



The umbrella value of caribou management strategies for biodiversity conservation in boreal forests under global change

Guillemette Labadie^{a,*}, Ilhem Bouderbala^{b,c}, Yan Boulanger^d, Jean-Michel Béland^d, Christian Hébert^d, Antoine Allard^c, Mark Hebblewhite^e, Daniel Fortin^a

^a Centre d'Étude de la Forêt, Département de biologie, Université Laval, Québec, QC G1V 0A6, Canada

^b Département de biologie, Université Laval, Québec, QC G1V 0A6, Canada

^c Département de physique, de génie physique et d'optique, Université Laval, Québec, QC G1V 0A6, Canada

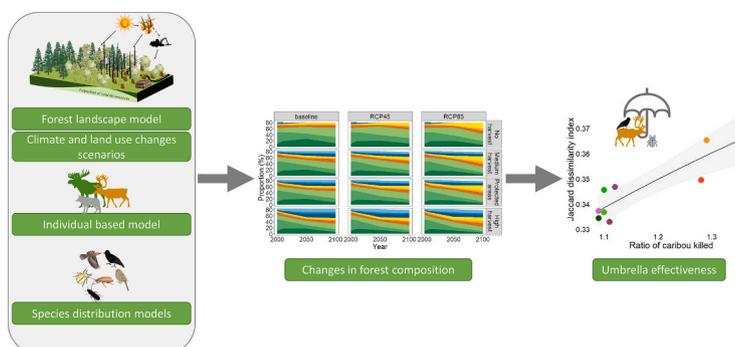
^d Canadian Forest Service, Natural Resources Canada, Quebec City, QC G1V4C7, Canada

^e Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, Franke College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA

HIGHLIGHTS

- Predictive models of occurrence are developed for 31 bird and 77 beetle species.
- Land-use change exerts stronger effects on biodiversity than climate change.
- Strategies mitigating human impact on caribou promote bird and beetle conservation.
- Boreal caribou is an effective umbrella in the face of global change.
- Single-species management can offer umbrella benefits.

GRAPHICAL ABSTRACT



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ABSTRACT

Single-species conservation management is often proposed to preserve biodiversity in human-disturbed landscapes. How global change will impact the umbrella value of single-species management strategies remains an open question of critical conservation importance. We assessed the effectiveness of threatened boreal caribou as an umbrella for bird and beetle conservation under global change. We combined mechanistic, spatially explicit models of forest dynamics and predator-prey interactions to forecast the impact of management strategies on the survival of boreal caribou in boreal forest. We then used predictive models of species occupancy to characterize concurrent impacts on bird and beetle diversity. Landscapes were simulated based on three scenarios of climate change and four of forest management. We found that strategies that best mitigate human impact on boreal caribou were an effective umbrella for maintaining bird and beetle assemblages. While we detected a stronger effect of land-use change compared to climate change, the umbrella value of management strategies for caribou habitat conservation were still impacted by the severity of climate change. Our results showed an interplay among changes in forest attributes, boreal caribou mortality, as well as bird and beetle species assemblages. The

* Corresponding author at: Département de biologie - Pavillon Alexandre-Vachon, 1045, av. de la Médecine, Université Laval, Québec, QC G1V 0A6, Canada.

E-mail address: guillemette.labadie.1@ulaval.ca (G. Labadie).

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conservation status of some species mandates the development of recovery strategies, highlighting the importance of our study which shows that single-species conservation can have important umbrella benefits despite global change.

1. Introduction

Global climate and land-use changes are affecting biodiversity and food webs by modifying environmental conditions (Wilmers and Getz, 2005; Blois et al., 2013). Different approaches of biodiversity conservation have thus been proposed to mitigate the impact of global change on ecosystems. Single-species approaches to animal conservation are one of them. Instead of predicting the impact of global change on all species, conservation and management plans focus on a single species (i.e., an umbrella species, (Roberge and Angelstam, 2004)) with the intent for sympatric species to be concurrently protected. The conservation strategy of an effective umbrella species must therefore represent the conservation needs of sympatric species, and must ideally provide protection from vertebrates to invertebrates (Rubinoff, 2001). Usually, umbrella species are organisms with large home ranges, sensitive to human-induced habitat changes, and typical of their ecosystem (Caro, 2010). Umbrella species can also be a flagship species, generating conservation interest, funding, and public support. Climate change already increases the impact of natural disturbances in most ecosystems (Dale et al., 2001; Flannigan et al., 2006; IPCC, 2021). Combined with human disturbances, it could alter species assemblages to the point that an umbrella species and management strategies aimed at conserving it may no longer be associated with the same species assemblages over the long term. Few studies, however, have assessed the consequences of global change on the effectiveness (i.e., the umbrella value) of conservation strategy designed around the needs of a given umbrella species for biodiversity conservation (Lindenmayer and Westgate, 2020).

In forest ecosystems, for example, changes in temperature and precipitation induced by climate change (CC) will influence the occurrence, duration, frequency, size, and intensity of natural disturbances such as wildfire and insect outbreaks (Dale et al., 2001; IPCC, 2021). In addition to CC, ecological communities are also largely shaped by anthropogenic disturbances. Land-use changes (LUC), the direct effect of human activities on landscape without a change in land-cover class (Bürgi et al., 2017), are causing widespread biodiversity declines through habitat loss and fragmentation (IPBES, 2018). CC and LUC thus jointly modify forest ecosystems, affecting the composition, structure, age classes and spatial configuration of forests, notably by increasing disturbed areas or inducing changes in the speed and pathways of forest succession (Baker, 1995; Bergeron et al., 2006; Yamasaki et al., 2008). Also, the cumulative effects of anthropogenic and natural disturbances can interactively compound ecosystem change, resulting in massive species losses and decline, and restructuring biological communities (Chapin III et al., 2000). Understanding the impact of global change on the distribution and abundance of species and their trophic interactions is thus valuable to predict future changes in the face of such complex habitat modifications (Fuller et al., 2011).

Boreal caribou (*Rangifer tarandus caribou*) is an umbrella species of North American boreal forests (Bichet et al., 2016; Drever et al., 2019) because of its large range and sensitivity to human-induced habitat changes, and because the management of its populations requires large areas of intact forests (Brown et al., 2003; Courtois et al., 2007; Hins et al., 2009; Fortin et al., 2013). Anthropogenic disturbances, such as logging and oil and gas extraction, are a major conservation challenge for all boreal biodiversity, including caribou (Trombulak and Frissell, 2001; Environment Canada, 2012). Co-occurrence of boreal caribou and their main predator, the gray wolf (*Canis lupus*), has increased dramatically due to repercussions of anthropogenic disturbances on their habitat (Environment Canada, 2012). Disturbed areas provide high-quality food for deciduous-browsing Cervidae species like moose

(*Alces alces*) and deer (*Odocoileus* spp.). The subsequent increases in these prey populations trigger a positive numerical response in wolves, which intensifies predation rate on boreal caribou, causing apparent-competition induced declines (i.e., the increase in predator numbers, sustained by one prey, intensifies the predation pressure on the secondary prey; Wittmer et al., 2005). In addition, the increase in wildfire induced by climate change will lead to further increase in the proportion of young stands containing more deciduous thermophilous species (Boulanger and Pascual Puigdevall, 2021), and thus herbivore species browsing on deciduous vegetation (i.e., apparent competitors for caribou). These interactive effects of climate and land-use changes cumulatively impact all biodiversity that rely on mature conifer for at least some portion of their life history (Norvez et al., 2013; Tremblay et al., 2018; Cadieux et al., 2020; Leston et al., 2020). For example, boreal bird species associated with mature forest, such as Canada warblers (*Cardellina canadensis*) (Ball et al., 2016) and Olive-sided Flycatcher (*Contopus cooperi*) (Environment Canada, 2015), are also declining as a result of these anthropogenic-induced loss in mature and old-growth coniferous forests (Imbeau et al. 2015).

Boreal caribou populations are threatened in Canada (Government of Canada, 2018), and are theoretically protected by provincial and national recovery plans across Canada (Environment and Climate Change Canada, 2017, 2018). In the province of Quebec, the management strategies under consideration, including measures to mitigate the impact of human activities, involve the protection of remaining intact old-growth forests on which caribou depend (Ministère des Forêts de la Faune et des Parcs, 2019a). As predation by wolves is considered the main driver of population decline (Rettie and Messier, 1998; Équipe de rétablissement du caribou forestier du Québec, 2013), and predation is closely linked to moose abundance and change in landscape composition (Serrouya et al., 2021), the effectiveness of these theoretical management strategies must be evaluated by considering the caribou-moose-wolf system entirely. As an umbrella species, the delineation of protected areas targeted for the conservation of boreal caribou could be an effective management strategy to maintain current biodiversity typical of boreal forest (Branton and Richardson, 2010; Thornton et al., 2016). Considering future changes in forest landscapes induced by CC and LUC, it is yet unclear if management strategies based on the current needs of boreal caribou would be effective at maintaining biodiversity. Moreover, it is also unclear to what extent the delineation of protected areas will succeed in protecting sufficient high-quality habitats under global changes. In fact, the impact of global change on the value of the umbrella approach remains unknown for most single-species management.

In previous studies, Bouderbala et al. (2023) as well as Labadie et al. (2023) examined the anticipated long-term changes in bird and beetle communities resulting from forest management and climate change scenarios, and predicted the impact of global change on the caribou food web. In this study, we profit from these analyses by comparing the umbrella value of forest management strategies designed around the needs of a single species (i.e., boreal caribou) for biodiversity conservation in a context of global change in the Canadian boreal forest. More precisely, we evaluated the potential umbrella effectiveness of different management strategies for maintaining sympatric bird and beetle species assemblages and high-quality habitat for those species. By integrating previous simulations from Labadie et al. (2023) with new simulations, we linked a landscape simulation model (Fig. 1.1) with individual-based models of caribou, moose and wolf agents (Fig. 1.2) and empirical models of bird and beetle species distribution developed by Bouderbala et al. (2023) (Fig. 1.3) to: (1) Evaluate the effectiveness of

management strategies and their landscape characteristics, through four scenarios of forest management (i.e., LUC), combined with three scenarios of CC; (2) Compare how species occurrences differ among LUC and CC scenarios; (3) contrasted LUC scenarios on biodiversity integrity; and (4) evaluate the extent to which management measures aiming at maintaining caribou populations also maintain biodiversity following global change (Fig. 1.4). Boreal caribou are under top-down control (Seip, 1992), and wolf predation risk is tightly linked to the level of disturbances (Environment Canada, 2012). Accordingly, as boreal caribou is an umbrella species, the management strategies associated with relatively low caribou mortality should perform as an umbrella and be linked to bird and beetle assemblages similar to undisturbed landscapes. More specifically, we used animal (birds and beetles) community dissimilarity between assemblages in disturbed and undisturbed landscapes as an index of biodiversity integrity (Bradford et al., 1998; Bichet et al., 2016), and boreal caribou mortality as an index of the effectiveness of the management strategy.

