Global Ecology and Conservation 39 (2022) e02294

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

There is still time to reconcile forest management with climate-driven declines in habitat suitability for boreal caribou

Mathieu Leblond[a,*], Yan Boulanger[b], Jesus Pascual Puigdevall[b], Martin-Hugues St-Laurent[c]

[a] *Science and Technology Branch, Environment and Climate Change Canada, Ottawa, ON, Canada*
[b] *Laurentian Forestry Centre, Canadian Forest Service, Natural Resources Canada, Québec, QC, Canada*
[c] *Département de biologie, chimie et géographie and Centre for Forest Research, Université du Québec à Rimouski, Rimouski, QC, Canada*

ARTICLE INFO

Keywords:
Climate change
Climate scenarios
Habitat loss
Human disturbance
Rangifer tarandus
Timber harvesting
Woodland caribou

ABSTRACT

Many boreal populations of woodland caribou in Canada are declining, mainly due to the prevalence of anthropogenic disturbances which alter predator-prey dynamics. Climate change is expected to exert an additional negative influence on caribou populations in coming decades, but it is unclear whether or how human activities and climate change will interact to influence habitat suitability for caribou, and how important these agents of change will be relative to each other. In this study, we used the LANDIS-II forest landscape model to forecast boreal caribou habitat suitability across its distribution within the harvestable boreal forest in Québec for the period 2020–2100, under three increasing anthropogenic radiative forcing scenarios (baseline, Representative Concentration Pathways [RCP] 4.5 and 8.5), and two contrasting harvest scenarios (with and without harvest). Our simulations revealed that harvesting was the dominant agent explaining future variations in caribou habitat suitability, although climate change also decreased habitat suitability, especially under RCP 8.5. Climate-induced decreases in habitat suitability mostly originated from increases in wildfires that burned mature conifer-dominated forests, i.e., high-quality habitat for caribou. Habitat suitability by 2100 was also predicted to vary spatially, with the northeastern and northwestern parts of the study area supporting better caribou habitat conditions regardless of scenarios. We show that reducing harvest activities in areas where habitat suitability is currently high could help maintain high-quality caribou habitat even under the most intense climate change scenario. Our results also suggest that highly-disturbed regions which currently provide low-quality habitat may not improve in the future unless active habitat restoration is performed. Our study helps disentangle the potential future effects of forest management and climate change as threats to caribou habitat, emphasizing the urgency of reconciling forest management with the conservation of this species at risk in Canada.

1. Introduction

Habitat loss and climate change are among the greatest threats to ecosystems and biodiversity (Travis, 2003) and largely contribute to the rapid rate of extinction of wildlife around the world (Ceballos et al., 2015; WWF, 2020). Many countries have enacted legislation

---

* Correspondence to: National Wildlife Research Centre, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada.
E-mail address: mathieu.leblond@ec.gc.ca (M. Leblond).

https://doi.org/10.1016/j.gecco.2022.e02294
Received 4 May 2022; Received in revised form 22 September 2022; Accepted 26 September 2022

for the protection of endangered species to put a stop to these extinctions. In Canada, the federal government is responsible for the development of recovery strategies for species at risk under the Species at Risk Act (S.C. 2002, c.29). In 2012, Environment Canada (EC) published the recovery strategy for the woodland caribou (*Rangifer tarandus caribou*), boreal population (hereafter boreal caribou), a species of conservation concern across its entire distribution. The recovery strategy identified critical habitat for 50 local populations of boreal caribou in Canada, most of which were deemed unlikely to be self-sustaining in the long term (EC, 2012). This generalized decline was mainly attributed to the ubiquity of anthropogenic disturbances in boreal caribou ranges, which largely favors predators and increases predation pressure on caribou (Wittmer et al., 2007; EC, 2011). Landscape-level planning and local restoration efforts were identified as essential steps for the successful recovery of this species. The Canadian Government also proposed a management threshold, i.e., the reduction of areal disturbances (from both natural and anthropogenic sources) below 35% over any population range, which, on average, should grant a 60% probability of maintaining a self-sustaining population (EC, 2011; 2012). This threshold was chosen as a compromise to limit the negative impacts of anthropogenic disturbances on boreal caribou while preserving some level of human land-use activities in caribou ranges. However, the recovery strategy for boreal caribou is relatively quiet about potential actions to mitigate impacts of climate change, a characteristic that it shares with many other recovery strategies for species at risk in Canada (Naujokaitis-Lewis et al., 2021) and the world (Hoeppner and Hughes, 2019).

Climate change will likely pose a threat to the long-term persistence of boreal caribou in Canada (e.g., Murray et al., 2015; Barber et al., 2018; Neilson et al., 2022; Palm et al., 2022). Boreal regions in North America are currently warming at least twice as fast as the rest of the world on average, with further warming projected to reach + 4 to + 8 °C by the end of the 21st century (Price et al., 2013). Climate change could negatively influence boreal caribou by modifying forest landscapes and large mammal communities, with potential impacts on habitat and predator-prey interactions (Barber et al., 2018). For instance, climate-induced increases in wildfires could increase the availability of early seral stands of deciduous trees (e.g., trembling aspen *Populus tremuloides*, white birch *Betula papyrifera*) which are most favorable to alternate prey such as moose *Alces alces*, at the expanse of old-growth coniferous stands preferred by caribou (Racey, 2005; but see DeMars et al., 2019). Further temperature increases in the southernmost parts of the boreal caribou distribution range, where remnant populations are on the brink of extinction after decades of anthropogenic pressure (e.g., Vors et al., 2007; Rudolph et al., 2017), could favor thermophilous deciduous species to the detriment of coniferous stands (Boulanger and Pascual Puigdevall, 2021). Within managed forests, climate-induced changes in caribou habitat could cumulate – and potentially interact – with timber harvesting (St-Laurent et al., 2022), leading to new landscape conditions typical of more temperate climates (Price et al., 2013). These new conditions could favor species such as white-tailed deer *Odocoileus virginianus*, thereby increasing the risk of spread of fatal neurological diseases such as *Parelaphostrongylus tenuis* or chronic wasting disease to caribou (Racey, 2005; Arifin et al., 2020). It remains unclear how current conservation strategies will perform under rapid climate-induced changes in forested landscapes. Thus, improved knowledge regarding the relative influence of anthropogenic disturbances and climate change is urgently needed to assist recovery actions for boreal caribou.

Ecological models are useful tools to predict future environmental conditions under specific assumptions, and can support conservation planning (Travers et al., 2019). Forest landscape models have been used to assess harvesting and climate change impacts on various wildlife species in the boreal forest (e.g., Tremblay et al., 2018; Micheletti et al., 2021), including caribou (St-Laurent et al., 2022). Similarly, habitat suitability models have been used to map habitat and predict the distribution of threatened species (Cianfrani et al., 2010) such as caribou (Leblond et al., 2014). Combining a forest landscape model with a habitat suitability model for boreal caribou would offer a unique opportunity to assess the cumulative and interactive impacts of timber harvesting and climate change. This work would enhance our collective knowledge on the complex relationships linking human disturbances, climate, and boreal caribou distribution presently (Neilson et al., 2022) and into the future (St-Laurent et al., 2022).

In this study, we assessed temporal and spatial trends in boreal caribou habitat suitability across its distribution within Québec's commercial forest (i.e., lands subject to industrial timber harvesting; Jobidon et al., 2015) over the 2020–2100 horizon. To do so, we combined a forest landscape model developed in LANDIS-II by Boulanger and Pascual Puigdevall (2021) with a habitat suitability model for boreal caribou developed by Leblond et al. (2014). Our objectives were to 1) simulate future habitat suitability for boreal caribou according to different forest management and climate change scenarios, and 2) assess the relative importance of each agent of change, i.e., timber harvesting and climate change, on variations in habitat suitability for boreal caribou occurring in the commercial forests of Québec. We developed our simulations at scales relevant for caribou management and conservation by summarizing them both globally and across six local boreal caribou ranges. We predicted that spatially heterogeneous changes in climate regimes combined with dissimilar initial habitat conditions would generate variability in the relative importance of agents of change across local populations. For instance, drier conditions in northwestern Québec are predicted to cause more wildfires, resulting in sharp shifts in forest age structure and composition (Boulanger and Pascual Puigdevall, 2021). Conversely, in moister regions such as northeastern Québec, fire activity is expected to be low, likely resulting in subtler changes in habitat suitability for boreal caribou. Results obtained at the broadest distribution range scale are also relevant as they may help identify potential “climate refugia” (i.e., areas that could maintain high-quality habitat locally despite global changes in climate; Stralberg et al., 2015). With this study, we aimed to better understand the effects of timber harvesting and climate change on boreal caribou habitat suitability across one of the largest areas ever simulated in a forest landscape model, to provide recommendations for actions that, if implemented now, would aid conservation of this species-at-risk in the context of land use and climate change.

2. Material and methods

2.1. Study area

We simulated changes in forest landscapes over the area covered by the habitat suitability model developed by Leblond et al. (2014), which included the entire commercial forest in the province of Québec (56.4 M ha). However, contrary to Leblond et al. (2014), we restrained analyses to the balsam fir (*Abies balsamea*) – yellow birch (*Betula alleghaniensis*), balsam fir – white birch, and black spruce (*Picea mariana*) – feather moss bioclimatic subdomains, because boreal caribou are extirpated from the southernmost temperate ecosystems. This generated a final study area of 368,186 km^2 (Fig. 1) encompassing the entire distribution of boreal caribou on lands subject to industrial timber harvesting. In this area, valleys covered by glacial till and humo-ferric podzols are intermingled with broadly rolling mosaics of upland plateaus at 200 – 800 m above sea level. Landform and soils are dominated by uplands and wetlands, where Precambrian granitic bedrock outcrops alternate with ridges encompassing coarse texture hummocky deposits of glacial origin. In the southern part of the study area, climate was more typical of the temperate continental region, whereas the northern part was more typical of boreal regions. As such, the study area covered wide latitudinal and longitudinal temperature gradients (mean annual temperature: south = 6.6 °C, north = −3.1 °C; total annual precipitation: west = 600 mm, east = 1200 mm; Robitaille and Saucier, 1998). A wide variety of forest ecosystems occurred within the area. Deciduous forests gradually transitioned to mixed and finally to conifer-dominated forests with increasing latitude. Recurrent spruce budworm outbreaks were the most prevalent natural disturbance in the mixedwood forest region (Boulanger et al., 2012), whereas wildfires were most frequent within the boreal portion, with fire return intervals ranging from ca. 400 years in the east to ca. 100 years in the drier, western part (Couillard et al., 2022). Timber harvest occurred at various rates over the entire study area, with cutblock size typically increasing with latitude (OIFQ, 2009). Single-tree and small-patch harvest were most prevalent in the deciduous stands found in the south of the study area, whereas cutblocks reaching more than several hundred hectares were more common in boreal forests (OIFQ, 2009).

