assign stand age, ranging from 0 to 100 yr, to the underlying vegetation cover type, such that areas that burned more often were assigned a younger forest age class. We account for the stochasticity of fire location and size by averaging the thirty 100-iteration parcels into a single vegetation cover/age raster.

RESULTS

Fire

Fire frequency was projected to decrease under the CanESM2 scenario from a median burn probability of 1.03% under baseline conditions to 1.00% in the 2050s and increasing to 1.10% in the 2080s (Table 3). Under the HadGEM2 scenario, median burn probability was projected to decrease to 0.90% in the 2050s and recover to 1.00% by the 2080s (Appendix S1: Table S1). Under the CSIRO-Mk3 scenario, we projected a median burn probability of 1.10% for the 2050s and the 2080s (Appendix S1: Table S1). The northern regions of the study area, characterized

by coniferous forest in the baseline period, had the highest burn probability (Fig. 2). This high fire frequency in the north was reduced by the 2080s as coniferous forest was replaced with deciduous forest and grassland, although residual coniferous forest burned at a higher rate (Fig. 2). Expansion of deciduous forest lowered burn probability throughout the study area wherever deciduous forest was projected to expand (Figs. 3 and 4). Coniferous forests in the center and south were relatively sheltered from increases in burn probability as surrounding uplands had partially transitioned from mixed-wood forest to deciduous forest or grasslands (Figs. 3 and 4). However, these coniferous forests faced increasing burn probability by the 2080s, particularly under the CanESM2 scenario (Fig. 2).

Vegetation

Simulated changes in vegetation cover were largely due to the replacement of upland mixed-wood forest by extensive grasslands under all three GCM scenarios (Fig. 4), with over half of the study area transitioning to grassland by the 2080s under the CanESM2 scenario. As a percentage of the total landscape, grassland cover increased from <1% of the landscape to 21%, 22%, and 51% under the HadGEM2, CSIRO-Mk3, and CanESM2 scenarios, respectively, which represented 36%, 37%, and 86% of all upland sites. Deciduous forest cover increased slightly across all three GCM scenarios, whereas coniferous cover on upland sites declined from 20% in the baseline to 11%, 12%, and 2% for the HadGEM2, CSIRO-Mk3, and CanESM2 scenarios, respectively (Fig. 4). When considered across upland and wetland sites together, pure coniferous cover declined from 47% in the baseline to 41%, 42%, and 36%, for the HadGEM2, CSIRO-Mk3, and CanESM2 scenarios, respectively. Similar patterns of decline were projected for upland mixedwood forests. The greatest vegetation change was projected for the CanESM2 scenario, with over half of the study area transitioning to grassland by the 2080s.

Pine forest, as the major upland coniferous forest type within the study area, represented the majority of the decline in coniferous cover (Appendix S1: Fig. S3). Changes in mean coniferous stand age varied less than five years across all scenarios

Table 3. Result summary for the CanESM2 scenario, including burn probability; nutrition; predation and disease risk; and 60% predation dominant habitat-quality.

	1st Quartile	Median	3rd Quartile
Baseline			
Burn probability (%)	0.80	1.03	1.33
Nutrition	0.30	0.42	0.49
Predation risk	0.19	0.51	0.74
Habitat-quality ₇₀	0.27	0.48	0.72
CanESM2 2050s			
Burn probability (%)	0.73	1.00	1.30
Nutrition	0.30	0.45	0.49
Predation risk	0.18	0.46	0.74
Habitat-quality ₇₀	0.27	0.51	0.72
CanESM2 2080s			
Burn probability (%)	0.83	1.10	1.43
Nutrition	0.48	0.50	0.50
Predation risk	0.19	0.82	0.82
Habitat-quality ₇₀	0.27	0.27	0.71