2. Methods

2.1. Model overview

Our study integrates the results that Labadie et al. (2023) obtained with an individual-based model (IBM) that caribou, moose and wolf agents interact in managed boreal forests. Specifically, the IBM provided caribou mortality rates in virtual landscape forests impacted by each of three levels of forest harvesting (No harvest, Medium harvest and High harvest), combined to three climate change scenarios (i.e., baseline, RCP 4.5, RCP 8.5). In addition to these simulations, we used the same IBM to assess the mortality rate expected in a landscape managed under a “Protected areas” scenario. This last scenario was designed specifically for boreal caribou conservation, in the territories covered by the

management strategy for boreal caribou under consideration in 2019 in Quebec (Ministère des Forêts de la Faune et des Parcs, 2019a, MFFP). The resulting dataset was used to assess the effectiveness of the Protected areas scenario in reducing caribou mortality, relative to the three other forest management scenarios (No harvest, Medium harvest and High harvest) in the context of climate change. Then, to evaluate the impact of caribou management on biodiversity, we estimate the overall probability of occurrence of bird and beetle species that can be expected in the different simulated landscapes based on the models of Bouderbala et al. (2023). Leveraging this comprehensive dataset, we examined the interaction between variation in caribou mortality rates between management scenarios and the concurrent change in bird and beetle assemblages (Table 1). Through this comparative analysis, we aimed to provide valuable insights into the efficacy of the newly developed management scenario and its implications for caribou, bird and beetle conservation efforts in the face of climate change.

Below, we provide an overview of the main model components and their behavior. Readers interested in the details of these components may also refer to Boulanger and Pascual Puigdevall (2021) (for the forest simulation model), Labadie et al. (2023) (for the IBM) and Bouderbala et al. (2023) (for bird and beetle species distribution models). For the IBM, empirical movement rules were derived from empirical data collected between 2005 and 2018. To project future scenarios, we examined the interactions among agents from the three species for two specific years (2000 and 2100), representing different expected landscape conditions. In all simulations, the caribou density remained constant at 2996 individuals, while the wolf and moose populations were adjusted based on available resources (Appendix A Table A.1).

2.2. Study area

The study area (48°N-54°N, 63°W-73°W) covers 115,470 km² of

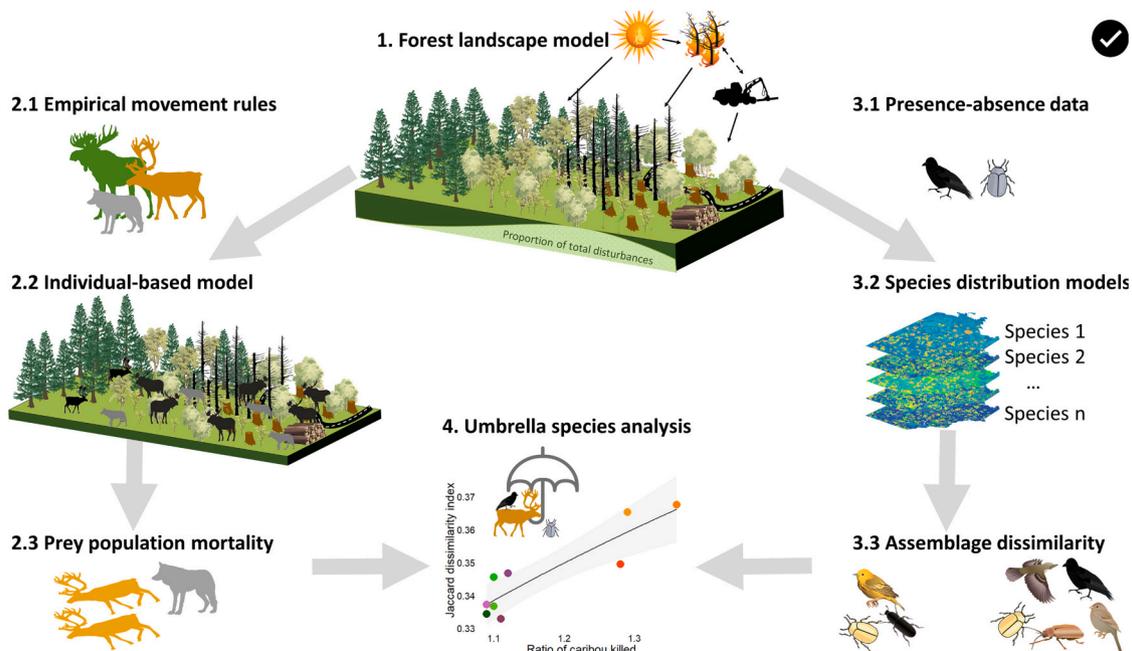


Fig. 1. Conceptual representation of the simulation design implemented in this study. (1) A forest landscape model was used to simulate stand-scale (i.e., individual tree establishment, growth and mortality) and landscape-scale dynamics (seed dispersal, natural and anthropogenic disturbances), allowing climate change and land use to individually impact forest landscapes. Forest landscape simulation outputs were then combined with empirical movements rules from boreal caribou, moose and wolves (2.1) to calibrate the individual based model (IBM – 2.2), and ultimately project prey mortalities (2.3) under each forest management and climate scenarios. In addition, we used presence-absence data of birds and beetles and models of species occurrence (3.1) to create species distribution models (3.2) and project species occurrence and assemblage dissimilarity (3.3) in landscapes developed from different land-use (LUC, logging) and climate change (CC, fire) scenarios. To evaluate if boreal caribou management strategies would be effective at maintaining biodiversity in the future under global change, we combined results of assemblage dissimilarity and caribou mortality (4). Tree, bird and beetle symbols courtesy of (UMCES, 2021). Schematic representation of the simulation design was adapted from Labadie et al. (2023).

Table 1

Characteristics of the four forest management scenarios cumulated with three climate scenarios used in LANDIS-II. For each scenario, the associated reference scenario and the land-use change characteristics were indicated.

Scenarios	Reference scenario	Land-use change characteristics
Baseline-Protected areas	Baseline-No harvest	Protected areas + Planned of the harvestable forest area per 10 years
Baseline-Medium harvest		4 % of the harvestable upland area per 10 years
Baseline-High harvest		8 % of the harvestable upland area per 10 years
RCP45-Protected areas	RCP 4.5-No harvest	Protected areas + Planned of the harvestable forest area per 10 years
RCP45- Medium harvest		4 % of the harvestable upland area per 10 years
RCP45-High harvest		8 % of the harvestable upland area per 10 years
RCP85-Protected areas	RCP 8.5-No harvest	Protected areas + Planned of the harvestable forest area per 10 years
RCP85- Medium harvest		4 % of the harvestable upland area per 10 years
RCP85-High harvest		8 % of the harvestable upland area per 10 years

boreal forest within the Côte-Nord region of Québec, Canada (Fig. 2). Natural disturbances, such as spruce budworm (SBW, *Choristoneura fumiferana*) outbreaks recurring every 35–40 years and frequent wildfires (with fire return intervals of approximately 250–400 years) are the dominant environmental events in this region (Boucher et al., 2017; Labadie et al., 2021). The study area exhibits a gradient in forest composition along its latitudinal axis. Towards the north, there are old-growth coniferous forests and open woodlands dominated by black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*). Moving southward, the forests transition to young and mature mixed forests containing black spruce, balsam fir, white birch (*Betula papyrifera*), white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*). Historically, forest harvesting was primarily concentrated in the southern part of the study area, gradually expanding northward, while wildfires were more prevalent in the northern regions.

2.3. Spatially explicit forest simulation model (Fig. 1.1)

2.3.1. Climate scenarios

Future climate projections for the study area were derived from two Representative Concentration Pathways (RCP, see Van Vuuren et al. (2011) for more information) known as RCP 4.5 and RCP 8.5. These projections were obtained from the Canadian Earth System Model version 2 (CanESM2) and downscaled using the ANUSPLIN method to a 10-km resolution. By the year 2100, compared to 2000, the study area is expected to experience an increase in mean annual temperatures ranging from approximately 3 °C (under RCP 4.5) to 7.5 °C (under RCP 8.5). Additionally, average precipitation is projected to increase by 7 % (under RCP 8.5) to 10 % (under RCP 4.5). Forest landscape simulations were parameterized using monthly time series data from each climate scenario.

2.3.2. Forest landscapes simulations with LANDIS-II

The forest landscape simulations were conducted using LANDIS-II v7.0 (Scheller and Mladenoff, 2004), a spatially explicit raster-based model that captures forest ecosystem processes at both stand and landscape scales (Scheller and Mladenoff, 2004). This model represents trees as cohorts, allowing for the assessment of ecological processes across broad spatial and temporal scales. It has been extensively used and validated in boreal regions (Boulanger et al., 2017; Taylor et al., 2017;

Tremblay et al., 2018; Boulanger and Pascual Puigdevall, 2021). A complete description of the model can be found in Labadie et al. (2023) and Tremblay et al. (2018). The spatial resolution for cell size was established at 250 m, equivalent to 6.25 ha. The simulations were initialized for the year 2000. To initialize the characteristics of forest composition and structure within each cell, data from the Canadian National Forest Inventory (NFI) and cohort information from provincial forest inventory plots (FIP), both permanent and temporary, were utilized. Using variables such as species biomass, mean annual temperature, and total annual precipitation, we conducted a nearest neighbor spectral analysis to assign the FIP plot with the closest resemblance, measured by Euclidean distance, to each 250-m cell. This imputation process was conducted in 20-year age intervals to ensure that the Euclidean distance primarily reflected site productivity rather than stand age. Subsequently, these cells were assigned to specific spatial units referred to as 'landtypes,' taking into consideration consistent soil conditions (as outlined by Mansuy et al., 2014) and uniform climate conditions. Cells on the grid that had non-forest cover types occupying >50 % of their area were categorized as 'inactive.' The model considers climate-sensitive tree growth, regeneration, and wildfire events.

2.3.3. Natural disturbances

In our study, we conducted fire simulations using the LANDIS-II Base Fire extension v 4.0. This extension replicates random fire events, considering factors like fire ignition, initiation, and spread. We organized fire data into 'fire regions,' aligning them with Canadian Homogeneous Fire Regime (HFR) zones. We aimed to maintain consistent fire characteristics to improve traceability and reproducibility, avoiding dynamic changes in simulations due to shifts in vegetation and climate. For both current and future fire regimes in each region, we used projections by Boulanger et al. (2017) under baseline and RCP climate scenarios.

To simulate outbreaks of Spruce Budworm (SBW), we used the Biological Disturbance Agent (BDA) extension (Sturtevant et al., 2004). This extension is designed to mimic tree mortality caused by insect infestations. We considered the vulnerability of host tree species to SBW, with balsam fir, white spruce, red spruce, and black spruce ranked from most to least susceptible. Outbreaks were modeled as probabilistic events at the cell level, influenced by site conditions, neighboring tree dominance, and regional outbreak status. The severity of these outbreaks and tree mortality depended on these probabilities and the susceptibility and age of host species. The parameters used in our study were calibrated and validated using various sources specific to the mixed boreal forest. Regional outbreaks were calibrated to reach the highest severity level possible using this extension, lasting for a maximum of one timestep (equivalent to 10 years) and occurring approximately every 40 years, consistent with observed regional patterns.