Eight local population ranges (Assinica, Témiscamie, Piraube, Côte-Nord, Coeurs, Portneuf, Charlevoix, and Val-d′Or) were delineated by the Québec Government using 100% minimum convex polygons around locations of GPS-collared individuals. The Témiscamie and Piraube as well as the Coeurs and Portneuf ranges overlapped by 77.8% and 56.6%, respectively, so we merged them into the Témiscamie – Piraube and Coeurs – Portneuf populations, for a total of six local population ranges (Fig. 1). We excluded additional boreal caribou populations known to occur in Québec, e.g., the Nottaway and Manicouagan populations, as their ranges were largely composed of areas beyond the northern limit for timber allocation (i.e., outside the commercial forest *sensu* Jobidon et al.,

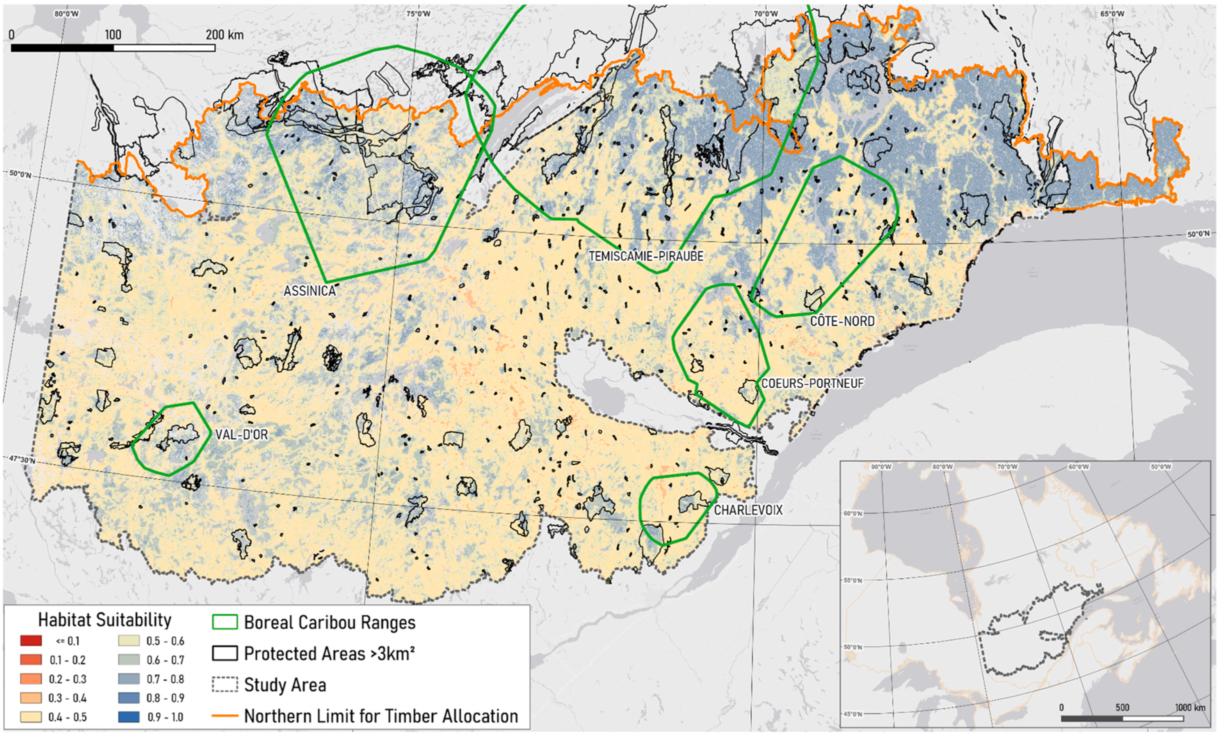

Fig. 1. Study area. Study area (dashed gray contour) in the commercial forest of Québec, Canada, where we estimated the habitat suitability index for boreal caribou by converting a habitat suitability model (Leblond et al., 2014) into LANDIS-II. We summarized analyses globally, as well as across the ranges of six local boreal caribou populations delineated in 2017 (green contours). In this figure, blue pixels (habitat suitability index = 1) represent the most suitable areas, whereas red pixels (habitat suitability index = 0) represent the least suitable areas for boreal caribou in the study area. Protected areas > 3 km^2 and the northern limit for timber allocation (i.e., northern limit of the commercial forest in Québec) are also shown.

2015). The number of caribou monitored and the period during which they were monitored varied by population. This information, along with additional details on the capture and handling of animals, are available in Appendix A.

2.2. *Modelling framework*

In this study we combined two previously-published models on simulated forest landscapes (Boulanger and Pascual Puigdevall, 2021) and boreal caribou habitat suitability (Leblond et al., 2014). Boulanger and Pascual Puigdevall (2021) simulated changes in forest composition and structure over time across all lands subject to industrial timber harvesting in Québec using LANDIS-II v. 6.2, a spatially-explicit raster-based forest landscape model that simulates disturbances, tree seed dispersal, and forest succession (Scheller et al., 2007). Leblond et al. (2014) developed a habitat suitability model for boreal caribou based on expert opinion and validated it using empirical data. This model weighed the relative importance of natural habitat types and human infrastructure for boreal caribou habitat suitability across a similarly broad landscape. This model identified mature conifer-dominated forests ≥ 70 years old and open woodlands as preferred habitat for boreal caribou (i.e., high-quality habitat), and identified proximity to roads and mines as deteriorating factors. A complete description of the habitat suitability model and how it was validated can be found in Leblond et al. (2014). We combined the two models by applying the habitat suitability model to the forest landscape model developed in LANDIS-II, and assessed how habitat suitability for boreal caribou responded to various scenarios of climate and land use change for the horizon 2020–2100.

During our simulations, we had to separate the study area into smaller parts because of computational constraints. We did so by dividing the study area into five bioclimatic sub-domains. We added a 50-km buffer around each sub-domain to consider seed dispersal and other landscape processes that might occur at the edges (Boulanger and Pascual Puigdevall, 2021). We simulated the five sub-domains and their overlapping buffers independently, and then combined results by averaging values in overlapping buffers to generate the final modelling extent across the whole study area. We used a 250-m cell resolution (6.25 ha) for all analyses.

2.3. *Climate data and climate scenarios*

We interpolated monthly time series of current climate from climate station data produced by McKenney et al. (2013). The baseline climate scenario corresponded to the climate observed during the 1981–2010 period. We obtained future climate projections from the Canadian Earth System Model v. 2 (CanESM2). We restrained future projections to two distinct climate change scenarios known as Representative Concentration Pathways (RCP) 4.5 and 8.5 (van Vuuren et al., 2011), which respectively assume that radiative forcing (i.e., the imbalance in Earth's radiation input vs. output) will reach 4.5 $W{\cdot}m^{-2}$ and 8.5 $W.m^{-2}$ by 2100. We used these two projections to provide a range of potential outcomes, as there is no consensus currently on which scenario is most likely to describe future climate (Hausfather and Peters, 2020; Schwalm et al., 2020). Compared to year 2000, the mean annual temperature over the entire study area was predicted to increase by approximately 3.9°C (RCP 4.5) or 8.5°C (RCP 8.5) by 2100. Total annual precipitation was projected to increase by 7 (RCP 8.5) to 10% (RCP 4.5). We bias-corrected CanESM2 data for the 2020–2100 period by expressing them as differences from (temperature) or ratios of (precipitation) monthly means for the 1961–1990 period.

2.4. *Forest landscape simulations*

In LANDIS-II, tree species are defined using unique life-history attributes and are represented in each grid cell as age cohorts in 10-year increments. We initialized forest composition and structure in each 250-m cell using forest properties data derived from the Canadian National Forest Inventory and cohort data from permanent and temporary forest inventory plots. We assigned cells to a specific spatial unit (i.e., "ecoregion") in which soil (see Sylvain et al., 2021) and climate conditions were considered homogeneous. Ecoregions are further described in Boulanger and Pascual Puigdevall (2021) and were delineated using ecological districts in Robitaille and Saucier (1998). We removed cells with less than 50% forest cover from simulations ($n = 1262{,}800$, or 21.4%). Removed cells were largely represented by water bodies, and to a lesser extent rocky outcrops, agricultural fields, and urban areas. More details regarding the calibration and validation of simulations can be found in Boulanger and Pascual Puigdevall (2021).

We used the LANDIS-II Biomass Succession extension v. 3.1 (Scheller, 2013) to simulate forest succession in each cell. This module considers cohort age, life-history traits, and species autecology (see Appendix B, Table B.1) as well as ecoregion- and climate-specific growth and reproduction parameters, to simulate changes in cohort biomass over time as each cohort regenerates, ages, and dies. We used PICUS v. 1.5 (Lexer and Hönninger, 2001; Taylor et al., 2017), a forest gap model, to obtain three sets of species-, climate-, and ecoregion-specific dynamic inputs used in the Biomass succession extension, namely *i*) species establishment probabilities, *ii*) maximum aboveground net primary productivity, and *iii*) maximum aboveground biomass. A complete description of PICUS can be found in Taylor et al. (2017). We derived climate- and soil-sensitive parameters for the 17 most common tree species occurring in the study area (Appendix B, Table B.2) for each ecoregion and climate conditions projected to occur in our scenarios.