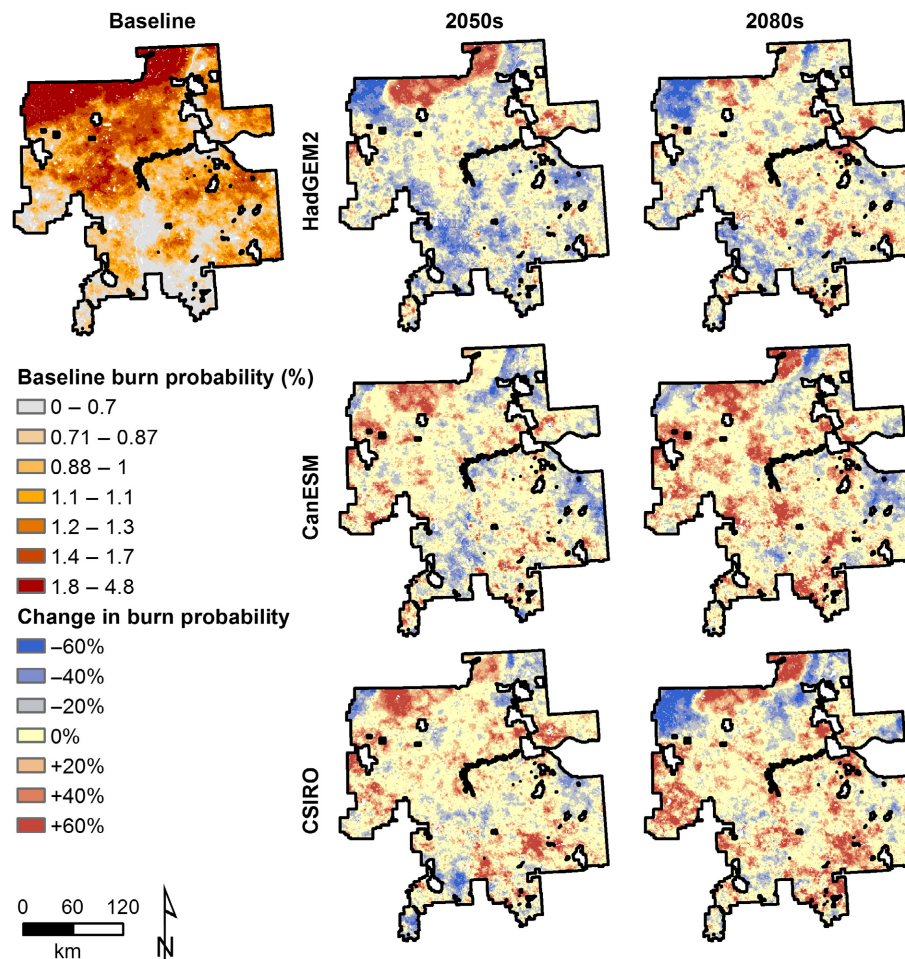


Fig. 2. Burn probability associated with the GCMs. Delta maps for the 2050s and 2080s indicate change in burn probability.

(Fig. 4). Although deciduous stand age fluctuated significantly across scenarios (Fig. 4), this was likely the result of a low proportion of deciduous vegetation cover, which would lead to individual simulated fire events causing disproportionately large impacts on simulated stand age. Mean stand age of mixedwood vegetation increased toward the 2080s, although this vegetation type represented a declining proportion of the landscape, so that by the 2080s, the mean stand age would be positively inflated by a very limited number of residual stands (Fig. 4). Mean grassland age increased 6–11 yr from the baseline scenario to the 2080s, although the relevance of grassland age in a boreal forest setting is unclear (Fig. 4).

Caribou habitat-quality

Median habitat-quality ($\text{habitat-quality}_{70}$) increased slightly from the baseline period to the 2050s (0.48–0.52) under the CanESM2 scenario (Table 3). The trend was similar under the CSIRO-Mk3 scenario (median 0.48–0.50), whereas median habitat-quality decreased under the HadGEM2 scenario (0.48–0.27). However, median overall habitat-quality declined substantially from the baseline to the 2080s under all three scenarios (median 0.48–0.27). We observed an increase in median predation and disease risk under the HadGEM2 and CSIRO-Mk3 scenarios, from 0.51 in the baseline scenario to 0.67 by the 2080s (Appendix S1: Table S1). The CanESM2 scenario