2.3.4. Forest harvesting and roads

We employed the model introduced in Labadie et al. (2023) to simulate caribou mortality rates under different forest disturbance levels (No harvest, Medium harvest and High harvest) and the newly developed species-specific management strategy (Protected areas). More precisely, the four simulated forest management scenarios (i.e., land-use change scenarios, LUC, Table 1) were determined according to a gradient of forest harvesting; i) no harvesting (No harvest); ii) medium-intensity clearcutting similar to half of the mean rate of the current forest harvesting (Medium harvest—applied to 4 % of the harvestable upland area per 10 years), iii) clearcutting with intensity similar to current management practices within the study area (High harvest—applied to 8 % of the harvestable upland area per 10 years), and iv) a scenario designed for boreal caribou conservation (Protected areas) consistent with the territories under consideration in 2019 in Quebec (Ministère des Forêts de la Faune et des Parcs, 2019a, MFFP). The strategy integrates the protection of large tracts of forest (i.e., protected areas with no forest harvest), and adaptive forestry practices designed to

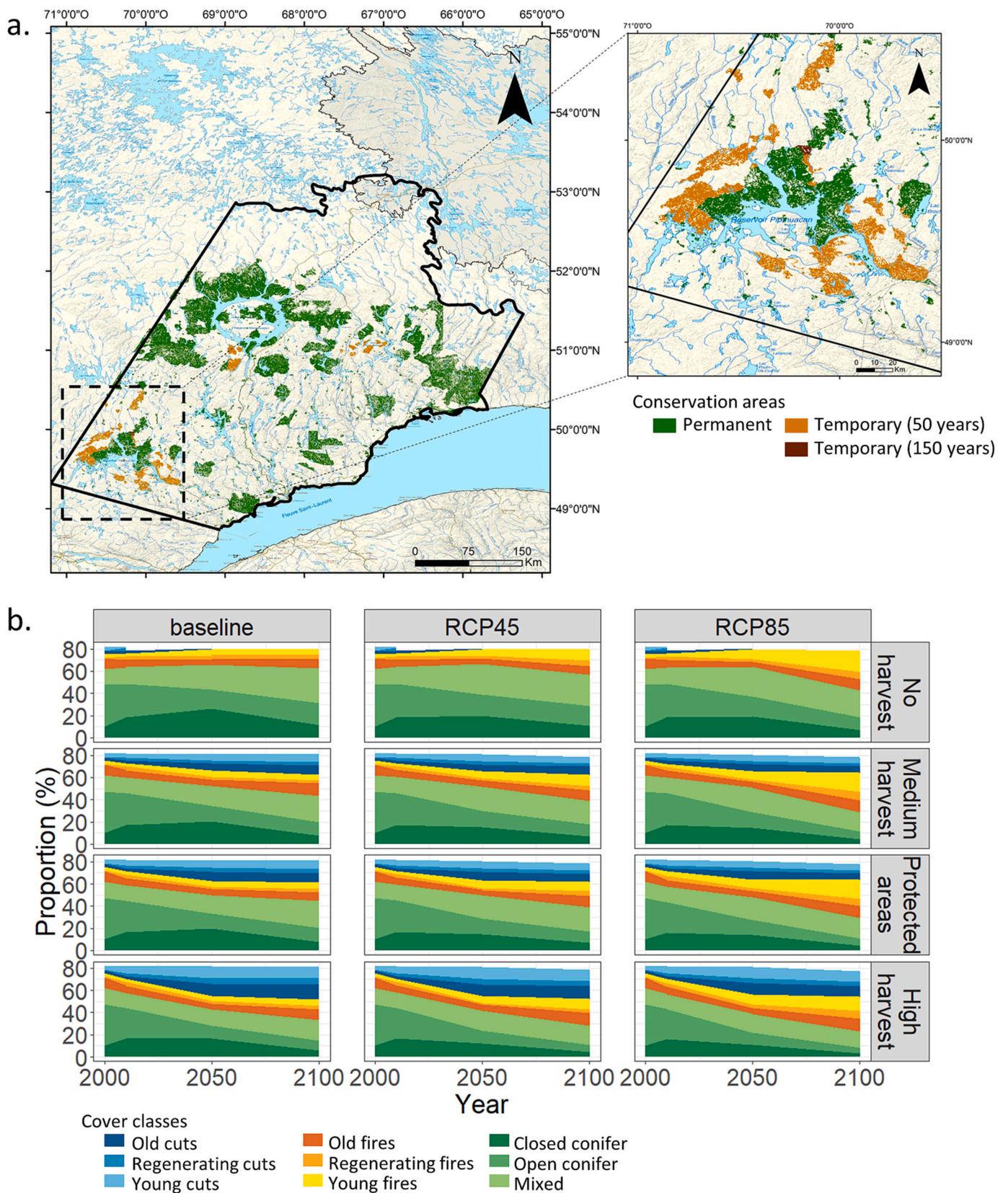


Fig. 2. Study area in the province of Quebec, Canada, with delineation of the conservation areas of the Protected areas scenario (a). Colors represent the temporary (50 or 150 years) or permanent conservation areas where no harvesting take place during the time period considered. Temporal changes in land cover (b). Stacked trends in the proportion of cover classes for each of the four forest management scenarios under either Baseline, RCP 4.5 or RCP 8.5 climate scenario. The remaining percent correspond to cover classes 'Open areas' and 'Other'. RCP, representative concentration pathway.

avoid caribou habitat and reduce rates of logging (Ministère des Forêts de la Faune et des Parcs, 2019a). We integrated the protected areas and the adaptive logging rate within each targeted area to delineate temporary (50 or 150 years) or permanent conservation areas where no harvesting occurred (Fig. 2). In the remaining area, harvest rates were parameterized according to those proposed by the MFFP under this plan (variation between 3.3 and 10.6 % per 10 years by forest management unit). Protected patch size varied between 0.06 km² to 2037 km² (mean size = 4.44 km² and median size = 0.12 km²), for a total area of 15,931 km². Only stands that included tree cohorts older than 60 years were allowed for harvesting simulation. Mean harvested patch size varied between 40 km² to 150 km², following current practices. Harvest rates were held constant throughout the simulations unless not enough stands qualified for harvest. In this latter case, harvest proceeded until there were no more stands available. Forest harvesting was simulated using the Biomass Harvest extension (v5.0; Gustafson et al., 2000), while roads were drawn using the Forest Roads Simulation module (Hardy, 2021). Hence, the road networks varied among forest harvesting scenarios. For the scenario designed for boreal caribou conservation, the dismantle of forest roads was not simulated, although initially recommended (Ministère des Forêts de la Faune et des Parcs, 2019a).

2.3.5. Simulation design

LANDIS-II simulations were run for 100 years starting from the year 2000, considering each radiative forcing and forest harvesting scenario with a 10-year time step. For the next steps of the analysis, we used landscapes resulting from the LANDIS-II model for the years 2000 and 2100 to assess the cumulative impact of anthropogenic disturbances and climate change on caribou mortality in the IBM analysis as well as on bird and beetle species distribution.

2.3.6. Habitat characteristics of simulated landscapes

To assess the composition of the forest and generate the final forest cover maps to use with biodiversity and individual-based caribou models, we used the relative proportions of species groups (conifer and deciduous species), obtained from the biomass outputs of the LANDIS-II model. As LANDIS-II does not directly provide crown closure data, we developed a random forest model, following Labadie et al. (2023) methods, for predicting crown closure using Canadian National Forest Inventory (NFI) forest attribute maps (Beaudoin et al., 2014). These maps are a k-Nearest Neighbours interpolation of NFI photoplot data collected in 2001, encompassing over 130 forest attributes, including species-specific biomass, stand age, and crown closure at a 250-m resolution (refer to Beaudoin et al. (2014)). Subsequently, we constructed a random forest model to forecast cell-level crown closure in NFI products based on NFI species-specific biomass and stand age. This model demonstrated a high goodness of fit ($R^2 = 0.86$). We then applied this model to LANDIS-II outputs, enabling us to predict crown closure throughout the simulation for each cell, using simulated species-specific biomass and stand age. Using information on species group and predicted crown closure, we classified the land cover into five distinct classes from the Land Cover Classification of the Earth Observation for Sustainable Development of Forests (EOSD) (Beaubien et al., 1999): closed-canopy conifer forest (conifer >75 % and crown closure >60 %), open-canopy mature conifer forest (conifer >75 %, and crown closure ≤60 %), mixed forest (conifer >25 % and deciduous >25 %), open area (Vegetation >50 % and Vegetation (non-treed) ≥ Vegetation (treed)) and other (Non-Vegetation ≥50 %). Land cover maps were then updated by incorporating roads, as well as recent (≤10 years), regenerating (11–20 years) and old (21–50 years) cutblocks/burned areas that were simulated by LANDIS-II at each 10-year time step.

2.3.7. Analysis of landscape structure and composition

To assess changes in landscape composition, we analyzed the LANDIS-II outputs to determine the proportions of anthropogenic and natural disturbances, as well as the proportion of deciduous land cover

(Appendix A Table A.2.a-c.). The calculation of disturbance levels followed the methodology outlined by Environment Canada (2011), which involved measuring the percentage of nonoverlapping area covered by burns, roads, and cuts. To account for the influence of roads and cuts on the surrounding areas, we included 500-m buffer zones around them in the calculation of disturbed areas as assessed by Environment Canada (2011).

To assess changes in landscape configuration, we used the ‘landscape metrics’ package in R (Hesselbarth et al., 2019). Two metrics were chosen to capture different aspects of landscape structure, which could potentially mediate individual responses to LUC and CC. At the patch level (i.e., neighboring cells belonging to the same land cover class), the mean ‘isolation index’ was calculated to evaluate the connectedness of patches within the same land cover class (Hesselbarth et al., 2019). The isolation index is derived from the ‘cohesion index’ and is calculated as $1 - \text{‘cohesion index’}$. A lower value of the ‘isolation index’ indicates that patches of the same class are more aggregated, while a higher value suggests increased isolation of patches (Appendix A Table A.2.d). This metric serves as a proxy for assessing the fragmentation and loss of mature conifer stands. At the landscape level, the ‘homogenization index’ was calculated, reflecting the complexity of the landscape pattern configuration (Nowosad and Stepinski, 2019; Hesselbarth et al., 2019). The ‘homogenization index’ is calculated as $1 / \text{‘conditional entropy’}$. A small value of the ‘homogenization index’ indicates that cells of one category are adjacent to cells of many other categories, implying a more heterogeneous landscape. Conversely, high values of the ‘homogenization index’ values indicate that cells of one category are predominantly adjacent to only one other category of cells, suggesting a more homogeneous landscape (Appendix A Table A.2.e).

2.4. Movement rules derived from radio-collared caribou, moose and wolves (Fig. 1.2.1)

To determine the effectiveness and then the umbrella value of management strategies, we used simulation results of boreal caribou mortality as an index of strategy suitability. We thus ran a spatially explicit individual-based model (IBM) with simulated agents, representing individuals of the three species (moose, caribou and wolf). Species-specific movement rules determined from empirical data collected for caribou, moose, and wolves over the study area (Labadie et al., 2023) were implemented in the IBM.