2.5. *Natural and anthropogenic disturbance simulations*

We simulated fire, spruce budworm outbreaks, and windthrows as natural disturbances in LANDIS-II. We simulated fires as stochastic events using the Base Fire v. 3.0 extension (Scheller and Domingo, 2011). Fires occurred at frequencies and burned across areas corresponding to specific fire regime information, based on the Canadian homogeneous fire regime zones (Boulanger et al., 2014). We calibrated baseline (we used the 1961–1990 period for baseline fire) and future fire regime parameters within each fire region according to projections made by Gauthier et al. (2015) and we further updated them to consider the negative feedback of fire activity on stand age following Boulanger et al. (2017). We simulated spruce budworm outbreaks using the BDA v. 3.0 extension modified to account for specific budworm parameters (Sturtevant et al., 2004). We simulated outbreaks as probabilistic events at the cell level with probabilities and impacts as a function of the site and neighbourhood host abundance and vulnerability. Potential hosts included balsam fir and black and white spruce. We simulated windthrows using the Base Wind v. 2.0 extension (Mladenoff and He, 1999).

We simulated harvest using the Biomass Harvest extension v. 2.2 (Gustafson et al., 2000). We used harvest parameters developed by Boulanger et al. (2019) to simulate harvest throughout the study area. Briefly, we simulated large (150 ha) irregular shelterwood cuts and clearcuts, which respectively removed 40% and 90% of the biomass in ≥ 60-year-old coniferous and ≥ 80-year-old deciduous stands. We set minimum time between two shelterwood cuts on a given pixel to 30 and 40 years in coniferous and deciduous stands, respectively (OIFQ, 2009). Stands to be harvested were randomly selected among those that met harvesting criteria (i.e., minimum age according to the specific prescription). Cuts retrieved a fixed proportion of each forest management unit at each time step. When the proportion of harvestable stands available in a given forest management unit was lower than this fixed proportion, harvesting continued until no harvestable stands were left. We did not allow harvest operations in national and provincial parks, as well as in other types of protected areas where timber harvesting is prohibited (see Fig. 1).

2.6. *Timber harvesting and climate change scenarios*

We ran simulations across a factorial design, using two harvest scenarios (with and without harvest) in interaction with three climate change scenarios (baseline, RCP 4.5 and RCP 8.5). It is unlikely that timber harvesting or global warming will cease in the near future; however, we included baseline climate (i.e., in which climate-sensitive parameters did not change) and “no harvest” scenarios to better unravel the influence of agents of change relative to each other. For each combination of harvest and climate change scenario, we ran five simulation iterations over 80 years, starting in 2020 and ending in 2100, using a 10-year time interval. Except for scenarios involving the baseline climate, we allowed fire regime parameters to change in 2040 and 2070, thereby generating three periods with distinct fire regimes: 2011–2040, 2041–2070 and 2071–2100. We allowed dynamic growth and establishment parameters (species establishment probabilities, maximum aboveground net primary productivity, and maximum aboveground biomass) to change according to climate scenarios at the same years. We simulated spruce budworm outbreaks to occur every 40 years (i.e., 2021–2030 and 2061–2070) to fit observed regional recurrence cycles in our study area (Boulanger et al., 2012). Windthrows occurred under a mean return interval of 2500 years (OIFQ, 2009), with 0.4% of active cells being affected by a stand-replacing windthrow at each 10-year step.

2.7. *Impact of scenarios on habitat suitability for boreal caribou*

For the purposes of our analyses, we defined dynamic forest cover classes as those that were allowed to change over time throughout our simulations. These were *i*) old coniferous and mixed stands ≥ 70 years old, *ii*) coniferous and mixed stands 50–70 years old, *iii*) open woodlands (typically rich in terrestrial lichens), *iv*) harvested stands (<20 years, and where at least 60% of the biomass was harvested, thus excluding all partially harvested stands), *v*) natural disturbances, and *vi*) regenerating stands (≥20 years but <50 years after a disturbance; deciduous stands <120 years old). These dynamic forest cover classes closely matched those in the habitat suitability model for caribou (Leblond et al., 2014). We translated LANDIS-II outputs into dynamic forest cover classes using species-specific tree biomass, stand age, natural disturbance and harvest simulation results at the 250-m pixel level. Initial conditions for each of these dynamic forest cover classes are presented in Appendix A. Some cells (7.6%) could not be dynamically simulated by LANDIS-II. These cells, found in wetlands and existing open woodlands, were left static because no models were available to realistically simulate their spatial distributions following changes in climate and land use, at the scale of our study area. We included these cells in the calculation of the habitat suitability index due to the importance of these land cover classes for caribou. Moreover, human infrastructures were not allowed to change during the course of the simulations and were also considered static. We calculated habitat suitability at the pixel-level (hereafter the habitat suitability index) under all scenario combinations and at each 10-year step. We normalized (rescaled between 0 and 1) values obtained at the study area level under conditions prevailing in 2020. To estimate temporal and spatial trends in caribou habitat suitability, we measured the difference between projected and initial values. In other words, positive and negative habitat suitability index values respectively represent increases and decreases in predicted habitat suitability for boreal caribou compared to initial conditions in 2020. Initial habitat suitability values prevailing at the onset of simulations are described in Appendix A for the whole study area as well as the ranges of six local boreal caribou populations.

We validated the LANDIS-II version of the habitat suitability model across the study area by overlapping the original habitat suitability model developed by Leblond et al. (2014) in a geographic information system using 1:20,000 ecoforest maps provided by the Québec Government. We compared habitat suitability values from both models at the 250-m pixel level ($n = 6{,}533{,}286$) in 2020. We computed major-axis regression parameters (Legendre and Legendre, 2012), and found that outputs from both models were highly correlated ($R^2 = 0.74$, Appendix C), despite a slight temporal mismatch between the two models. The LANDIS-II version of the habitat suitability model slightly underestimated high habitat suitability values (slope of the major axis = 0.635) compared to the original model (Appendix C).

We averaged habitat suitability index values across simulation iterations pertaining to each climate and harvest scenario to produce study-area-wide maps of caribou habitat suitability at each time step. We created maps by estimating the proportion of each dynamic forest cover as well as habitat suitability indices within a 100-ha moving window and smoothing the results. We assessed temporal trends in dynamic forest cover and caribou habitat suitability in the study area according to each harvest and climate scenario. We report standard deviation from the mean of simulation iterations in Appendix D for both temporal and spatial trends in habitat suitability. Deviations originated from stochastic parameters, including probabilities of fire, spruce budworm epidemics, and tree reproduction and establishment. Other sources of uncertainty, e.g., spatial variation in the ability of the caribou habitat suitability model to correctly predict the locations of GPS-collared animals (validation *sensu* Leblond et al., 2014), were not considered in this study.

2.8. Relative importance of timber harvesting vs. climate change

We assessed the importance (effect size index; Albers and Lakens, 2018) of each agent of change, i.e., timber harvest and climate change, on variations in habitat suitability for boreal caribou in our study area. We measured importance (ω^2) using a 2-way factorial ANOVA where we considered harvest and climate change as factors. We calculated specific ω^2 values at each time step, for each landscape unit, using:

$$\omega^2 = [SS_i - (df_i)\times(MS_{error})] \,/\, [MS_{error} + SS_{tot}]$$

where SS_i is the sum of squares of agent of change *i* (i.e., harvest or climate change), df_i is degrees of freedom, MS_{error} is the mean square of the error and SS_{tot} is the total sum of squares. We performed the ANOVA and ω^2 calculations at the ecoregion scale for each simulated iteration in R v.3.6.3 (R Core Team, 2019).

Similar to dynamic forest cover and habitat suitability index, we compiled and mapped temporal trends in importance for the whole study area as well as across the six local boreal caribou ranges. We area-weighted ecoregion-level importance of each agent of change over each range. Results are expressed relative to those obtained under baseline climate and with harvest, also called the reference scenario.

3. Results

3.1. Dynamic forest cover projections

Both harvest and climate change influenced dynamic forest cover in our projections. In general, increasing radiative forcing from 4.5 to 8.5 $W{\cdot}m^{-2}$ resulted in more abundant regeneration and naturally disturbed stands and decreased coniferous and mixed stands 50 years and older (Fig. 2; see Appendix E for changes in dynamic forest cover by local population ranges, and Appendix F for spatial patterns in dynamic forest cover classes across the study area). Old coniferous and mixed stands $\geq$ 70 years old were the most reduced forest cover under strong climate change (i.e., under RCP 8.5) relative to the reference scenario (i.e., under baseline climate with harvest), whereas naturally disturbed areas concomitantly increased the most. These variations were strongest in the northern and central parts of the study area (Appendix F). Predictably, stopping harvest decreased the proportion of the study area covered by regenerating stands and increased coniferous and mixed stands (Fig. 2, Appendix E). Without harvest and under baseline climate, the proportion of old coniferous and mixed stands $\geq$ 70 years old increased by $>$ 30% on average. When including climate change a similar increase was observed but only in the southern and northeastern parts of the study area (Appendix F). Climate- and harvest-induced variations in open woodlands were minimal. We predicted declines in the proportion of harvested stands in northcentral Québec under increased climate change compared to the reference scenario, a phenomenon that was essentially driven by a decrease in the availability of harvestable stands resulting from increased wildfire activity.

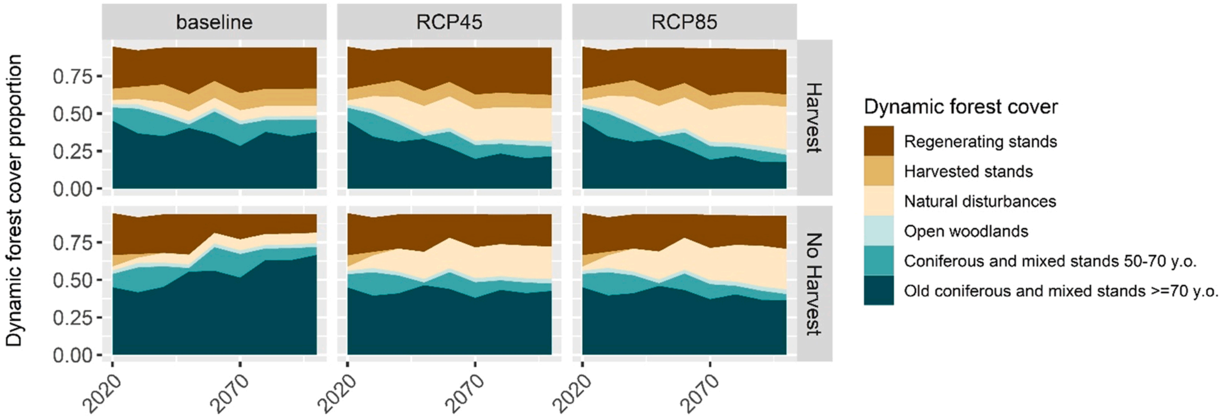

Fig. 2. Temporal trends in dynamic forest cover proportions. We used dynamic forest cover proportions to forecast boreal caribou habitat suitability in the commercial forest of Québec, Canada, during the period 2020–2100. Dynamic forest cover proportions represent averages across five simulation iterations under two timber harvest (with or without harvest) and three climate change scenarios (baseline, RCP 4.5, RCP 8.5) at the study area scale.