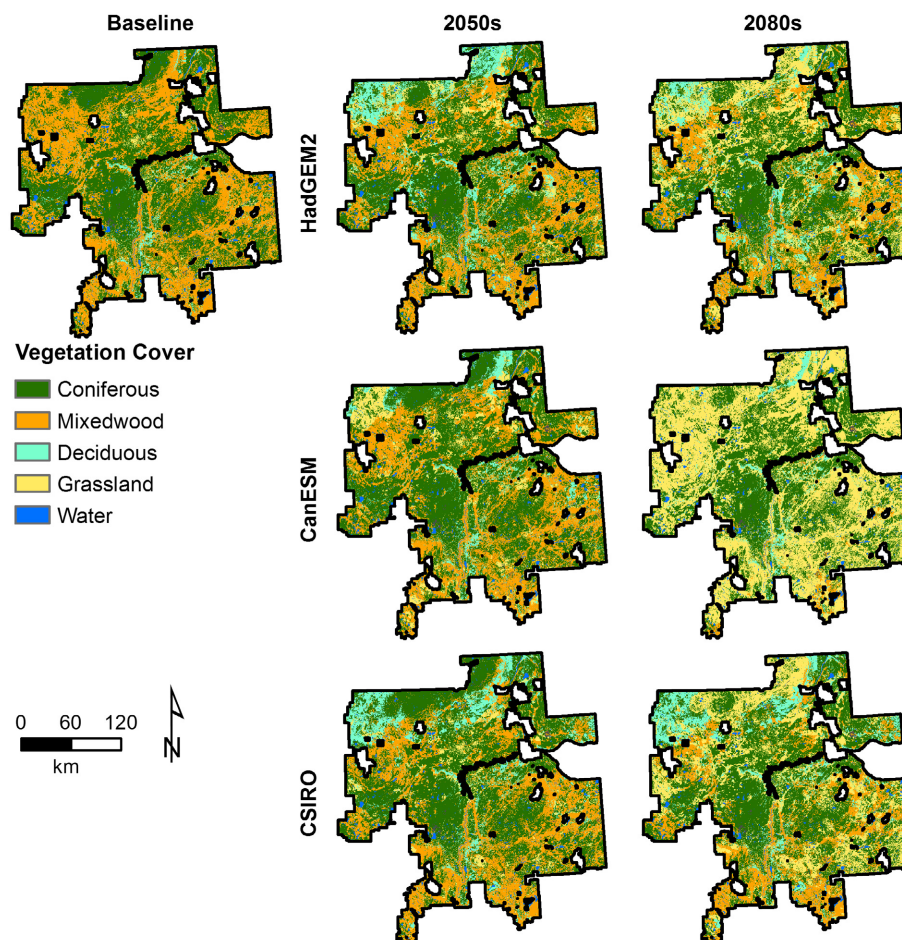


Fig. 3. Vegetation cover as modeled from GCM climate projections.

demonstrated a more substantial increase in median predation and disease risk, from 0.51 in the baseline scenario to 0.82 in the 2080s (Table 3). There was a minor increase in nutritional quality from the baseline scenario to the 2080s across all three GCMs.

Areas of high predation risk were generally associated with poor nutrition, but only in the baseline scenario. This correlation was reversed for the 2080s, such that the areas experiencing the greatest increase in nutritional resources also generally saw increasing predation and disease risk (Figs. 5, S4, and S5). Changes were spatially heterogeneous under the HadGEM2 and CSIRO-Mk3 scenarios, and generally more uniform under the CanESM2 scenario (Figs. 5, S4, and S5). Predation and disease risk was high in areas converting to grassland, and relatively low

in holdout bogs, fens, and coniferous stands. This grassland conversion was associated with increasing nutritional resources. Varying the weights of predation and disease risk and nutrition had little effect on the decreasing trend of habitat-quality. In general, habitat-quality declined as predation and disease risk was weighted higher (Appendix S1: Table S1).