Briefly, we used 68 GPS-collared adult female caribou, 16 wolves, and 15 moose monitored between March 2005 and December 2018. Our research primarily focused on the winter season, as this period is associated with higher caribou mortality rates (Losier et al., 2015; Labadie et al., 2021). To examine the extent to which individuals alter their movement behavior in response to environmental characteristics, step selection functions (SSFs; (Fortin et al., 2005)), specific for each species were used. Details on GPS data and SSF models can be found in Appendix S1 in Labadie et al. (2023).

Habitat was characterized from 2004 to 2018 using the Canadian NFI forest cover maps (Beaudoin et al., 2014), and information provided annually by local forestry companies (Ministère des Forêts de la Faune et des Parcs, 2019b) and from the Canadian National Fire Database (Canadian Forest Service, 2019) for anthropogenic and natural disturbances.

2.5. Individual-based model (IBM) (Fig. 1.2.2)

A complete description of the model and how it was parameterized, calibrated and validated can be found in Labadie et al. (2023). Below, we outline the major model components.

Briefly, the IBM simulations were conducted in a spatially explicit representation of the Côte-Nord region using simulated landscapes generated from the forest landscape model for projections. The IBM was used to simulate the movements and interactions of individual agents,

including prey species (caribou and moose) and predators (wolves). These movements and predation events were influenced by species-specific behavior and the characteristics of the surrounding landscape. Each species exhibited distinct responses to landscape features, such as cuts and roads (Fortin et al., 2013, 2015; Gagné et al., 2016), resulting in variations in the types of land cover where the likelihood of predator-prey encounters was highest for each prey species (Courbin et al., 2009, 2013). When an individual agent moved, 21 random steps were generated within a buffer surrounding their current position. Subsequently, the agent relocated to the position that exhibited the highest SSF score. The maximum distance that an individual of a given species could cover in a single step was determined based on the 99th percentile of the species-specific empirical step length distribution (Dickie et al., 2017) (Appendix A Table A.3). Prey could only die from predation, and they were then removed from the simulation.

2.5.1. Moose and wolf numerical response

Simulations accounted for the typical numerical response of moose that follows timber harvesting (Potvin et al., 2005; Anderson et al., 2018), and the subsequent increase in wolf density (Messier, 1984). The number of moose in a simulation was adjusted to the proportion of deciduous vegetation available in simulated landscapes (Appendix A Table A.1), and then the number of wolf packs was adjusted to moose density based on Messier (1984), Appendix A Table A.1).

2.5.2. Model projections

To simulate the movements of wolf, moose and caribou, and to estimate the predation rate of wolves under various scenarios, IBM simulations were conducted for a duration of one year in both the years 2000 and 2100. Each simulation was replicated ten times. Consequently, a total of 130 (12 scenarios in 2100 + 1 reference scenario in 2000) x10 replicates) simulations were performed.

2.6. Analysis of outputs of individual-based models (Fig. 1.2.3)

2.6.1. Analysis of prey mortality

To evaluate the effectiveness of conservation strategy in mitigating caribou mortality and the influence of the cumulative effects of LUC and CC, we compared the predicted caribou mortalities simulated by the IBM across different scenarios of CC and LUC. To assess how changes in forest structure and composition impacted the proportion of caribou killed (i.e., number of caribou killed/total number of caribou), we used a generalized linear mixed model (GLMM) with a binomial distribution. We thus analyzed the relationship between the proportion of caribou mortalities and several covariates related to forest characteristics, including the proportion of areas disturbed by cuts and roads, burned areas, and landscape features, such as mean stand age, proportion of deciduous vegetation, landscape homogenization and isolation of mature conifer stands. To account for the variation in the proportion of caribou killed among LUC scenarios because of CC, we created a factor from the combination of LUC and CC (i.e., LUC × CC) that was used as a random effect, with the factor “No harvest _baseline” as reference. We considered a logit link and binomially distributed errors.

2.7. Bird and beetle occurrence data (Fig. 1.3.1)

We characterized boreal biodiversity based on predictive models of occupancy of birds and beetles previously developed from field observations (Bouderbala et al., 2023). For birds, models were based on presence-absence data from the Second Atlas of Breeding Birds of Québec (Regroupement QuébecOiseaux, 2018). All birds were identified at the species level. For beetles, species abundance datafiles collected in 2004, 2005, 2007, 2011, and 2018 from June to August (Janssen et al., 2009; Légaré et al., 2011; Bichet et al., 2016) were merged, and then transformed into a presence-absence database (Bouderbala et al., 2023). The beetles were identified at the species level when possible; otherwise,

the identification to the genus level was standardized (92 % identifications were at the species level).

2.8. Species distribution models (Fig. 1.3.2)

As a result of these models, Bouderbala et al. (2023) provides predicted density for 31 bird and 77 beetle species for each simulated landscapes generated from the forest landscape model for projections (The species list used for the model is in Appendix B Table B.1), which we used to evaluate the umbrella value of management strategies designed around the needs of boreal caribou. In addition to the expected species distribution maps provided by Bouderbala et al. (2023), we generated maps of the predicted occurrence for bird and beetle species for the caribou conservation scenario (i.e., Protected areas). Briefly, these models only included species that were recorded at $\geq 1\%$ and $\geq 5\%$ of all sites for birds and beetles, respectively, and that also had high goodness-of-fit (i.e., Area under the curve (AUC) diagnostic ≥ 0.7). Presence-absence data of bird and beetle species were used to estimate the probability of occurrence related solely to habitat characteristics using GLMMs with a random intercept to account for differences among sampling years (see Bouderbala et al. (2023) for more details).

Similarities in predicted probability of occurrence combined with expert opinion allowed to classify bird species according to their main habitat associations (mature forests or early-to-mid succession forests, Appendix B Table B.1). Early-to-Mid succession forest included the following land covers: wetland and young stands of deciduous, mixed-wood and coniferous species. On a total of 31 bird species, 7 were associated with mature forests, 20 with early-to-mid succession forests and 4 were considered as generalist. Knowledge regarding beetle habitat associations was too scarce to allow similar classification and further habitat-related investigations. The occurrence probability maps of every included species were then computed for each scenario.

2.9. Analysis of outputs of species distribution models (Fig. 1.3.3)

Impacts of LUC and CC on bird and beetle species assemblages were assessed by comparing occupancy and assemblage dissimilarity under each CC and LUC scenario in 2100. We used the predicted probability of occurrence of species s (p_s) for every pixel of the landscape, as a function of environmental characteristics associated with a given CC and LUC scenario. An occupancy index of species s (P_s) was estimated as its mean probability of occurrence in the landscape for each of the climate j and forest management scenario k :

$$P_{sjk} = \frac{\sum_{pixels} \log(p_{sjk} + 1)}{N_{pixels}}$$

We evaluated the percent change in P_s between the reference scenario (No harvest under climate j scenario, Table 1) and each of the climate j and forest management scenario k , as:

$$\Delta P_{sjk-ref} = \frac{P_{sjk} - P_{sjref}}{P_{sjref}} \times 100$$

We then computed the Jaccard dissimilarity index (JDI; (Jaccard, 1908, Rahel, 2000)) on occupancy indices to assess the biodiversity change across scenarios (i.e., the degree of the dissimilarity in assemblage composition between the compared scenarios). Biodiversity change was calculated from the equation:

$$JDI_{jk-ref} = \frac{2BC_{jk-ref}}{1 + BC_{jk-ref}}$$

Where BC is the Bray-Curtis dissimilarity index determined from the relationship:

$$BC_{jk-ref} = \frac{\sum_{\text{species}} |P_{sjk} - P_{sref}|}{\sum_{\text{species}} (P_{sjk} + P_{sref})}$$

where P_{sjk} and P_{sref} refer to the index of occupancy of a species s in landscapes under climate j and forest management scenario k and No harvest (i.e., reference), respectively (Oksanen et al., 2020).

To assess how changes in forest structure and composition impacted variation in biodiversity (i.e., the Jaccard Dissimilarity Index, JDI), we used a linear regression to relate the biodiversity change to each covariate of forest characteristics: the proportion of areas disturbed by cuts and roads, burned areas, and landscape characteristics, such as the mean stand age, proportion of deciduous vegetation, landscape homogenization and isolation of mature conifer stands. As the JDI is an index that compare two scenarios (scenario jk compared to the scenario of reference, Table 1), we calculated the percentage of change of each covariate of forest characteristics following:

$$\text{Percentage of change (Covariate}_{x_{jk}}) = \left(\frac{\text{Covariate}_{x_{jk}}}{\text{Covariate}_{x_{ref}}} - 1 \right) \times 100$$

where $\text{Covariate}_{x_{jk}}$ is the value of the landscape characteristics x under the climate scenario j and forest management k . For example, for the covariate 'mean stand age', we used the value of the mean stand age of the landscape under the scenario RCP 8.5-Medium harvest and the value of the mean stand age of the landscape under the reference scenario (RCP 8.5-No harvest, Table 1). This method was used to get a direct assessment of the effects of LUC while controlling for CC.

2.10. Umbrella effectiveness of a conservation strategy under global change (Fig. 1.4)

To test the umbrella value of the boreal caribou management strategies' ability to conserve associated biodiversity, we calculated the Pearson's correlation coefficient between the ratio of caribou killed, an index of the effectiveness of management strategies for maintaining the species, and biodiversity change (i.e., the Jaccard Dissimilarity Index, JDI) from both avian and beetle taxa between scenarios with harvest (Protected areas, Medium and High harvest) and the No harvest scenario in 2100 while controlling for CC (Table 1). To determine the cumulative impact of LUC and CC on the umbrella value of a management strategy, we calculated the Pearson's correlation coefficient between the ratio of caribou killed and biodiversity change from both taxa between scenarios with harvest (Protected areas, Medium and High harvest) and the Baseline-No harvest scenario in 2100 as a unique reference for each CC scenario.

3. Results

3.1. Projection of forest cover

LUC changed the composition of boreal landscapes by initiating widespread secondary succession (Fig. 2), and by decreasing the proportion of old forests. Under the Protected areas scenario, the average stand age across the landscape was 71-year-old, showcasing the successful preservation of mature forest stands compared to the High harvest scenario, where the average stand age was 53-year-old under the baseline climate scenario. This prediction of increasing deciduous vegetation and decreasing proportion of old-growth forests was further exacerbated by CC (Fig. 2). Under each climate scenario, the proportion of post-harvest stands <50-year-old were comparable under the Medium harvest and Protected areas scenarios (Appendix C Table C.1). Simulation outputs of Medium harvest and Protected areas scenarios were similar: at the end of 100 years (Appendix C Table C.1), both scenarios ended up with comparable amounts of most forest age-class types and

habitat available for species (Fig. 2, Appendix C Table C.1). CC also altered landscape composition mainly through an important surge in area burned (e.g., the proportion of burned areas doubled under RCP85 compared to baseline climate scenario under No harvest scenario in 2100, Appendix C Table C.1). Indeed, the proportion of deciduous vegetation in the study area was mainly driven by disturbance-induced increases in boreal, co-occurring deciduous species (e.g., trembling aspen) rather than through a climate-induced northward expansion of thermophilous species. The shift to deciduous and younger vegetation was characterized by the increase in mixed stands and in regenerating cuts and burned areas (Fig. 2). Forest disturbance levels (i.e., Proportion of cuts and roads, and burned areas) increased with the intensification of LUC and CC. Moreover, CC caused a steep decline in landscape complexity by causing an increase in proportion of burned areas (Pearson's correlation $r = -0.87$, $P < 0.01$, in 2100). Protected areas scenario had more aggregated cuts than Medium harvest scenarios, which increased landscape complexity; the complexity index was 1.83 and 1.73 respectively under Baseline climate scenario. The scenario with the lowest landscape complexity was High harvest under RCP 8.5 scenario (value of the complexity index = 1.51). In addition, the change in landscape structure can also be characterized by the isolation of mature conifer stands which was correlated with the increase in LUC (Pearson's correlation $r = 0.68$, $P = 0.01$, in 2100), and the increase in the proportion of deciduous vegetation within the landscape (Pearson's correlation $r = 0.84$, $P < 0.01$, in 2100).