3.2. Projected changes on boreal caribou habitat suitability

Both climate change and timber harvesting decreased habitat suitability for boreal caribou throughout the study area (Fig. 3A), as well as across the six local boreal caribou ranges (Fig. 3B, Appendix E). Under harvest, both climate change scenarios generally led to decreases in habitat suitability by 2100 compared to the baseline climate scenario (Fig. 4). Timber harvesting led to habitat suitability declines in all local ranges, even in those where habitat suitability index values were lowest at the onset of our simulations (Charlevoix, Coeur – Portneuf; Figs. 3B and 4). Among climate change scenarios, the largest reductions in habitat suitability were predicted to occur under RCP 8.5, especially in the northernmost part of the study area, in the ranges of the Assinica and Témiscamie – Piraube populations (Figs. 3B and 4). The noticeable drop in habitat suitability occurring in 2070 (Fig. 3) was related to a spruce budworm outbreak set to occur during the 2061–2070 time step. This outbreak decreased habitat suitability through a reduction in old coniferous and mixed stands ≥ 70 years old (also visible on Fig. 2), i.e., forest cover classes where outbreaks were parameterized to have the most severe impacts.

Stopping harvest completely helped mitigate climate-induced decreases in boreal caribou habitat suitability throughout the study area (Fig. 3). Most notably, the northeastern part of the study area which, in 2020, showed the highest habitat suitability for boreal caribou (Appendix A) remained highly suitable even under RCP 8.5 when harvest was stopped (Fig. 4, Appendix F). Similarly, in the southern part of the study area, but outside of the six local population ranges, scenarios under climate change but without harvest resulted in increased proportions of old coniferous and mixed stands ≥ 70 years old (Appendix F). Globally, the northeastern and northwestern parts of the study area showed the highest habitat suitability by 2100, despite relatively large climate- and harvest-induced decreases in habitat suitability (Fig. 4).

3.3. Relative importance of harvest and climate change

There were clear spatial gradients and temporal trends in the magnitude of effects of harvest vs. climate change on boreal caribou habitat suitability in our simulations. Spatially, harvest had a higher importance (i.e., higher ω^2) than climate change over most of the northeastern and northwestern parts of the study area, and more so under RCP 4.5 (Fig. 5). Conversely, climate change tended to have a higher importance than harvest in the northcentral part of the study area, where it generally explained between 40% and 80% of variations in habitat suitability by 2100, regardless of climate change scenario (Fig. 5). Globally, as well as at the scale of local

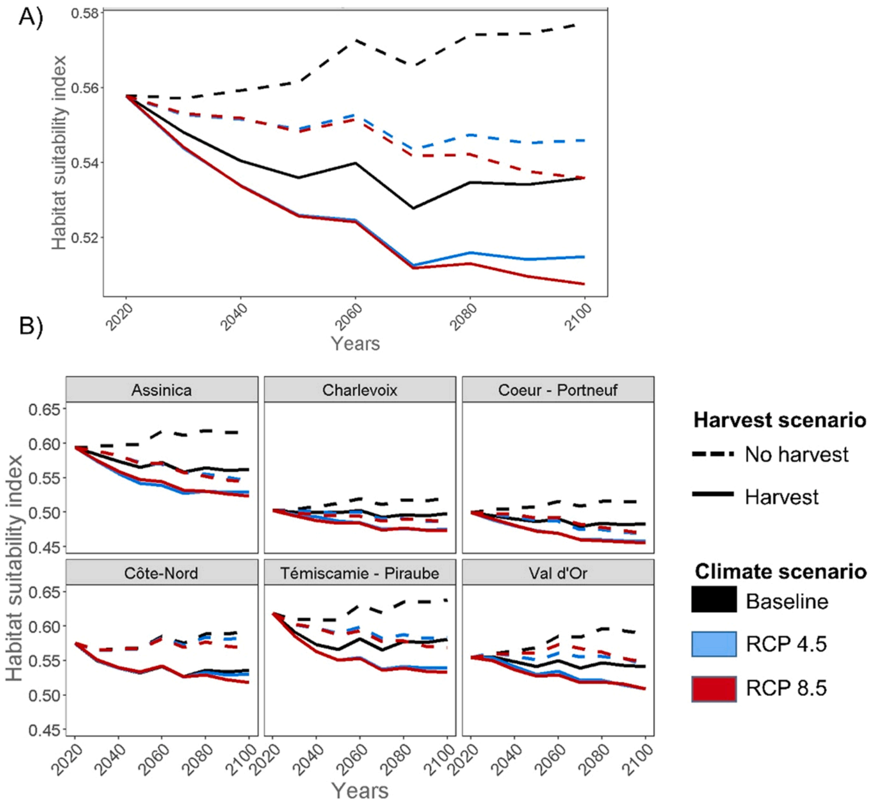

Fig. 3. Temporal trends in the boreal caribou habitat suitability index during the period 2020–2100. A) Temporal trends for the whole study area and B) for six local boreal caribou ranges in the commercial forest of Québec, Canada. The habitat suitability index represents the average of five simulation iterations under two timber harvest (with or without harvest) and three climate change scenarios (baseline, RCP 4.5, RCP 8.5).

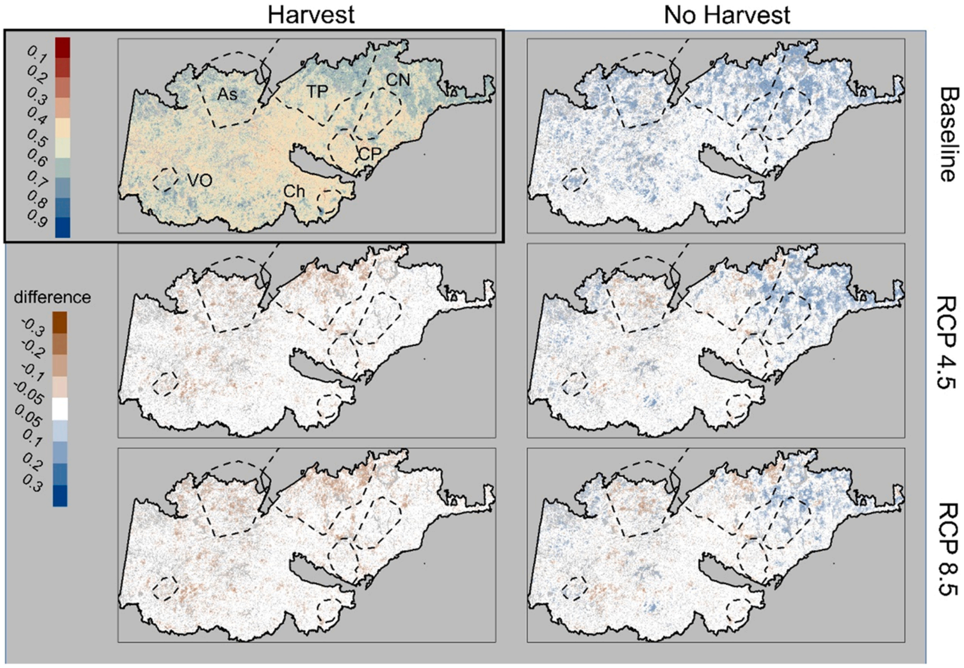

Fig. 4. Changes in the boreal caribou habitat suitability by 2100. Changes are relative to the reference scenario (top left) under two timber harvest (columns: with or without harvest) and three climate change scenarios (rows: baseline, RCP 4.5, RCP 8.5). For all scenarios other than the reference scenario, blue pixels indicate an increase, and red pixels indicate a decrease in average habitat suitability compared to the reference scenario. Local boreal caribou ranges, located in the commercial forest of Québec, Canada, are delineated using dashed lines. As: Assinica; Ch: Charlevoix; CN: Côte-Nord; CP: Coeurs – Portneuf; TP: Témiscamie – Piraube; VO: Val d′Or.

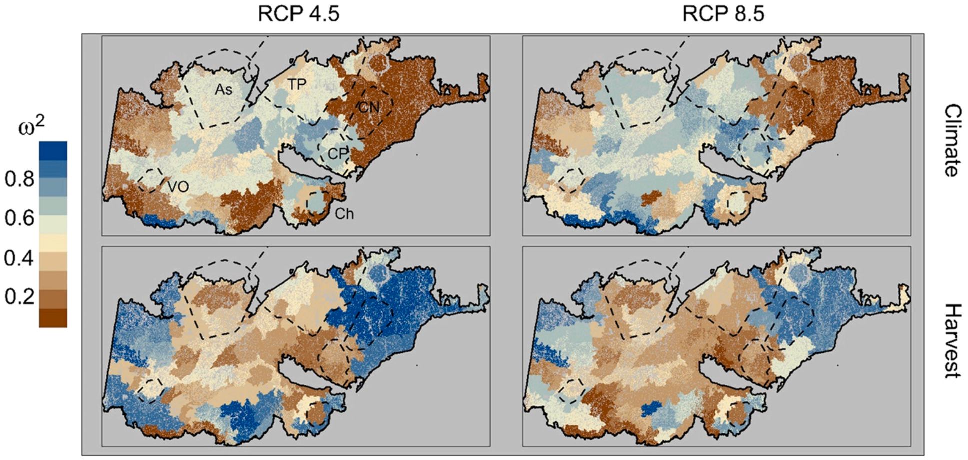

Fig. 5. Importance of harvest vs. climate change in 2100. Mean relative importance (ω^2) of climate change (top row) and timber harvest (bottom row) on boreal caribou habitat suitability at the ecoregion level under two climate change scenarios: RCP 4.5 (left column) and RCP 8.5 (right column). Ecoregions had homogeneous soil and climate conditions, explaining the apparent patchwork in the spatial distribution of importance (see Boulanger and Pascual Puigdevall, 2021), for details about ecoregions). Local boreal caribou ranges, located in the commercial forest of Québec, Canada, are delineated using dashed lines. As: Assinica; Ch: Charlevoix; CN: Côte-Nord; CP: Coeurs – Portneuf; TP: Témiscamie – Piraube; VO: Val d′Or.

population ranges, timber harvesting was the most important agent of change explaining boreal caribou habitat suitability at the beginning of our simulations (Fig. 6). The importance of harvest tended to decrease with time. Harvest remained the most important agent of change for the whole study area until the end of our simulations (RCP 4.5) or 2090 (RCP 8.5). Climate change replaced timber harvesting as the most important agent of change for four of the six ranges after 2070 or 2090 (Fig. 6).