DISCUSSION

Changing vegetation and fire

Our projections of vegetation change suggest that our study area will be dramatically altered by the 2080s. Expansion of early-seral deciduous forests was projected for the 2050s, with general declines of mixedwood cover and minor grassland expansion. By the 2080s, large areas of

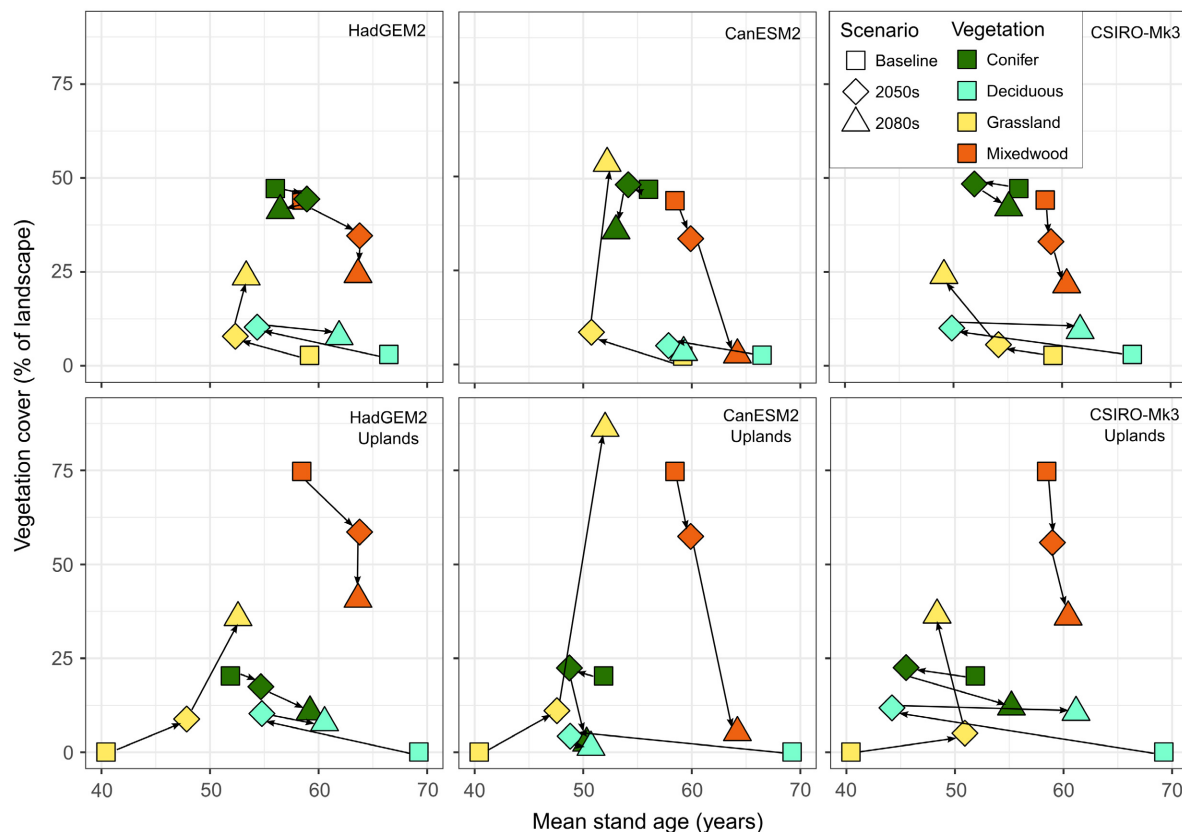


Fig. 4. Projected change in vegetation cover and mean stand age for all three GCMs. Land cover types were grouped into four general types as defined in Stralberg et al. (2018). Arrows indicate temporal trajectory from baseline to 2080s. Vegetation change was only allowed to occur in uplands for all scenarios.

upland coniferous forest were projected to give way to grasslands, such that grasslands covered between 20% and 50% of the study area by the 2080s. Such widespread change is generally in agreement with other modeling studies, including conversion to grassland vegetation cover (Schneider et al. 2009, 2016, Rooney et al. 2015). In fact, by the 2080s the study area is expected to have a climate resembling the modern-day fescue grassland and parkland (Schneider et al. 2016), or, when considered at the biome scale, the Great Plains Grassland biome (Rehfeldt et al. 2012). The southern limits of the boreal are strongly associated with climatic moisture limitations (Hogg 1994), and there has recently been extensive drought-induced mortality in aspen along the boreal-grassland transition zone (Michaelian et al. 2011). This suggests that temperature increases and drought stress will lead to boreal forest

fragmentation and vegetation cover change, which may occur rapidly (Soja et al. 2007).