3.2. Effectiveness of forest management for reducing boreal caribou mortality

We determined the effectiveness of management strategies to reduce mortality of the boreal caribou by analyzing the simulated proportion of caribou killed by wolf for each scenario. The effectiveness of the two boreal caribou management strategies through the decrease in forest harvesting rate (Medium harvest scenario) or the delineation of protected areas (Protected areas scenario) was equivalent as the proportion of caribou killed was nearly the same under both scenarios (Appendix C Fig. C.1). Moreover, the proportion of caribou killed by wolves increased with the increase in the proportion of cuts and roads (Pearson's correlation $r = 0.67$, $P < 0.01$), and deciduous vegetation (Pearson's correlation $r = 0.88$, $P < 0.01$). CC and LUC also affected landscape structure by increasing the homogeneity of the landscape and the isolation of mature conifer stands which are both predicted to increase the proportion of caribou killed by wolves (Pearson's correlation $r = 0.58$, $P < 0.01$, and Pearson's correlation $r = 0.70$, $P < 0.01$, respectively) (Appendix C Fig. C.2). An overall increase in stand age, which is predicted to be favored by caribou conservation strategies, is expected to reduce the proportion of caribou killed by wolves (Pearson's correlation $r = -0.83$, $P < 0.01$) (Appendix C Fig. C.2).

3.3. Projected bird and beetle occupancy following climate change and forest management

The simulations indicate that, compared to the uncut landscape (No harvest), the probability of decrease or increase in the occurrence of beetle species should remain approximately the same in landscapes altered by the three forest management scenarios (i.e., Protected areas, Medium and High harvest scenarios), regardless of CC (Fig. 3). For bird species associated with early-to-mid succession forests, approximately 90 % of species were predicted to increase their probability of occurrence under the three LUC scenarios compared with the No harvest scenario, regardless CC (Fig. 3). The great majority of increasing bird species were early successional species (94 % associated with young forest and/or harvested forest <20-year-old, Appendix B Table B.1 and Appendix C Table C.2). The highest decrease in the probability of occurrence was obtained for bird species associated with mature forests, with the highest decrease under High harvest scenario, regardless of CC

(Fig. 3). Those species were associated with old forests and/or harvested forests older than 20-year-old (Appendix B Table B.1). In addition, bird species associated with mature forests that were disadvantaged by natural and anthropogenic disturbances (i.e., with a negative percentage of change in species index of occupancy), were predicted to have an even larger decrease in their probability of occurrence with CC, resulting in a larger negative percentage of changes in species index occupancy in addition to the impact of LUC (Fig. 3). For example, under RCP 8.5 species associated with mature forests that are expected to decrease their probability of occurrence will decrease by 28 %, 24 % and 34 % respectively depending on forest harvesting scenarios (i.e., Medium harvest, Protected areas and High harvest), while under the baseline scenario, they are expected to decrease their probability of occurrence by 21 %, 16 % and 30 % respectively (Fig. 3).

3.4. Variations in bird and beetle assemblages following climate change and forest management

Compared to the No harvest scenario, the biodiversity change (i.e., Jaccard dissimilarity index; JDI) for all taxa under Medium harvest and Protected areas scenarios were very similar regardless of CC scenarios (Table 2). Biodiversity change increased with increasing forest harvesting rates for all taxa (Table 2). LUC had a more important impact than CC on biodiversity change. An 11 % increase in cuts (Medium harvest [16 % of cuts] to High harvest [27 % of cuts]) increased biodiversity change by 38 %, when averaging all climate scenarios. Compared to Baseline-No harvest, the cumulated effects of LUC and CC resulted, on average, in 25 % and 9 % higher dissimilarity under RCP 8.5 and RCP 4.5 respectively than under no climate change (Appendix C Table C.3). When considering the cumulative effects of LUC and CC (i.e., with the unique reference scenario Baseline-No harvest), the biodiversity change under Protected areas scenario was smaller than the biodiversity change under Medium harvest scenario for all taxa and CC scenarios (Appendix C Table C.3).

More precisely, biodiversity change (JDI) increased with the growing proportion of cuts and roads (Pearson's correlation $r = 0.88, P < 0.01$) and deciduous vegetation (Pearson's correlation $r = 0.95, P < 0.01$)

Table 2

Biodiversity change shown through the Jaccard dissimilarity index (JDI) contrasting prediction of species assemblages between the reference scenario and harvested landscapes in 2100, given climate change, for the boreal forest in Canada. All taxa column includes the value of JDI calculated from beetle and bird (Mature, Early-Mid succession forests and generalist species) data.

Scenarios	Birds (Mature)	Birds (Early-Mid)	Beetles	All taxa	Reference scenario
Baseline-Protected areas	0.14	0.13	0.10	0.13	Baseline-No harvest
Baseline-Medium harvest	0.17	0.15	0.12	0.15	
Baseline-High harvest	0.23	0.19	0.17	0.20	
RCP45-Protected areas	0.15	0.13	0.10	0.13	RCP 4.5-No harvest
RCP45-Medium harvest	0.18	0.13	0.11	0.14	
RCP45-High harvest	0.25	0.19	0.16	0.20	
RCP85-Protected areas	0.13	0.10	0.08	0.11	RCP 8.5-No harvest
RCP85-Medium harvest	0.16	0.11	0.09	0.12	
RCP85-High harvest	0.21	0.16	0.12	0.17	

(Fig. 4). Biodiversity change decreased, however, as landscapes become increasingly comprised of older forests (Pearson's correlation $r = -0.90, P < 0.01$) (Fig. 4). Changes in landscape structure induced by CC and LUC, through the increase in the homogeneity of the landscape, were predicted to increase the biodiversity change (Pearson's correlation $r = 0.82, P < 0.01$) (Fig. 4). Our analysis did not detect a significant link between the proportion of burned areas, the isolation of mature conifer

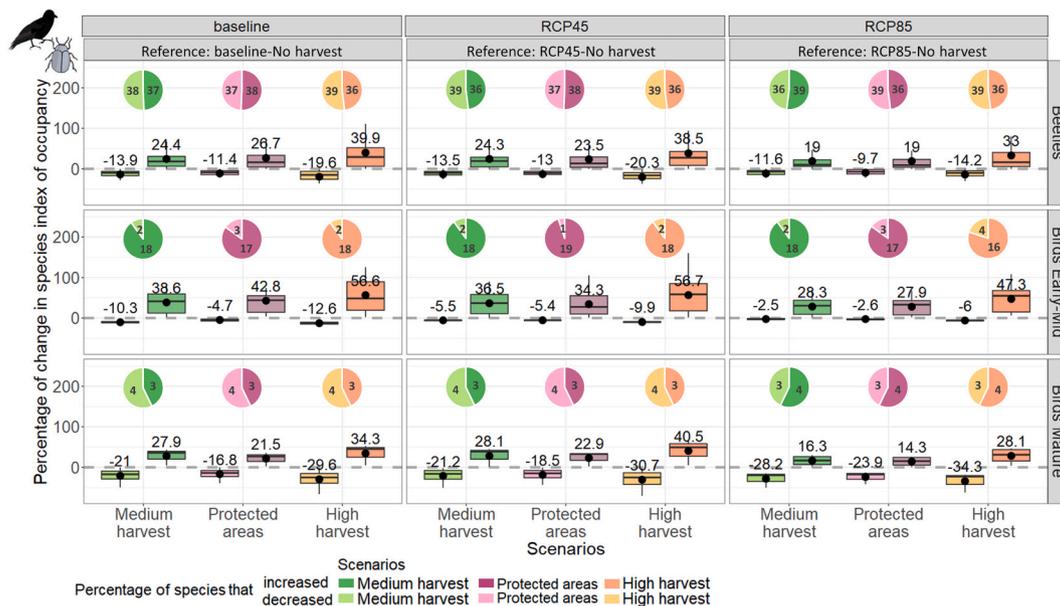


Fig. 3. Percentage of change (boxplot) in species occupancy index between the harvested landscapes and the uncut landscape (No harvest) in 2100. Black points represent the mean percentage of change in species occupancy index and error bars represent 95 % confidence intervals. Pie charts represent the percentage of species for which the probability of occurrence respectively increased or declined with harvest, relative to the scenario with no harvest, under each climate change scenario. For each scenario, the black values within the pie chart represent the number of species for which the probability of occurrence respectively increased or declined. The grey dashed line represents a percentage of change in species index of occupancy equal to zero.