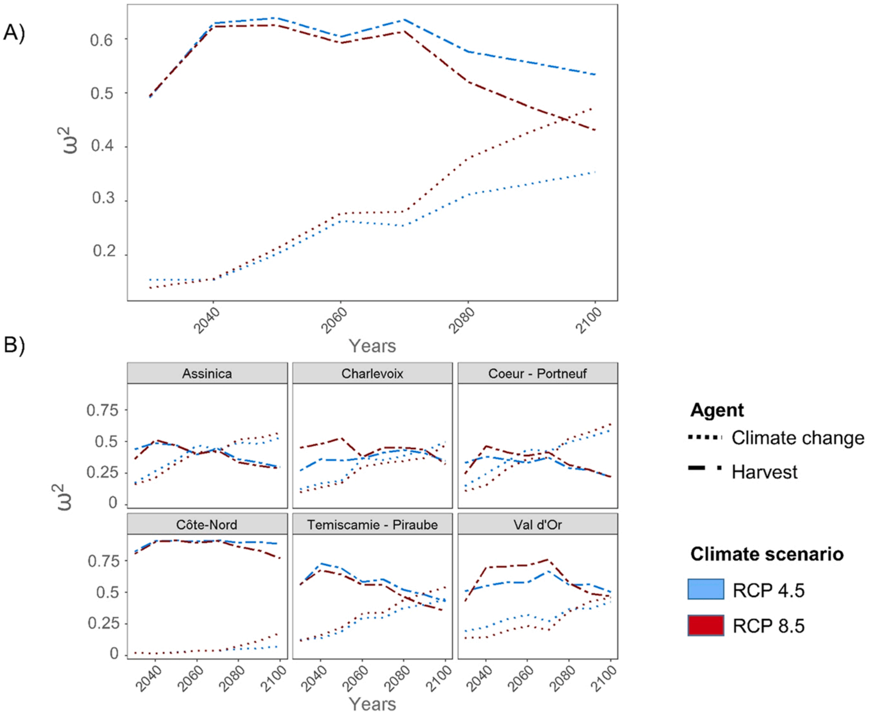

Fig. 6. Temporal trends in the importance of harvest vs. climate change during the period 2020–2100. Change in mean relative importance (ω^2) of timber harvest (dash-dotted line) and climate change (dotted line) on variations in boreal caribou habitat suitability under two climate change scenarios: RCP 4.5 (in blue) and RCP 8.5 (in red), A) for the whole study area and B) for six local boreal caribou ranges in the commercial forest of Québec, Canada.

4. Discussion

We combined a forest landscape model and a habitat suitability model to simulate the influence and relative importance of two major agents of change, timber harvesting and climate change, on future habitat suitability for boreal caribou in the commercial forest of Québec. We found that combined impacts of timber harvesting and climate change led to a significant decrease in habitat suitability for boreal caribou over the 2020–2100 horizon, with strong spatial and temporal variations driven by both initial habitat conditions and the severity of harvest and climate scenarios.

Timber harvesting was the main agent of change explaining habitat suitability for boreal caribou across the whole study area as well as at the scale of six local caribou ranges, at least up until 2070. Harvesting impacts were particularly important in relatively pristine regions (e.g., northeast of the study area), where they depleted highly suitable habitat that otherwise would have been maintained without harvest, even under strong climate change. These results echo those of St-Laurent et al. (2022), who recently used a similar approach to model changes in boreal caribou habitat based on data from 121 GPS-collared females. These authors found that decreases in habitat quality across their smaller study area (encompassed within ours) were mostly driven by high harvest rates which reduced the availability of mature conifer forests up until 2050. Our results also corroborate those of Neilson et al. (2022), who found that human disturbances were a stronger driver of boreal caribou occurrence across Canada, compared to climate.

The boreal caribou habitat suitability model we used in this study was strongly driven by changes in the age class of forest stands, with older coniferous and mixed stands (≥70 years old) providing the most suitable habitat to caribou (as detailed in Leblond et al., 2014). Harvesting practices generally target the same stands to maximize yield, and this was emulated by our harvesting scenario. Under harvest, old coniferous forests were gradually replaced by regenerating stands at the landscape scale, and more so in areas where large quantities of mature trees were available, i.e., where harvesting activities were historically low. As a result, harvest levels simulated in our study largely and directly contributed to the loss of suitable boreal caribou habitat throughout the study area, regardless of climate change scenarios.

Climate change cumulated with harvesting to further decrease caribou habitat suitability, but mostly during the later half of our simulation horizon (i.e., 2070–2100). Climate change gained more importance with time and became the most important agent of change for four of six local population ranges after 2070 or 2090. In our simulations, climate change decreased caribou habitat suitability mostly through an increase in fire activity. This became most notable after 2070, following a lengthening of the fire season as well as an intensification of fire-conducive weather conditions during the fire season, mechanisms also highlighted by Wang et al. (2017). Our results showed that the central part of the harvestable boreal forest within the province sustained a higher rate of wildfires (also shown by Boulanger et al., 2014), which prevented the maturation of coniferous and mixedwood stands (Tremblay et al., 2018) and promoted the growth of pioneer deciduous species such as trembling aspen (Bouchard et al., 2019). Boulanger and Pascual Puigdevall (2021) also found that climate-induced changes in Québec's boreal forests would mostly be driven by an increase in fire frequency and annual area burned, especially in the northwestern part of the province. Alterations to caribou habitat caused by wildfires were also projected in western Canada where increases in area burned could combine with more frequent droughts to convert coniferous stands into parklands and grasslands unsuitable to caribou (Barber et al., 2018).

Other climate-induced changes in forest landscapes, such as the direct conversion from boreal coniferous to temperate deciduous stands, were not a major pathway leading to changes in our analyses, likely in part due to the relatively short temporal scale of our study (see also St-Laurent et al., 2022). In fact, strictly climate-driven transitions of boreal forests to temperate forests were most likely to occur at the southern fringe of our study area where thermophilous deciduous species could outcompete co-occurring boreal conifers under warmer-than-average conditions (Fisichelli et al., 2014; Brice et al., 2019). However, such climate-induced alterations are much less likely to impact caribou, as they were extirpated from most of this area several decades ago (Courtois et al., 2003).

4.1. Climate change, caribou, and the forestry sector

Our simulations showed that declines in boreal caribou habitat suitability after 2070 were largely due to strong increases in fire activity caused by climate change, most notably in the northcentral part of the study area. These fire-induced changes caused a gradual decrease in average stand age, with mature conifer-dominated stands preferred by caribou being converted to lower-quality regenerating stands (Bergeron et al., 2017; St-Laurent et al., 2022). Our simulations also predicted a decline in the proportion of stands available for harvest in this region, leading to a decline in the relative importance of harvest – as compared to climate change – on habitat suitability for boreal caribou. This result suggests that the increased relative importance of climate change on caribou habitat in our analyses after 2070 was the result of both the increase in climate change severity and the decrease in timber harvesting impacts due to a lack of available timber. This result highlights how intrinsically intertwined the forestry sector will be to climate in the future (Brecka et al., 2020), a notion that is yet to be entirely captured by timber management plans across the country (Williamson et al., 2019). In view of this, it could be tempting to write off caribou has being condemned to disappear following climate change, and as a corollary, to push for the maximization of short-term socioeconomic gains provided by timber, including the pre-emptive harvesting of fire-prone stands. We caution against this near-sighted tactic for several reasons.

First, from a wildlife habitat perspective, fire represents a stochastic "risk" at the local scale (Gauthier et al., 2015): a fire could occur, or not; it could burn down a whole area or only parts of it; it could be severe or relatively minor; or it could occur in the near future or only in a few decades. In practice, this means that high-quality caribou habitat is highly likely to remain available at the range scale. This is why the recovery strategy for boreal caribou in Canada treats its critical habitat has a proportion of undisturbed areas above a management threshold, instead of a static area – to capture the dynamic nature of fire-prone boreal ecosystems where caribou occur, and where they have evolved over millennia (EC, 2012; Lafontaine et al., 2019). As such, pre-emptively harvesting all fire-prone forests over a very short period of time would be catastrophic for caribou (as well as for a plethora of other species), as it would guarantee that virtually no high-quality habitat remains over extensive areas. Moreover, burned areas, in stark contrast with harvested areas, are frequently used by caribou (Dalerum et al., 2007; Lafontaine et al., 2019), and may act as "island" refugia from predators (Skatter et al., 2017). Burned areas also have a lesser impact on caribou calf recruitment and adult survival compared to human disturbances such as cutblocks (Johnson et al., 2020).