With little grassland cover at the present day, it is difficult to appreciate fully how such a change would alter the underlying ecology and fire behavior of the study area. The expansion of grasslands will not depend on seed from southern ecozones, as small natural grasslands are already present and grasses (often non-native species) have been established along roadways and industrial infrastructure throughout the Boreal Plain (Schneider et al. 2003). This forest decline could occur even more quickly and extensively if fire activity is more intense than we project. However, vegetation transition from mixedwood cover to a predominantly deciduous forest entails a negative feedback process by which fire activity is subdued (Terrier et al. 2013, Wang et al. 2016). Our results show that this

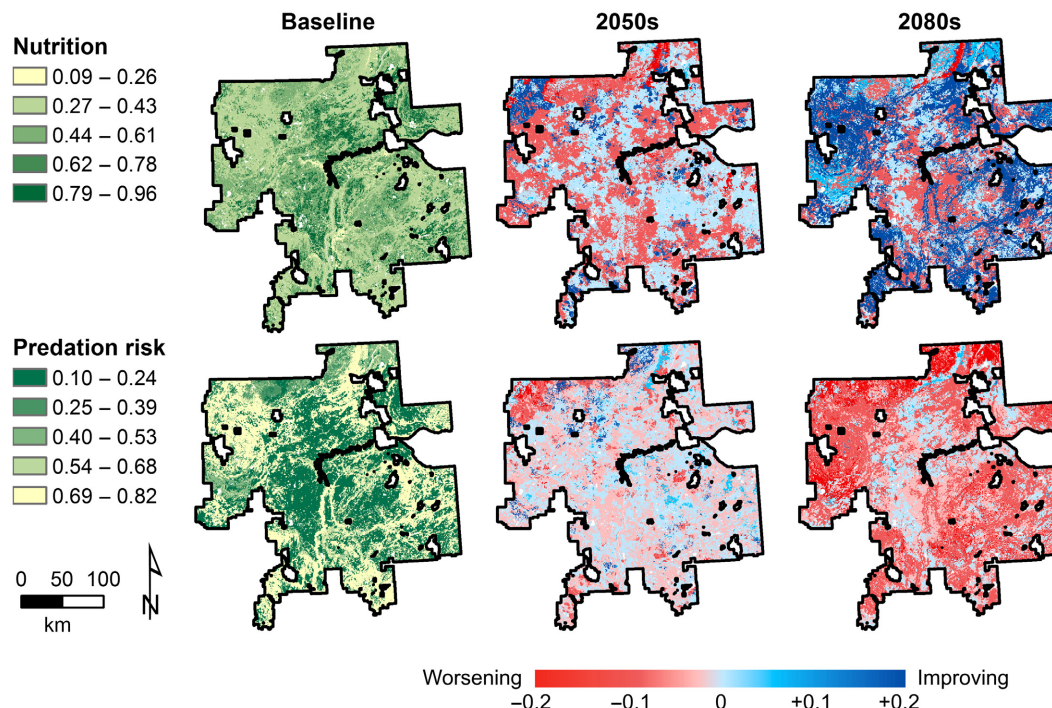


Fig. 5. Maps of habitat-quality modules from the CanESM2 scenario for the baseline period, the 2050s, and the 2080s. Delta maps indicate change in index, with red indicating worsening conditions for caribou and blue indicating improving conditions. Other GCMs are presented in Appendix S1.

effect will end by the 2080s as the climate begins to resemble the modern prairie and parkland regions, driving grasslands to expand and replace deciduous forest. Caribou would not be expected to persist long term in grassland systems, considering their current habitat; however, given climatic resilience of forests and the patchiness of wildfire patterns, it would seem unlikely that coniferous forests will disappear entirely from the uplands (Whitman et al. 2018).

Our conclusions depend on the assumption that key caribou habitat (forested peatlands) persists into the 2100s, given their resilience to warming and drying trends (Waddington et al. 2015, Schneider et al. 2016, McLaughlin et al. 2017). Low-lying coniferous forests, in particular treed fens and bogs, are crucial for caribou as a source of winter forage and as refugia from wolves (Rettie and Messier 1998, Shepherd 2006). Our vegetation models prohibit change in these environments, and consequently, habitat-quality changes within the WSAR and ESAR ranges are relatively modest; however, linear anthropogenic features threaten these late-seral

habitats with increasing fragmentation, exposing them to elevated predation and disease risk from sources originating in the uplands, even though peatlands are comparatively resilient to climate change. In light of this, our estimates of future caribou habitat suitability should be viewed as conservative, and it is possible that fire and other disturbances will reduce the availability of high-quality habitat further than is modeled here.