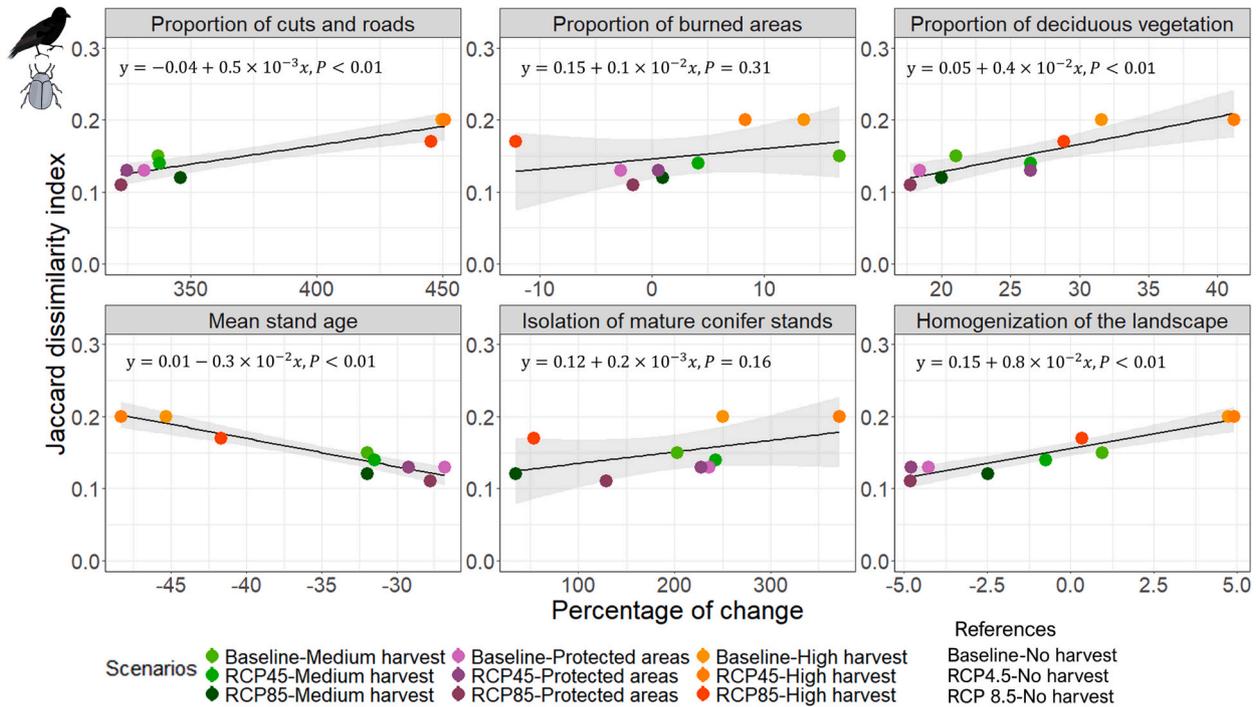


Fig. 4. Change in biodiversity shown through the Jaccard dissimilarity indices (JDI) of animal species assemblages (all taxa combined) comparing landscape characteristics (Proportion of cuts and roads, Proportion of burned areas, Proportion of deciduous vegetation, Mean stand age, Isolation of mature conifer stands and homogenization of the landscape) to the reference landscape in 2100. Equations came from linear models to relate the biodiversity change to each covariate of forest characteristics. The x-axis corresponded to the percentage of change of landscape characteristics indicated in each strip between the tested scenarios and the reference scenario indicated in the figure.

stands and biodiversity change (Pearson's correlation $r = 0.30, P = 0.43$ and Pearson's correlation $r = 0.62, P = 0.07$, respectively) (Fig. 4).

3.5. Umbrella effectiveness of conservation strategies

Finally, we found a positive relationship between the ratio of the proportion of caribou killed and biodiversity change (JDI) from both taxa (Pearson's correlation $r = 0.89, P < 0.01$, Fig. 5a), which implies that bird and beetle assemblages are less impacted (i.e., lower JDI) when conditions are more suitable for caribou survival (lower mortality).

Biodiversity change and boreal caribou mortality decreased when a management strategy was implemented compared to the current practice (High harvest scenario) (Table 2, Appendix C Fig. C.1). When we used the Baseline-No harvest scenario as a unique reference to determine the cumulative effects of LUC and CC, we observed that biodiversity change and the ratio of the proportion of caribou killed increased under RCP 8.5, regardless of LUC (Fig. 5b and Appendix C Table C.3). These results demonstrate that the effectiveness of management strategies also depends on the cumulative impacts of CC and LUC.

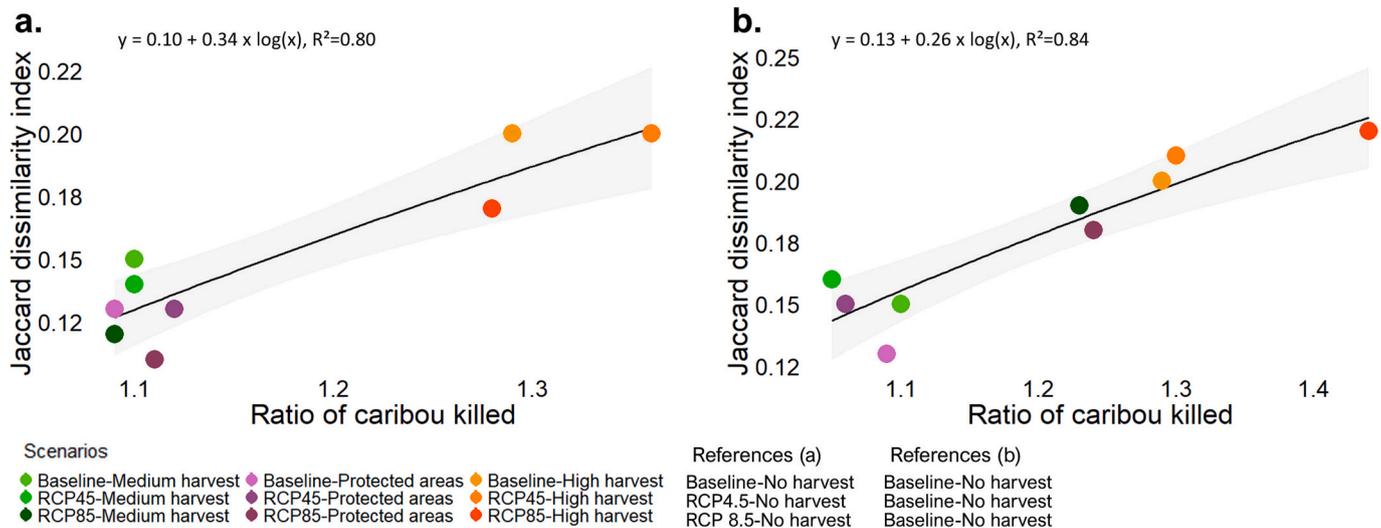


Fig. 5. Change in biodiversity shown through the Jaccard dissimilarity indices (JDI) of animal species assemblages (all taxa combined) comparing the ratio of the proportion of caribou killed by wolf to the reference landscape in 2100. a) shows the effects of LUC, regardless of CC and b) shows the cumulative effects of LUC and CC. The reference scenarios used to calculate the biodiversity change and the ratio of caribou killed were the same. The grey ribbon indicates 95 % CI.

4. Discussion

This work highlights future cumulative effects of climate change and various land-uses resulting from different management strategies on forest characteristics, animal assemblages, and the umbrella value of boreal caribou for biodiversity conservation. Our results show an interplay among changes in vegetation structure and composition, boreal caribou mortality and biodiversity assemblages (Fig. 4, Appendix C Fig. C.2). Our findings also point to LUC induced by forest harvesting as a key driving force of community assembly. In accordance with Bichet et al. (2016), we show that management strategy designed around the needs of boreal caribou populations (Protected areas scenario) and management strategy that reduce the level of forest harvesting (Medium harvest scenario) can serve as an effective umbrella for preserving bird and beetle assemblages, but we further predict that their umbrella value will depend on the severity of climate change. In addition to the similar forecasted response of boreal caribou and bird and beetle assemblages to global change, management strategies designed to maintain boreal caribou can serve for conserving sufficient high-quality habitat of co-occurring species. As an effective umbrella species for biodiversity, boreal caribou could alleviate the effect of global change on animal species assemblages without having to identify all the sympatric species and their independent responses to CC and LUC.

We emphasize that the main goal of this study was to determine whether scenarios aiming at the conservation of one umbrella species also maintain the integrity of regional biodiversity under climate change, not testing how well caribou performs as an umbrella to other potential umbrella species. Among the possible management measures aimed at preserving boreal caribou populations, we tested two possible management actions. The first one, Medium harvest, was simulated to evaluate the effect of the reduction of the level of forest harvesting. The second one, Protected areas, was simulated to evaluate the effect of the delineation of specific conservation areas, aiming at minimizing the threat of anthropogenic disturbances while maximizing patches of high habitat quality for boreal caribou. The delineation of protected areas influenced the location of cuts, and subsequently the structure of the landscape. Our results highlighted that species assemblages were more similar to the uncut landscape under which we observed complex landscape with large mature stands (i.e., landscapes under conservation strategy scenarios). Previous studies have reported that landscape complexity has a positive effect on biodiversity (Janssen et al., 2009), and could be used to manipulate species interactions with the aim of increasing or decreasing the predation rate on target populations according to management objectives (Smith et al., 2019; Vanlandeghem et al., 2021). Our results emphasize an opportunity to increase the umbrella value of the proposed management strategies by focusing on human activities while maintaining landscape complexity.

Projected increases in fire activity due to CC cumulate with forest harvesting are expected to be important drivers of landscape changes and subsequently in boreal assemblages. The use of a spatially explicit and mechanistic forest model allowed us to simulate changes in forest stand composition, an important driver of bird and beetle occurrences (Cadieux et al., 2019; Mason et al., 2021) and caribou mortality (Courbin et al., 2009; Gagné et al., 2016). In our simulations, a significant proportion of coniferous stands transitioned to deciduous-dominated stands after a disturbance. For caribou, the proportion of deciduous vegetation induced by forest harvesting and wildfire determined the numerical response of moose and wolf, and consequently the predation risk for boreal caribou (Serrouya et al., 2021). Therefore, impact of forest composition on caribou mortality through apparent competition is expected to be higher compared to the change in forest structure as determined in Labadie et al. (2023). While lichen availability is not currently a limiting resource for caribou in boreal forest, a reduction in lichen availability can be expected due to the increasing occurrences of fires with climate change (Rupp et al., 2006). However, the rapid and asymmetrical change in vegetation composition due to the

induced increase in deciduous vegetation would be a major threat for boreal caribou. Management strategies that are expected to decrease or control for the proportion of deciduous vegetation are thus predicted to have a high umbrella value. Indeed, the proportion of deciduous vegetation is also predicted to greatly impact bird and beetle assemblages. Overall, our results indicate that the predicted large-scale conversion of the boreal forest to higher deciduous cover may be one of the most important threats to the integrity of boreal assemblages (Drapeau et al., 2000; Carroll, 2007; Janssen et al., 2009; Légaré et al., 2011; Cadieux et al., 2020; Labadie et al., 2021). As a result, the long-term ecological consequences of LUC and CC could be an ecological state shift (Folke et al., 2004) in assemblage structure, in which the outcomes are predicted to depend on the potential change in fire regime from CC and the rate of LUC (i.e., forest harvesting).

The transition from conifer to mixed forests, with more deciduous trees, represents not only a large change in forest composition but also a major net loss of old growth stands on which many forest species depend. Decrease in old-growth forest was one of the most important variables that significantly affected the response of modeled species and thus the dissimilarity in species assemblages. In accordance with other studies in western Canada (Schneider et al., 2003; Cadieux et al., 2020), we identified that boreal caribou and bird species requiring old-growth habitats were likely to be the most negatively affected by cumulative disturbances. More specifically, we show that the probability of occurrence of bird species associated with mature forests – such as Bay-breasted Warbler (*Setophaga castanea*), Cape May warbler (*Setophaga tigrine*), Brown creeper (*Certhia americana*), Swainson's thrush (*Catharus ustulatus*) and Evening grosbeak (*Coccothraustes vespertinus*) – would have the highest decrease while the probability of occurrence of bird species associated with early-to-mid succession forests would have the highest increase (Appendix C Table C.2). Furthermore, loss of old growth stands would also have major consequences on saproxylic beetles (i.e., those depending on dead wood during some part of their life cycle). Indeed, old forests present a multitude of microhabitats favorable to insect biodiversity but above all, it is the large amount of dead trees of various sizes and species which are necessary for maintaining saproxylic beetle assemblages (Ulyshen, 2018). More globally, the consequences of the loss of mature stands or the degradation of forests for biodiversity are in accordance with many other worldwide systems (Gibson et al., 2011; Haddad et al., 2015; Lindenmayer et al., 2017; Chase et al., 2020). For example, in Australia, there was concern for the population viability of several threatened mammals following the widespread collapse of old trees (Lindenmayer et al., 2015). Furthermore, in regions such as Finland and Sweden, the depletion of mature forests had devastating consequences for a broad range of taxa (Berg et al., 1994; Bauhus et al., 2009). Forests are important globally because of their economic resources, ecosystem services and biodiversity (Gauthier et al., 2015), especially older forest with their specific structural attributes (e.g., large trees with cavities and coarse woody debris) (Kuuluvainen et al., 2012; Kuuluvainen and Gauthier, 2018). Strategies aiming at maintaining old-growth stands should thus have a higher value for an umbrella species such as the boreal caribou.