Second, from a forest management perspective, ignoring the incidence of forest fires during harvest planning could have dramatic consequences on the forestry sector. The evidence is substantial. For instance, Daniel et al. (2017) showed that adopting precautionary targets for allowable timber that consider increases in climate uncertainty could improve the resilience of this economic sector by stabilizing timber supply over time (see also Raulier et al., 2014; Leduc et al., 2015). In contrast, maintaining current harvesting rates or increasing them could cause extensive regeneration failures (Splawinski et al., 2019; Cyr et al., 2021) with additional long-term impacts on timber supply and biodiversity. Predictions from these studies suggest reducing the level of allowable harvest today to buffer against future losses, which is in total opposition with compensating for future losses today with no plans for the future. This idea is not new; Paul Dayton wrote in 1998: "*The challenge to management of any wild resource is to provide a buffer for uncertainties to safeguard the future health of the population or ecosystem*" (Dayton, 1998). As counter-intuitive as it may seem, reducing harvest levels may be beneficial for both forest ecosystems and the forestry sector, representing a win-win situation between values that are often considered irreconcilable.

Our simulations showed that several local boreal caribou ranges in Québec were susceptible to reductions in habitat suitability following climate change. However, the northeastern part of the study area remained highly suitable even under the most aggressive climate change scenario. These predictions could be used by land managers to plan future actions that could benefit both caribou and the forestry sector. For instance, this region could serve as a potential climate refugium for boreal caribou (Stralberg et al., 2015). This highly inertial and stable area could play an important role in helping boreal caribou and other late-seral conifer specialists to "track" the northward displacement of their climatic niche (Chen et al., 2011). In other parts of our study area such as in the south, our simulations predicted an increase in the proportion of old coniferous and mixed stands by 2100. These areas, provided they are harvested in a sustainable manner, could continue to provide wood for the foreseeable future. In other parts of the province where caribou occur, we propose that reducing landscape-level harvesting rates could help maintain caribou habitat by mitigating climate-induced decreases in mature conifer-dominated stands.

4.2. Limits inherent to our modelling framework

Human infrastructures such as roads were not allowed to change during the course of our simulations. This likely had the consequence of underestimating the impacts of timber harvesting, because road network development usually occurs concurrently with harvesting. Roads cause habitat fragmentation (Lesbarrères and Fahrig, 2012), increase encounter rates between caribou and their predators (Newton et al., 2017), and intensify predation pressure on caribou (Mumma et al., 2018). Consequently, roads can jeopardize the sustainability of caribou populations via direct increases in mortality, or (indirect) functional habitat loss (Polfus et al., 2011). By ignoring how road networks may develop in the future, we presented a conservative perspective on the synergistic impacts of climate change and timber harvesting on caribou habitat suitability. In this regard, we predicted low habitat suitability and important inertia in regions where the road network is already very dense (such as in the center of the study area). To the best of our knowledge, no models exist that are capable of providing spatially explicit forecasts of road network development and other human footprint at the scale of our study area. Other land types such as wetlands and existing open woodlands were also held static. The consequences of this limitation are unknown, although we note that sparsely treed forests such as those occupying wetlands and open woodlands are less likely to burn (Schaefer and Pruitt, 1991) or be harvested, and thus less likely to transition to a different land cover class over a 100-year time span.

Our simulations modeled the impacts of timber harvesting and climate change on habitat suitability, but not directly on the physiology (e.g., thermoregulation capacity) or demography (e.g., reproductive output) of caribou. However, we note that habitat alteration and loss have already been shown to influence several aspects of caribou behavior and demography, such as space use (Beauchesne et al., 2013), calf survival (Leclerc et al., 2014), adult survival (Losier et al., 2015), population size and growth rate (Stewart et al., 2020). For instance, the cumulative climate- and harvest-induced changes in habitat quality simulated in this study could reduce the survival of boreal caribou through imbalances in trophic interactions (Labadie et al., 2021). Increases in the proportions of early seral deciduous stands caused by fire and harvesting could benefit moose and deer, which would then support higher wolf populations and thus increase predation risk for caribou (Wittmer et al., 2007; Barber et al., 2018). Next steps should aim at measuring the influence of harvesting and climate change on caribou vital rates and population trends (Rudolph et al., 2017; Fryxell et al., 2020; Johnson et al., 2020).

Finally, harvest levels simulated in this study were representative of current harvesting practices in Québec, but did not consider potential modifications to forest management strategies that may be proposed to cope with the impacts of climate change. Such climate change adaptation strategies could include assisted migration through planting or seeding (Ste-Marie et al., 2011), selective cutting, or silvicultural treatments retaining higher proportions of fire- or insect-tolerant species to reduce stand vulnerability (e.g., Girardin et al., 2013). Once identified, these strategies and their effectiveness could be assessed using the analytical framework used in this study.

5. Conclusion

Boreal caribou are legally protected under Canada's Species at Risk Act and under Québec's *Loi sur les Espèces en Péril*. Despite these regulations, they were extirpated from the southern part of their historical distribution in Canada (COSEWIC, 2014; Neilson et al., 2022) and Québec (Courtois et al., 2003), and their distribution range continues to be pushed northwards by anthropogenic pressures (Schaefer, 2003). Harvest-induced habitat alterations occurring under climate change could represent a deadly anthropogenic cocktail for boreal caribou (*sensu* Travis, 2003). Urgent actions will be required to protect remnant caribou habitat that still exists in small patches across their current distribution, as well as restore suitable habitat conditions in their historical range. Our simulations suggest that highly suitable habitat for boreal caribou could be maintained in the landscape, even in the face of acute climate change, but only under a strict timber harvesting strategy.

Boreal caribou recovery may require improving landscape connectivity between caribou ranges to help mitigate the negative impacts of climate change (Bauduin et al., 2018). Recovery may also depend on complementary management strategies, which should be implemented with the greatest haste possible. Examples of potential management strategies include increasing fire suppression efforts (although the costs may be prohibitive in remote northern areas; Podur and Wotton, 2010; Hope et al., 2016), using more extensive silvicultural practices (e.g., Nadeau-Fortin et al., 2016), actively restoring deteriorated habitat (e.g., Lacerte et al., 2021), or resorting to interim actions such as the penning of females during reproduction to improve recruitment (e.g., Lamb et al., 2022). Simulations emulating these strategies may also help assess their efficacy a priori, especially in the context of future climate change (e.g., Bauduin et al., 2018).

In light of our results, however, we argue that temporary ad hoc strategies may be insufficient to save boreal caribou in regions where habitat conditions are already severely deteriorated. Current harvest levels are likely too high to maintain suitable caribou habitat throughout the province, and intensification of fire activity, a major pathway of climate change effects in our simulations, could endanger currently stable boreal caribou populations, notably those located in northcentral and northwestern Québec. Reducing harvest levels in these regions and allowing the reestablishment of a significant coniferous cover thus appears essential to maintain caribou habitat in the future.

Our results do not support the common assertion that the extirpation of boreal caribou is inevitable as a consequence of climate-induced habitat loss. Although we show a non-negligible contribution of climate change in future decreases in caribou habitat suitability, we also show that there is still room to adjust our land-use practices and contribute to the conservation of boreal caribou. Notably, by reducing harvest intensity in areas where habitat suitability is currently high, it could be possible to maintain high-quality caribou habitat even under the most intense climate change predictions. In line with our national and international commitments, it is our nations' obligation to protect biodiversity and species at risk such as boreal caribou.

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.

Data Availability

Data will be made available on request.

Acknowledgments

We thank C. Dussault and the Ministère des Forêts, de la Faune et des Parcs du Québec for their contribution during the elaboration of the boreal caribou habitat suitability model, as well as for sharing data used in this study. We thank S. Moran for his assistance with Fig. 1, as well as J. Schaefer and two anonymous reviewers for their insightful comments which greatly helped improve this manuscript. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02294.

References

Albers, C., Lakens, D., 2018. When power analyses based on pilot data are biased: Inaccurate effect size estimators and follow-up bias. J. Exp. Soc. Psychol. 74, 187–195. https://doi.org/10.1016/j.jesp.2017.09.004.

Arifin, M.I., Staskevicius, A., Shim, S.Y., Huang, Y., Fenton, H., McLoughlin, P.D., et al., 2020. Large-scale prion protein genotyping in Canadian caribou populations and potential impact on chronic wasting disease susceptibility. Mol. Ecol. 29, 3830–3840. https://doi.org/10.1111/mec.15602.

Barber, Q.E., Parisien, M.-A., Whitman, E., Stralberg, D., Johnson, C.J., St-Laurent, M.-H., et al., 2018. Potential impacts of climate change on the habitat of boreal woodland caribou. Ecosphere 9, e02472. https://doi.org/10.1002/ecs2.2472.

Bauduin, S., McIntire, E., St-Laurent, M.-H., Cumming, S.G., 2018. Compensatory conservation measures for an endangered caribou population under climate change. Sci. Rep. 8, 16438. https://doi.org/10.1038/s41598-018-34822-9.

Beauchesne, D., Jaeger, J.A.G., St-Laurent, M.-H., 2013. Disentangling woodland caribou movements in response to clearcuts and roads across temporal scales. PLoS One 8, e77514. https://doi.org/10.1371/journal.pone.0077514.

Bergeron, Y., Irulappa Pillai Vijayakumar, D.B., Ouzennou, H., Raulier, F., Leduc, A., Gauthier, S., 2017. Projections of future forest age class structure under the influence of fire and harvesting: implications for forest management in the boreal forest of eastern Canada. Forestry 90, 485–495. https://doi.org/10.1093/forestry/cpx022.

Bouchard, M., Aquilué, N., Périé, C., Lambert, M.-C., 2019. Tree species persistence under warming conditions: a key driver of forest response to climate change. . Ecol. Manag. 442, 96–104. https://doi.org/10.1016/j.foreco.2019.03.040.

Boulanger, Y., Pascual Puigdevall, J., 2021. Boreal forests will be more severely affected by projected anthropogenic climate forcing than mixedwood and northern hardwood forests in eastern Canada. Landsc. Ecol. 36, 1725–1740. https://doi.org/10.1007/s10980-021-01241-7.

Boulanger, Y., Arseneault, D., Morin, H., Jardon, Y., Bertrand, P., Dagneau, C., 2012. Dendrochronological reconstruction of spruce budworm (*Choristoneura fumiferana*) outbreaks in southern Quebec for the last 400 years. Can. J. . Res. 42, 1264–1276. https://doi.org/10.1139/X2012-069.

Boulanger, Y., Gauthier, S., Burton, P.J., 2014. A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. Can. J. . Res. 44, 365–377. https://doi.org/10.1139/cjfr-2013-0372.