Several authors have explored less conservative fire scenarios based strictly on future climate conditions (i.e., independent of fuels) and have reported an explosive increase in fire frequency and area burned. As examples, Boulanger et al. (2014) reported a 370% increase in modeled annual area burned and a 300% increase in number of fires, and Flannigan et al. (2005) found increases of 74–118% in modeled annual area burned (also, Wang et al. 2016). Under such large increases in fire extent and frequency, the landscape would transition more rapidly from mature coniferous forest to extensive grassland regions with relatively small islands of unburned forest.

Shifts in modeled landscape drivers

Predation risk and nutritional value were negatively correlated in the baseline period, but are positively correlated in the future, particularly in grassland-dominated portions of the landscape. This changing relationship may have implications of caribou ecology as they seek to maximize their fitness, alternately attracting them to new forage opportunities or driving them away from open landscapes and associated predation risk. However, our habitat-quality index is dependent on our expert-driven weighting factors, which are necessarily subjective and uncertain. Therefore, it is important to consider the individual components of our index, not just the combined habitat-quality value.

While observed population declines (Hervieux et al. 2013) may paint a bleak picture for the future of some populations of boreal caribou, our models highlight that nutritional resources are unlikely to become limiting in the study area. Our models result in a widespread but modest increase in nutritional resources when averaged across the study area. Caribou consume a wide variety of forage species, including lichens, deciduous shrubs, forbs, fungi, and graminoids (Denryter et al. 2017). Expanding grasslands may actually increase the availability of forage for caribou by displacing mixedwood and deciduous forests, albeit at the cost of increasing predation and disease risk.

Depending on the yearly weather variability, climate change may also aid caribou in accessing ground forage by shortening winters and decreasing average snowpack depth (IPCC 2013), since caribou typically access ground forage by cratering or digging through overlying snow (Bradshaw et al. 1995). Alternately, repeated freeze-thaw cycles and rain-on-snow events could form a layer of ice on the snowpack (Dau 2005, Joly et al. 2009), preventing access to underlying forage, including lichens. Although not captured by our model, these phenomena could significantly impact the availability of forage during winter.

Through further anthropogenic habitat destruction and climate-induced vegetation cover change, rising predation likely represents the greatest risk for caribou populations in the near future. Grassland vegetation types and early-seral forests provide less cover for caribou than mature forests, and there is evidence from southern

forests that white-tailed deer frequently forage in grasslands near forest edges (Beier and McCullough 1990). Therefore, the novel boreal grasslands are likely to be associated with white-tailed deer (Côté et al. 2004) and wolves (Latham et al. 2011b). High mortality is the limiting factor for many populations of boreal caribou (McLoughlin et al. 2003, DeMars and Boutin 2017, Rudolph et al. 2017), and increasing predation and disease risk is the primary factor in our projected decrease in overall habitat-quality. Thus, increased disease, in the form of chronic wasting disease and brain worm, as well as greater predation would offset the apparent gains in habitat-quality associated with more nutritious spring and summer forage. This will depend on the frequency of wolves entering peatlands, which have historically acted as refugia from predators (Rettie and Messier 1998, Shepherd 2006), and whether these peatlands continue to be fragmented by anthropogenic features (Latham et al. 2011c, DeMars and Boutin 2017).

SCOPE AND LIMITATIONS

This study was intended as an exploratory investigation into the future of caribou habitat across a portion of the boreal forest in western Canada. Our findings provide new insights into the relationship among future vegetation cover change, fire regime, and habitat-quality. There is a substantial amount of uncertainty in predictions of future fire behavior within novel vegetation communities, and considering that uncertainty, we make two conservative assumptions: that the number of fire-conducive days (i.e., duration of burning) did not increase from the baseline period and that the number of ignitions did not increase from the baseline period. This decision was justified as it is highly uncertain how wildfire activity will respond to changes in vegetation in the study area, especially if the already intense fire suppression policies are maintained or expanded. For example, it is uncertain whether fires in future grasslands will smolder overnight in extant coniferous stands, or whether they will self-extinguish, which would reduce average fire duration in a landscape with extensive grasslands. Similarly, it is uncertain whether fewer fires will escape initial suppression activities, given that it is likely

there will be less forested area in the future (Schneider et al. 2009).