We show that management strategies aiming at reducing harvest rates, notably those specifically targeted for caribou conservation, decreased caribou mortality and biodiversity change compared to a business-as-usual forest harvesting scenario. These results highlight that the key factor to preserve boreal biodiversity is to reduce the level of forest harvesting at the regional scale. We show that management aimed at reducing the level of forest harvesting per se or to favour protected areas, should mitigate the increase in the proportion of deciduous vegetation, and the loss of mature forests. The efficacy of management strategies focused on umbrella species is better over large spatial extents, because the design of management action will naturally accommodate the needs of many species at regional scales (Thornton et al., 2016) by preserving a large variety of environmental characteristics. We show that a management plan that focuses on the protection of boreal

caribou habitat through the decrease in harvesting levels trigger a decrease in encounter rates with wolves and allows to represent conditions at multiple levels (i.e., stand, landscape, and ecosystem) leading to the protection of a large number of other species. As complementary analyses to our study, it would be also very interesting to use additional metrics, such as those based on species conservation status or functional traits to provide valuable insights into specific aspects of biodiversity conservation.

In conclusion, while there are many uncertainties surrounding global change effects on boreal ecosystems, there is clear evidence for the positive effects of strategies that aimed to mitigate the impact of human activities. We found that management strategies designed by targeting specific species with large home ranges and with special habitat requirements, such as rare or threatened species, can be used to evaluate the effects of environmental changes, and at broader scale for biodiversity conservation (Brashares, 2010). Our study provides guidance to conservation strategies by clarifying mechanisms through which CC and LUC threaten biodiversity. The determination of the umbrella value of the boreal caribou conservation strategy shows that a single-species management strategy can be critical for governments, such as in Canada and in USA, because they have the legal obligation of developing a conservation strategy for the recovery of individual endangered and threatened species (U.S. Fish and Wildlife Service, 1973; Government of Canada, 2002). In this context, our study emphasizes that surrogate species, like umbrella species, which benefit from governmental action plans (e.g., conservation strategy), can act as a catalyst for research informing biodiversity conservation approaches.

Declaration of competing interest

The authors declare no competing interests.

Data availability

The datasets generated during and analyzed during the current study will be made available in the Dryad repository, if the paper gets accepted for publication: <https://doi.org/10.5061/dryad.djh9w0w5z>

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CRedit authorship contribution statement

G.L. and D.F. conceived the project. Y.B. simulated landscapes with the forest simulation model. J.-M.B. and C.H. were in charge of the insect database. G.L. calibrated the individual-based model, analyzed the data and produced results. IB did the distribution models for birds and beetles. G.L., D.F., M.H., and Y.B. wrote the paper. All authors discussed the analyses and results, and edited the manuscript text, and gave final

approval for publication. Y.B. provided constant good humor to the team by making dad's jokes and dad's noise from his office and also by buying Vachon Billot-Logs to the whole team.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.168087>.

References

- Anderson, M., Sciences, B., Building, B.S., McLellan, B.N., Serrouya, R., 2018. Moose response to high-elevation forestry: implications for apparent competition with endangered caribou. *J. Wildl. Manag.* 82, 299–309.
- Baker, W.L., 1995. Longterm Response of Disturbance Landscapes to Human Intervention and Global Change, 10, pp. 143–159.
- Ball, J.R., Hache, S., Bayne, E., Schieck, J., Sólomos, P., Schmiegelow, F.K.A., 2016. Regional habitat needs of a nationally listed species, Canada Warbler (*Cardellina canadensis*), in Alberta, Canada. *Avian Conserv. Ecol.* 11, 10.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manag.* 258, 525–537.
- Beaubien, J., Cihlar, J., Simard, G., Latifovic, R., 1999. Land cover from multiple thematic mapper scenes using a new enhancement-classification methodology. *J. Geophys. Res. Atmos.* 104, 27909–27920.
- Beaudoin, A., Bernier, P.Y., Guindon, L., Villemare, P., Guo, X.J., Stinson, G., Bergeron, T., Magnussen, S., Hall, R.J., 2014. Mapping attributes of Canada's forests at moderate resolution through kNN and MODIS imagery. *Can. J. For. Res.* 44, 521–532.
- Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M., Weslien, J., 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conserv. Biol.* 8, 718–731.
- Bergeron, Y., Cyr, D., Drever, C.R., Flannigan, M., Gauthier, S., Kneeshaw, D., Lauzon, É., Leduc, A., Le Goff, H., Lesieur, D., Logan, K., 2006. Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. *Can. J. For. Res.* 36, 2737–2744.
- Bichet, O., Dupuch, A., Hébert, C., Le Borgne, H., Fortin, D., 2016. Maintaining animal assemblages through single-species management: the case of threatened caribou in boreal forest. *Ecol. Appl.* 26, 612–623.
- Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C., Finnegan, S., 2013. Climate change and the past, present, and future of biotic interactions. *Science* 341, 499–504.
- Boucher, Y., Perrault-Hébert, M., Fournier, R., Drapeau, P., Auger, I., 2017. Cumulative patterns of logging and fire (1940–2009): consequences on the structure of the eastern Canadian boreal forest. *Landsc. Ecol.* 32, 361–375.
- Bouderbala, I., Labadie, G., Béland, J., Boulanger, Y., Hébert, C., Desrosiers, P., Allard, A., Fortin, D., 2023. Effects of global change on bird and beetle populations in boreal forest landscape: an assemblage dissimilarity analysis. *Divers. Distrib.* 29, 757–773.
- 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.
- Boulanger, Y., Girardin, M.P., 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. For. Res.* 47, 755–764.
- Bradford, D.F., Franson, S.E., Neale, A.C., Heggem, D.T., Miller, G.R., Canterbury, G.E., 1998. Bird species assemblages as indicators of biological integrity in Great Basin rangeland. *Environ. Monit. Assess.* 49, 1–22.
- Branton, M.A., Richardson, J.S., 2010. Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. *Conserv. Biol.* 25, 9–20.
- Brashares, J.S., 2010. Filtering Wildlife. *Science* 329, 402–403.
- Brown, G.S., Mallory, F.F., Rettie, J., 2003. Range size and seasonal movement for female woodland caribou in the boreal forest of northeastern Ontario. *Rangifer* 23, 227.
- Bürgi, M., Ostlund, L., Mladenoff, D.J., 2017. Legacy effects of human land use: ecosystems as time-lagged systems. *Ecosystems* 20, 94–103.
- Cadioux, P., Boulanger, Y., Cyr, D., Taylor, A.R., Price, D.T., Tremblay, J.A., 2019. Spatially explicit climate change projections for the recovery planning of threatened species: the Bicknell's thrush (*Catharus Bicknelli*) as a case study. *Glob. Ecol. Conserv.* 17, e00530.
- Cadioux, P., Boulanger, Y., Cyr, D., Taylor, A.R., Price, D.T., Sólomos, P., Stralberg, D., Chen, H.Y.H., Brecka, A., Tremblay, J.A., 2020. Projected effects of climate change on boreal bird community accentuated by anthropogenic disturbances in western boreal forest, Canada. *Divers. Distrib.* 26, 668–682.
- Canadian Forest Service, 2019. Canadian National Fire Database – Agency Fire Data. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta. <http://cwfis.cfs.nrcan.gc.ca/ha/nfdb>.
- Caro, T.M., 2010. Conservation by Proxy: Indicator, Umbrella, Keystone, Island Press, Flagship and other surrogate species.
- Carroll, C., 2007. Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: Marten and Lynx in the northern Appalachians. *Conserv. Biol.* 21, 1092–1104.

- Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- Chase, J.M., Blowes, S.A., Knight, T.M., Gerstner, K., May, F., 2020. Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature* 584, 238–243.
- Courbin, N., Fortin, D., Dussault, C., Courtois, R., 2009. Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. *Landscape Ecol.* 24, 1375–1388.
- Courbin, N., Fortin, D., Dussault, C., Fargeot, V., Courtois, R., 2013. Multi-trophic resource selection function enlightens the behavioural game between wolves and their prey. *J. Anim. Ecol.* 82, 1062–1071.
- Courtois, R., Ouellet, J.-P., Breton, L., Gingras, A., Dussault, C., 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience* 14, 491–498.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate change and forest disturbances. *BioScience* 51, 723–734.
- Dickie, M., Serrouya, R., McNay, R.S., Boutin, S., 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *J. Appl. Ecol.* 54, 253–263.
- Drapeau, P., Leduc, A., Giroux, J., Savard, J.L., Bergeron, Y., Vickery, W.L., 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. *Ecol. Monogr.* 70, 423–444.
- Drever, C.R., Hutchison, C., Drever, M.C., Fortin, D., Ann, C., Wiersma, Y.F., Johnson, C.A., Wiersma, Y.F., Ann, C., Wiersma, Y.F., 2019. Conservation through co-occurrence: woodland caribou as a focal species for boreal biodiversity. *Biol. Conserv.* 232, 238–252.
- Environment and Climate Change Canada, 2017. Report on the Progress of Recovery Strategy Implementation for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal population, in Canada for the Period 2012–2017. Page Species at Risk Act Recovery Strategy Series, Ottawa.
- Environment and Climate Change Canada, 2018. Action Plan for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada: Federal Actions. Species at Risk Act Action Plan Series, Ottawa.
- Environment Canada, 2011. Scientific Assessment to Inform the Identification of Critical Habitat for Woodland Caribou (*Rangifer tarandus*), Boreal Population, in Canada : 2011 Update. Ontario, Canada, Ottawa.
- Environment Canada, 2012. Recovery Strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal population, in Canada. Species at Risk Act Recovery Strategy Series:138.
- Environment Canada, 2015. Recovery Strategy for Olive-Sided Flycatcher (*Contopus cooperi*) in Canada. Species at Risk Act Recovery Strategy Series, Ottawa.
- Équipe de rétablissement du caribou forestier du Québec, 2013. Plan de rétablissement du caribou forestier (*Rangifer tarandus caribou*) au Québec- 2013-2023. produit par Flannigan, M.D., Amiro, B.D., Logan, K.A., Stocks, B.J., Wotton, B.M., 2006. Forest fires and climate change in the 21ST century. *Mitig. Adapt. Strateg. Glob. Chang.* 11, 847–859.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.* 35, 557–581.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., Mao, J.S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone national park. *Ecology* 86, 1320–1330.
- Fortin, D., Buono, P.-L., Fortin, A., Courbin, N., Tye Gingras, C., Moorcroft, P.R., Courtois, R., Dussault, C., 2013. Movement responses of Caribou to human-induced habitat edges Lead to their aggregation near anthropogenic features. *Am. Nat.* 181, 827–836.
- Fortin, D., Buono, P.-L., Schmitz, O.J., Courbin, N., Losier, C., St-Laurent, M.-H., Drapeau, P., Heppell, S., Dussault, C., Brodeur, V., Mainguy, J., 2015. A spatial theory for characterizing predator–multiprey interactions in heterogeneous landscapes. *Proc. R. Soc. B Biol. Sci.* 282, 20150973.
- Fuller, R.A., Ladle, R.J., Whittaker, R.J., Posingham, H.P., 2011. Planning for persistence in a changing world. *Conserv. Biogeogr.* 161–189.
- Gagné, C., Mainguy, J., Fortin, D., 2016. The impact of forest harvesting on caribou-moose-wolf interactions decreases along a latitudinal gradient. *Biol. Conserv.* 197, 215–222.
- Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., Schepaschenko, D.G., 2015. Boreal forest health and global change. *Science* 349, 819–822.
- Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–381.
- Government of Canada, 2002. Species at Risk Act. Page S.C. 2002, c.29. Ottawa, Ontario, Canada.
- Government of Canada, 2018. Progress report on unprotected critical habitat for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal population, in Canada - April 2018. <https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/critical-habitat-reports/woodland-caribou-boreal-population-2018.html#toc7>.
- 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. For. Res.* 30, 32–43.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D., Townshend, J.R., 2015. Habitat Fragmentation and Its Lasting Impact on Earth ' s Ecosystems: 1–10.
- Hardy, C., 2021. Klemet/LANDIS-II-Forest-Roads-Simulation-module: Release of v1.3.1 (1.3.1). Zenodo.
- Hesselbarth, M.H., Sciaini, M., With, K.A., Wiegand, K., Nowosad, J., 2019. Landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* 42, 1648–1657.
- Hins, C., Ouellet, J.P., Dussault, C., St-Laurent, M.-H., 2009. Habitat selection by forest-dwelling caribou in managed boreal forest of eastern Canada: evidence of a landscape configuration effect. *For. Ecol. Manag.* 257, 636–643.
- IPBES, 2018. The IPBES assessment report on land degradation and restoration. Page (L. Montanarella, R. Scholes, and A. Brainich, Eds.). In: Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.
- IPCC, 2021. Climate Change 2021: The Physical Science Basis.
- Jaccard, P., 1908. Nouvelles recherches sur la distribution florale. *Bulletin de la Société Vaudoise des Sciences Naturelles* 44, 223–270.
- Janssen, P., Fortin, D., Hébert, C., 2009. Beetle diversity in a matrix of old-growth boreal forest: influence of habitat heterogeneity at multiple scales. *Ecography* 32, 423–432.
- Kuuluvainen, T., Gauthier, S., 2018. Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. *For. Ecosyst.* 2, 1–15.
- Kuuluvainen, T., Tahvonen, O., Aakala, T., 2012. Even-aged and uneven-aged forest management in boreal fennoscandia: A review. *Ambio* 41, 720–737.
- 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.* 118, e2022892118.
- Labadie, G., Hardy, C., Boulanger, Y., Vanlandeghem, V., Hebblewhite, M., Fortin, D., 2023. Global change risks a threatened species due to alteration of predator–prey dynamics. *Ecosphere* 14, e4485.
- Légaré, J.P., Hébert, C., Ruel, J.C., 2011. Alternative silvicultural practices in irregular boreal forests: response of beetle assemblages. *Silva Fennica* 45, 937–956.
- Leston, L., Bayne, E., Dzus, E., Solyomos, P., Moore, T., Andison, D., Cheyne, D., Carlson, M., 2020. Quantifying long-term bird population responses to simulated harvest plans and cumulative effects of disturbance. *Front. Ecol. Evol.* 8, 1–25.
- Lindenmayer, D.B., Westgate, M.J., 2020. Are flagship, umbrella and keystone species useful surrogates to understand the consequences of landscape change? *Curr. Landscape Ecol. Rep.* 5, 76–84.
- Lindenmayer, D., Blair, D., McBurney, L., Banks, S., 2015. Mountain Ash: Fire. Csiro Publishing, Logging and the Future of Victoria's Giant Forests.
- Lindenmayer, D., Thorn, S., Banks, S., 2017. Please do not disturb ecosystems further. *Nat. Ecol. Evol.* 1, 0031.
- Losier, C.L., Couturier, S., St-Laurent, M.-H., Drapeau, P., Dussault, C., Rudolph, T., Brodeur, V., Merkle, J.A., Fortin, D., 2015. Adjustments in habitat selection to changing availability induce fitness costs for a threatened ungulate. *J. Appl. Ecol.* 52, 496–504.
- Mansuy, N., Thiffault, E., Paré, D., Bernier, P., Guindon, L., Villemaire, P., Poirier, V., Beaudoin, A., 2014. Digital mapping of soil properties in Canadian managed forests at 250m of resolution using the k-nearest neighbor method. *Geoderma* 235–236, 59–73.
- Mason, S.C., Shirey, V., Ponisio, L.C., Gelhaus, J.K., 2021. Responses from bees, butterflies, and ground beetles to different fire and site characteristics: A global meta-analysis. *Biol. Conserv.* 261, 109265.
- Messier, F., 1984. Moose-wolf dynamics and the natural regulation of moose. *Oecologia* 65, 203–512.
- Ministère des Forêts de la Faune et des Parcs, 2019a. La stratégie pour les caribous forestiers et montagnards. <https://mfpp.gouv.qc.ca/la-faune/especes/caribou-quebec/amenagement-habitat-caribou-forestier/>.
- Ministère des Forêts de la Faune et des Parcs, 2019b. Cartographie Récolte et reboisement. <https://www.donneesquebec.ca/recherche/fr/dataset/recolte-et-reboisement>.
- Norvez, O., Hébert, C., Bélanger, L., 2013. Impact of salvage logging on stand structure and beetle diversity in boreal balsam fir forest, 20 years after a spruce budworm outbreak. *For. Ecol. Manag.* 302, 122–132.
- Nowosad, J., Stepinski, T.F., 2019. Information theory as a consistent framework for quantification and classification of landscape patterns. *Landscape Ecol.* 34, 2091–2101.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2020. Vegan: Community Ecology Package. Available online at <https://cran.r-project.org/package=vegan>. (Accessed 2 October 2023).
- Potvin, F., Breton, L., Courtois, R., 2005. Response of beaver, moose, and snowshoe hare to clear-cutting in a Quebec boreal forest: A reassessment 10 years after cut. *Can. J. For. Res.* 35, 151–160.
- Rahel, F.J., 2000. Homogenization of fish faunas across the United States. *Science* 288, 854–856.
- Regroupement Québec Oiseaux, 2018. Atlas des oiseaux nicheurs du Québec. Données obtenues en réponse à une demande présentée aux bureaux de l'Atlas (www.atlas-oiseaux.qc.ca). Service canadien de la faune d'Environnement Canada et Études d'Oiseaux Canada. Québec, Québec, Canada.
- Rettie, W.J., Messier, F., 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Can. J. Zool.* 76, 251–259.
- Roberge, J.M., Angelstam, P., 2004. Usefulness of the umbrella species concepts as a conservation tool. *Conserv. Biol.* 18, 76–85.
- Rubinoff, D., 2001. Evaluating the California Gnatcatcher as an umbrella species for conservation of southern California coastal sage scrub. *Conserv. Biol.* 15, 1374–1383.

- Rupp, T.S., Olson, M., Adams, L.G., Dale, B.W., Joly, K., Henkelman, J., Collins, W.B., Starfield, A.M., 2006. Simulating the influence of various fire regimens on caribou winter habitat. *Ecol. Appl.* 16, 1730–1743.
- Scheller, R.M., Mladenoff, D.J., 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. *Ecol. Model.* 180, 211–229.
- Schneider, R.R., Stelfox, B.J., Boutin, S., Wasel, S., 2003. Managing the cumulative impacts of land uses in the Western Canadian sedimentary basin: a modeling approach. *Ecol. Soc.* 7.
- Seip, D.R., 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Can. J. Zool.* 70, 1494–1503.
- Serrouya, R., Dickie, M., Lamb, C., van Oort, H., Kelly, A.P., DeMars, C., McLoughlin, P. D., Larter, N.C., Hervieux, D., Ford, A.T., Boutin, S., 2021. Trophic consequences of terrestrial eutrophication for a threatened ungulate. *Proc. R. Soc. B Biol. Sci.* 288, 20202811.
- Smith, J.A., Donadio, E., Pauli, J.N., Sheriff, M.J., Bidder, O.R., Middleton, A.D., 2019. Habitat complexity mediates the predator–prey space race. *Ecology* 0, e02724.
- 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. Model.* 180, 153–174.
- Taylor, A.R., Boulanger, Y., Price, D.T., Cyr, D., McGarrigle, E., Rammer, W., Kershaw, J. A., 2017. Rapid 21st century climate change projected to shift composition and growth of Canada's Acadian Forest Region. *For. Ecol. Manag.* 405, 284–294.
- Thornton, D., Zeller, K., Rondinini, C., Boitani, L., Crooks, K., Burdett, C., Rabinowitz, A., Quigley, H., 2016. Assessing the umbrella value of a range-wide conservation network for jaguars (*Panthera onca*). *Ecol. Appl.* 26, 1112–1124.
- 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.
- Trombulak, S.C., Frissell, C. a, 2001. Review of ecological effects of roads on terrestrial and aquatic communities. *Conserv. Biol.* 14, 18–30.
- U.S. Fish & Wildlife Service, 1973. Endangered Species Act of 1973, As Amended through the 108th Congress.
- Ulyshen, M.D. (Ed.), 2018. Saproxylic Insects: Diversity, Ecology and Conservation. Springer International Publishing, Cham.
- UMCES, 2021. Integration and Application Network. University of Maryland Center for Environmental Science. ian.umces.edu/symbols/.
- Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative concentration pathways: an overview. *Clim. Chang.* 109, 5–31.
- Vanlandeghem, V., Drapeau, P., Prima, M.C., St-Laurent, M.-H., Fortin, D., 2021. Management-mediated predation rate in the caribou-moose-wolf system: spatial configuration of logging activities matters. *Ecosphere* 12, e03550.
- Wilmers, C.C., Getz, W.M., 2005. Gray wolves as climate change buffers in Yellowstone. *PLoS Biol.* 3, 0571–0576.
- Wittmer, H.U., Sinclair, A.R.E., McLellan, B.N., 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144, 257–267.
- Yamasaki, S.H., Duchesneau, R., Doyon, F., Russell, J.S., Gooding, T., 2008. Making the case for cumulative impacts assessment: modelling the potential impacts of climate change, harvesting, oil and gas, and fire. *For. Chron.* 84, 349–368.