Boulanger, Y., Girardin, M., Bernier, P.Y., Gauthier, S., Beaudoin, A., Guindon, L., 2017. Changes in mean forest age in Canada's forests could limit future increases in area burned but compromise potential harvestable conifer volumes. Can. J. Res. 47, 755–764. https://doi.org/10.1139/cjfr-2016-0445.

Boulanger, Y., Arseneault, D., Boucher, Y., Gauthier, S., Cyr, D., Taylor, A.R., et al., 2019. Climate change will affect the ability of forest management to reduce gaps between current and presettlement forest composition in southeastern Canada. Landsc. Ecol. 34, 159–174. https://doi.org/10.1007/s10980-018-0761-6.

Brecka, A.F.J., Boulanger, Y., Searle, E.B., Taylor, A.R., Price, D.T., Zhu, Y., et al., 2020. Sustainability of Canada's forestry sector may be compromised by impending climate change. Ecol. Manag. 474, 118352 https://doi.org/10.1016/j.foreco.2020.118352.

Brice, M.-H., Cazelles, K., Legendre, P., Fortin, M.-J., 2019. Disturbances amplify tree community responses to climate change in the temperate–boreal ecotone. Glob. Ecol. Biogeogr. 28, 1668–1681. https://doi.org/10.1111/geb.12971.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. Sci. Adv. 1 https://doi.org/10.1126/sciadv.1400253.

Cianfrani, C., Le Lay, G., Hirzel, A.H., Loy, A., 2010. Do habitat suitability models reliably predict the recovery areas of threatened species? J. Appl. Ecol. 47, 421–430. https://doi.org/10.1111/j.1365-2664.2010.01781.x.

COSEWIC, 2014. Assessment and status report on the Caribou *Rangifer tarandus*, Newfoundland population, Atlantic-Gaspésie population and Boreal population, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada, p. 151.

Couillard, P.-L., Bouchard, M., Laflamme, J., Hébert, F., 2022. Zonage des régimes de feux du Québec méridional. Mémoire de recherche forestière no. 189. Gouvernement du Québec, p. 23.

Courtois, R., Ouellet, J.-P., Gingras, A., Dussault, C., Breton, L., Maltais, J., 2003. Historical changes and current distribution of caribou, *Rangifer tarandus*, in Quebec. Can. Field-Nat. 117, 399–414. https://doi.org/10.22621/cfn.v117i3.742.

Cyr, D., Splawinski, T.B., Pascual Puigdevall, J., Valeria, O., Leduc, A., Thiffault, N., et al., 2021. Mitigating post-fire regeneration failure in boreal landscapes with reforestation and variable retention harvesting: At what cost? Can. J. . Res. 52, 1–14. https://doi.org/10.1139/cjfr-2021-0180.

Dalerum, F., Boutin, S., Dunford, J.S., 2007. Wildfire effects on home range size and fidelity of boreal caribou in Alberta, Canada. Can. J. Zool. 85, 26–32. https://doi.org/10.1139/Z06-186.

Daniel, C.J., Ter-Mikaelian, M.T., Wotton, B.M., Rayfield, B., Fortin, M.-J., 2017. Incorporating uncertainty into forest management planning: timber harvest, wildfire and climate change in the boreal forest. . Ecol. Manag. 400, 542–554. https://doi.org/10.1016/J.FORECO.2017.06.039.

Dayton, P.K., 1998. Reversal of the burden of proof in fisheries management. Science 279, 821–822. https://doi.org/10.1126/science.279.5352.821.

DeMars, C.A., Serrouya, R., Mumma, M.A., Gillingham, M.P., McNay, R.S., Boutin, S., 2019. Moose, caribou, and fire: have we got it right yet? Can. J. Zool. 97, 866–879. https://doi.org/10.1139/cjz-2018-0319.

Environment Canada (EC) (2011). Scientific assessment to inform the identification of critical habitat for woodland caribou (Rangifer tarandus caribou), boreal populations, in Canada: 2011 Update. Ottawa, Ontario, Canada. 591 pp.

Environment Canada (EC), 2012. Recovery Strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada. Species at Risk Act Recovery Strategy Series, Ottawa, Ontario, Canada, p. 150 pp.

Fisichelli, N.A., Frelich, L.E., Reich, P.B., 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography 37, 152–161. https://doi.org/10.1111/j.1600-0587.2013.00197.x.

Fryxell, J.M., Avgar, T., Liu, B., Baker, J.A., Rodgers, A.R., Shuter, J., et al., 2020. Anthropogenic disturbance and population viability of woodland caribou in Ontario. J. Wildl. Manag. 84, 636–650. https://doi.org/10.1002/jwmg.21829.

Gauthier, S., Bernier, P.Y., Boulanger, Y., Guo, J., Guindon, L., Beaudoin, A., et al., 2015. Vulnerability of timber supply to projected changes in fire regime in Canada's managed forests. Can. J. . Res. 45, 1439–1447. https://doi.org/10.1139/cjfr-2015-0079.

Girardin, M.P., Ali, A.A., Carcaillet, C., Blarquez, O., Hély, C., Terrier, A., et al., 2013. Vegetation limits the impact of a warm climate on boreal wildfires. N. Phytol. 199, 1001–1011. https://doi.org/10.1111/nph.12322.

Gustafson, E.J., Shifley, S.R., Mladenoff, D.J., Nimerfro, K.K., He, H.S., 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. Can. J. . Res. 30, 32–43. https://doi.org/10.1139/x99-188.

Hausfather, Z., Peters, G.P., 2020. Emissions – the 'business as usual' story is misleading. Nature 577, 618–620. https://doi.org/10.1038/d41586-020-00177-3.

Hoeppner, J.M., Hughes, L., 2019. Climate readiness of recovery plans for threatened Australian species. Conserv. Biol. 33, 534–542. https://doi.org/10.1111/cobi.13270.

Hope, E.S., McKenney, D.W., Pedlar, J.H., Stocks, B.J., Gauthier, S., 2016. Wildfire suppression costs for Canada under a changing climate. PLoS One 11, e0157425. https://doi.org/10.1371/journal.pone.0157425.

Jobidon, R., Bergeron, Y., Robitaille, A., Raulier, F., Gauthier, S., Imbeau, L., et al., 2015. A biophysical approach to delineate a northern limit to commercial forestry: the case of Quebec's boreal forest. Can. J. . Res. 45, 515–528. https://doi.org/10.1139/cjfr-2014-0260.

Johnson, C.A., Sutherland, G.D., Neave, E., Leblond, M., Kirby, P., Superbie, C., et al., 2020. Science to inform policy: linking population dynamics to habitat for a threatened species in Canada. J. Appl. Ecol. 57, 1314–1327. https://doi.org/10.1111/1365-2664.13637.

Labadie, G., McLoughlin, P.D., Hebblewhite, M., Fortin, D., 2021. Insect-mediated apparent competition between mammals in a boreal food web. Proc. Natl. Acad. Sci. USA 118, e2022892118. https://doi.org/10.1073/pnas.2022892118.

Lacerte, R., Leblond, M., St-Laurent, M.-H., 2021. Determinants of vegetation regeneration on forest roads following restoration treatments: implications for boreal caribou conservation. Restor. Ecol. 29, e13414 https://doi.org/10.1111/rec.13414.

Lafontaine, A., Drapeau, P., Fortin, D., Gauthier, S., Boulanger, Y., St-Laurent, M.-H., 2019. Exposure to historical burn rates shapes the response of boreal caribou to timber harvesting. Ecosphere 10, e02739. https://doi.org/10.1002/ecs2.2739.

Lamb, C.T., Willson, R., Richter, C., Owens-Beek, N., Napoleon, J., Muir, B., et al., 2022. Indigenous-led conservation: pathways to recovery for the nearly extirpated Klinse-Za mountain caribou. Ecol. Appl. https://doi.org/10.1002/eap.2581.

Leblond, M., Dussault, C., St-Laurent, M.-H., 2014. Development and validation of an expert-based habitat suitability model to support boreal caribou conservation. Biol. Conserv. 177, 100–108. https://doi.org/10.1016/j.biocon.2014.06.016.

Leclerc, M., Dussault, C., St-Laurent, M.-H., 2014. Behavioural strategies towards human disturbances explain individual performance in woodland caribou. Oecologia 176, 297–306. https://doi.org/10.1007/s00442-014-3012-9.

Leduc, A., Bernier, P.Y., Mansuy, N., Raulier, F., Gauthier, S., Bergeron, Y., 2015. Using salvage logging and tolerance to risk to reduce the impact of forest fires on timber supply calculations. Can. J. . Res. 45, 480–486. https://doi.org/10.1139/cjfr-2014-0434.

Legendre, P. and Legendre, L. (2012). Developments in numerical ecology. 3rd ed. 1006 pp.

Lesbarrères, D., Fahrig, L., 2012. Measures to reduce population fragmentation by roads: what has worked and how do we know? Trends Ecol. Evol. 27, 374–380. https://doi.org/10.1016/j.tree.2012.01.015.

Lexer, M.J., Hönninger, K., 2001. A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. . Ecol. Manag. 144, 43–65. https://doi.org/10.1016/S0378-1127(00)00386-8.

Losier, C.L., Couturier, S., St-Laurent, M.-H., Drapeau, P., Dussault, C., Rudolph, T.D., et al., 2015. Adjustments in habitat selection to changing availability induce fitness costs for a threatened ungulate. J. Appl. Ecol. 52, 496–504. https://doi.org/10.1111/1365-2664.12400.

McKenney, D.W., Pedlar, J.H., Hutchinson, M., Papadopol, P., Lawrence, K., Campbell, K., et al., 2013. Spatial climate models for Canada's forestry community. . Chron. 89, 659–663. https://doi.org/10.5558/tfc2013-118.

Micheletti, T., Stewart, F.E.C., Cumming, S.G., Haché, S., Stralberg, D., Tremblay, J.A., et al., 2021. Assessing pathways of climate change effects in SpaDES: An application to boreal landbirds of Northwest Territories Canada. Front. Ecol. Evol. 9, 679673 https://doi.org/10.3389/fevo.2021.679673.