Bioclimatic models, which drive our vegetation cover projections, are a necessary approximation and assume vegetation cover is in sync with climate. Change in vegetation will likely lag behind changes in climate (Camill and Clark 2000), and our projections should be interpreted as an approximation of future vegetation. In reality, vegetation may take decades to centuries longer to reach the steady state modeled here, largely due to the climatic resilience of mature trees (Schneider et al. 2016). However, our method of modeling vegetation change in the context of wildfire is a significant improvement over models that project rapid changes solely as a function of climate envelopes. We were not able to account for other sources of disturbance, such as forest pests or expanding anthropogenic footprint. Furthermore, we assume that all lowland vegetation types will not change during the study period but that changes in adjacent upland environments will affect caribou in spite of their preference for lowland environments. Dealing with imperfect data, uncertainty, and simplified model relationships is unavoidable in research designed to project future conditions; however, our projections should be interpreted as a plausible, long-term future scenario.

We used empirical data in the form of published resource selection functions, where available, to parameterize the caribou habitat-quality modules. Although there is a large body of literature focused on caribou ecology, we still needed to rely on expert knowledge and a qualitative interpretation of previously-reported coefficients to develop the nutrition and predation and disease risk modules. We based our parameterization on plausible relationships, but we were not able to validate these hypothesized parameters. Such an approach is justified when considering novel ecosystems and vegetation lags, as empirical predictions may not remain accurate for future conditions. In particular, further information is needed on how woodland caribou and white-tailed deer will utilize future grassland environments and different forest age classes (see Appendix S3).

Several important components of caribou ecology were not modeled, either to limit the complexity of the study, or because they were largely

unpredictable. First, we did not attempt to represent adaptive or maladaptive components of caribou biology and ecology relative to climate and vegetation change. We only considered changes in the abundance of white-tailed deer and associated diseases, and not in other species that may impact predation risk and disease. In considering white-tailed deer abundance, we make the implicit assumption that an expansion of habitat favorable to white-tailed deer will result in an increase in white-tailed deer abundance, thereby leading to an increase in wolf populations and higher risk of disease transmission to caribou. In the case of meningeal worm, we did not model the resource and climatic restrictions of the intermediate host, a number of poorly-studied gastropods (Anderson 1972). Also, *Rangifer* is a genus that is adapted to cold environments, but we did not model changes to snow conditions, biting insect abundance, or the impacts of a warmer climate on thermoregulation, which are known to play a role in caribou behavior and survival (Couturier et al. 2009, Raponi et al. 2018). Very little information is available on the relative importance of forage availability and predator avoidance for Alberta caribou; therefore, habitat-quality analyses are subjective and rely on sensitivity analysis rather than empirical data. Finally, integrating future changes in anthropogenic development would be a valuable addition to these projections. Future seismic line footprint will depend on resource prices, land management, and restoration practices, all of which are outside of the scope of this paper. Despite the exploratory nature of the study, it is a first step toward integrating climate change and disturbance into assessments of future habitat-quality, and these findings should provide insight into the nature of the threat facing caribou.

CONCLUSION

Our simulations suggest that vegetation change in the study area will be widespread by the 2080s, even when accounting for vegetation inertia in wetland areas. The transition of mixed-wood forest into grassland will likely lead to significant increases in predation and disease risk, factors which will prove a challenging obstacle for caribou population recovery. Treed peatlands may provide caribou with persistent forage and predator refugia, although fragmentation and

eventually wildfire will limit their long-term effectiveness. We projected a minor improvement to average nutritional resources for caribou in the study area, although increased white-tailed deer and wolf populations may render such nutritional resources meaningless. This type of modular modeling approach provides outcomes that, albeit highly uncertain at present, can be built upon as our understanding of woodland caribou ecology grows. It will hopefully become a useful and important tool—among others—in the pressing need for widespread woodland caribou conservation in Canada.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2472/full>