Mladenoff, D.J., He, H.S., 1999. Design, behavior and applications of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Mladenoff, D.J., Baker, W.L. (Eds.), Spatial Modeling of Forest Landscape Change: Approaches and Applications. Cambridge University Press, Cambridge, United Kingdom, pp. 125–162.

Mumma, M.A., Gillingham, M.P., Parker, K.L., Johnson, C.J., Watters, M., 2018. Predation risk for boreal woodland caribou in human-modified landscapes: Evidence of wolf spatial responses independent of apparent competition. Biol. Conserv. 228, 215–223. https://doi.org/10.1016/J.BIOCON.2018.09.015.

Murray, D.L., Majchrzak, Y.N., Peers, M.J.L., Wehtje, M., Ferreira, C., Pickles, R.S.A., et al., 2015. Potential pitfalls of private initiatives in conservation planning: a case study from Canada's boreal forest. Biol. Conserv. 192, 174–180. https://doi.org/10.1016/j.biocon.2015.09.017.

Nadeau-Fortin, M.-A., Sirois, L., St-Laurent, M.-H., 2016. Extensive forest management contributes to maintain suitable habitat characteristics for the endangered Atlantic-Gaspesie caribou. Can. J. . Res. 46, 933–942. https://doi.org/10.1139/cjfr-2016-0038.

Naujokaitis-Lewis, I., Endicott, S., Guezen, J., 2021. Treatment of climate change in extinction risk assessments and recovery plans for threatened species. Conserv. Sci. Pract. 3, e450 https://doi.org/10.1111/csp2.450.

Neilson, E.W., Castillo-Ayala, C., Beckers, J.F., Johnson, C.A., St-Laurent, M.-H., Mansuy, N., et al., 2022. The direct and habitat-mediated influence of climate on the biogeography of boreal caribou in Canada. Clim. Chang. Ecol. 3, 100052 https://doi.org/10.1016/j.ecochg.2022.100052.

Newton, E.J., Patterson, B.R., Anderson, M.L., Rodgers, A.R., Vander Vennen, L.M., Fryxell, J.M., 2017. Compensatory selection for roads over natural linear features by wolves in northern Ontario: Implications for caribou conservation. PLoS One 12, e0186525. https://doi.org/10.1371/journal.pone.0186525.

OIFQ. (2009). Manuel de foresterie, 2e Éd. Ordre des ingénieurs forestiers du Québec. Éditions MultiMondes, Québec, Canada. 1544 pp.

Palm, E.C., Suitor, M.J., Joly, K., Herriges, J.D., Kelly, A.P., Hervieux, D., et al., 2022. Increasing fire frequency and severity will increase habitat loss for a boreal forest indicator species. Ecol. Appl., e2549 https://doi.org/10.1002/eap.2549.

Podur, J., Wotton, M., 2010. Will climate change overwhelm fire management capacity? Ecol. Modell. 221, 1301–1309. https://doi.org/10.1016/j.ecolmodel.2010.01.013.

Polfus, J.L., Hebblewhite, M., Heinemeyer, K., 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. Biol. Conserv. 144, 2637–2646. https://doi.org/10.1016/j.biocon.2011.07.023.

Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R.A., Hogg, E.H., et al., 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems. Environ. Rev. 21, 322–365. https://doi.org/10.1139/er-2013-0042.

R Core Team, 2019. R, A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.r-project.org⟩.

Racey, G.D., 2005. Climate change and woodland caribou in Northwestern Ontario: a risk analysis. Rangifer 25, 123–136. https://doi.org/10.7557/2.25.4.1777.

Raulier, F., Dhital, N., Racine, P., Tittler, R., Fall, A., 2014. Increasing resilience of timber supply: how a variable buffer stock of timber can efficiently reduce exposure to shortfalls caused by wildfires. Policy Econ. 46, 47–55. https://doi.org/10.1016/j.forpol.2014.06.007.

Robitaille, A., Saucier, J.-P., 1998. Paysages régionaux du Québec méridional. Publications du Québec, Sainte-Foy, QC, Canada.

Rudolph, T.D., Drapeau, P., Imbeau, L., Brodeur, V., Légaré, S., St-Laurent, M.-H., 2017. Demographic responses of boreal caribou to cumulative disturbances highlight elasticity of range-specific tolerance thresholds. Biodivers. Conserv. 26, 1179–1198. https://doi.org/10.1007/s10531-017-1292-1.

Schaefer, J.A., 2003. Long-term range recession and the persistence of caribou in the taiga. Conserv. Biol. 17, 1435–1439. https://doi.org/10.1046/j.1523-1739.2003.02288.x.

Schaefer, J.A., Pruitt, W.O., 1991. Fire and woodland caribou in southeastern Manitoba. Wildl. Monogr. 116, 3–39.

Scheller, R.M. (2013). LANDIS-II Biomass Succession v3.1 Extension User Guide.

Scheller, R.M.and Domingo, J.B. (2011). LANDIS-II Base Fire v2.1 Extension User Guide.

Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., et al., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol. Modell. 201, 409–419. https://doi.org/10.1016/j.ecolmodel.2006.10.009.

Schwalm, C.R., Glendon, S., Duffy, P.B., 2020. Reply to Hausfather and Peters: RCP 8.5 is neither problematic nor misleading. Proc. Natl. Acad. Sci. USA 117, 27793–27794. https://doi.org/10.1073/pnas.2018008117.

Skatter, H.G., Charlebois, M.L., Eftestøl, S., Tsegaye, D., Colman, J.E., Kansas, J.L., et al., 2017. Living in a burned landscape: woodland caribou (*Rangifer tarandus caribou*) use of post-fire residual patches for calving in a high fire/low anthropogenic Boreal Shield Ecozone. Can. J. Zool. 95, 975–984. https://doi.org/10.1139/cjz-2016-0307.

Splawinski, T.B., Cyr, D., Gauthier, S., Jetté, J.-P., Bergeron, Y., 2019. Analyzing risk of regeneration failure in the managed boreal forest of northwestern Quebec. Can. J. . Res. 49, 680–691. https://doi.org/10.1139/cjfr-2018-0278.

Ste-Marie, C., Nelson, E.A., Dabros, A., Bonneau, M.-E., 2011. Assisted migration: Introduction to a multifaceted concept. . Chron. 87, 724–730. https://doi.org/10.5558/tfc2011-089.

Stewart, F.E.C., Nowak, J.J., Micheletti, T., McIntire, E.J.B., Schmiegelow, F.K.A., Cumming, S.G., 2020. Boreal caribou can coexist with natural but not industrial disturbances. J. Wildl. Manag. 84, 1435–1444. https://doi.org/10.1002/jwmg.21937.

St-Laurent, M.-H., Boulanger, Y., Cyr, D., Manka, F., Drapeau, P., Gauthier, S., 2022. Lowering the rate of timber harvesting to mitigate impacts of climate change on boreal caribou habitat quality in eastern Canada. Sci. Total Environ. 838, 156244 https://doi.org/10.1016/j.scitotenv.2022.156244.

Stralberg, D., Bayne, E.M., Cumming, S.G., Sólymos, P., Song, S.J., Schmiegelow, F.K.A., 2015. Conservation of future boreal forest bird communities considering lags in vegetation response to climate change: a modified refugia approach. Divers. Distrib. 21, 1112–1128. https://doi.org/10.1111/ddi.12356.

Sturtevant, B.R., Gustafson, E.J., Li, W., He, H.S., 2004. Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. Ecol. Modell. 180, 153–174. https://doi.org/10.1016/j.ecolmodel.2004.01.021.

Sylvain, J.-D., Anctil, F., Thiffault, É., 2021. Using bias correction and ensemble modelling for predictive mapping and related uncertainty: a case study in digital soil mapping. Geoderma 403, 115153. https://doi.org/10.1016/j.geoderma.2021.115153.

Taylor, A.R., Boulanger, Y., Price, D.T., Cyr, D., McGarrigle, E., Rammer, W., et al., 2017. Rapid 21st century climate change projected to shift composition and growth of Canada's Acadian Forest Region. . Ecol. Manag. 405, 284–294. https://doi.org/10.1016/j.foreco.2017.07.033.

Travers, H., Selinske, M., Nuno, A., Serban, A., Mancini, F., Barychka, T., et al., 2019. A manifesto for predictive conservation. Biol. Conserv. 237, 12–18. https://doi.org/10.1016/j.biocon.2019.05.059.

Travis, J.M.J., 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proc. R. Soc. Lond. Ser. B-Biol. Sci. 270, 467–473. https://doi.org/10.1098/rspb.2002.2246.

Tremblay, J.A., Boulanger, Y., Cyr, D., Taylor, A.R., Price, D.T., St-Laurent, M.-H., 2018. Harvesting interacts with climate change to affect future habitat quality of a focal species in eastern Canada's boreal forest. PLoS One 13, e0191645. https://doi.org/10.1371/journal.pone.0191645.

van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., et al., 2011. The representative concentration pathways: an overview. Clim. Change 109, 5–31. https://doi.org/10.1007/s10584-011-0148-z.

Vors, L.S., Schaefer, J.A., Pond, B.A., Rodgers, A.R., Patterson, B.R., 2007. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. J. Wildl. Manag. 71, 1249–1256. https://doi.org/10.2193/2006-263.

Wang, X., Parisien, M.-A., Taylor, S.W., Candau, J.N., Stralberg, D., Marshall, G.A., et al., 2017. Projected changes in daily fire spread across Canada over the next century. Environ. Res. Lett. 12, 025005 https://doi.org/10.1088/1748-9326/aa5835.

Williamson, T.B., Colombo, S.J., Duinker, P.N., Gray, P.A., Hennessey, R.J., Houle, D., et al., 2009. Climate change and Canada's forests: from impacts to adaptation. Sustainable Forest Management Network and Natural Resources Canada. Canadian Forest Service, Northern Forestry Center, Edmonton, Canada, p. 104.

Wittmer, H.U., McLellan, B.N., Serrouya, R., Apps, C.D., 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. J. Anim. Ecol. 76, 568–579. https://doi.org/10.1111/j.1365-2656.2007.01220.x.

WWF. (2020). Living Planet Report 2020 - Bending the curve of biodiversity loss. Almond, R. E. A., Grooten, M., and Petersen, T. (Eds). World Wildlife Fund. Gland, Switzerland.