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ARTICLE

Climate Ecology

Global change risks a threatened species due to alteration of predator–prey dynamics

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Abstract

Although global change can reshape ecosystems by triggering cascading effects on food webs, indirect interactions remain largely overlooked. Climate- and land-use-induced changes in landscape cause shifts in vegetation composition, which affect entire food webs. We used simulations of forest dynamics and movements of interacting species, parameterized by empirical observations, to predict the outcomes of global change on a large-mammal food web in the boreal forest. We demonstrate that climate- and land-use-induced changes in forest landscapes exacerbate asymmetrical apparent competition between moose and threatened caribou populations through wolf predation. Although increased prey mortalities came from both behavioral and numerical responses, indirect effects from numerical responses had an overwhelming effect. The increase in caribou mortalities was exacerbated by the cumulating effects of land use over the short term and climate change impacts over the long term, with higher impact of land use. Indirect trophic interactions will be key to understanding community dynamics under global change.

KEYWORDS
apparent competition, behavioral response, climate change, land use change, numerical response, species conservation, species interactions

INTRODUCTION

There is mounting evidence that global change (climate [CC] and land use [LUC]) can impact biodiversity by influencing species interactions. In low-productivity environments, for example, herbivore biomass may not sustain carnivore populations (Oksanen, 1992). As plant resources increase with global change, the associated numerical response of herbivores may allow carnivore populations to establish and increase. In turn, this can limit the growth of other herbivore populations and trigger indirect interactions across food webs. Indirect interactions arise when the effect of one species on another is mediated by the action of a third species (i.e., change in abundance and/or behavior) (Wootton, 1994). Recent studies demonstrate how climate variations can alter abiotic conditions (Peers et al., 2020) and primary production, with potential cascading effects across food webs (Rosenblatt & Schmitz, 2016; Stoner et al., 2018). CC can thus exacerbate the well-known impacts of anthropogenic disturbances (e.g., LUC, harvesting) on food webs (Brook et al., 2008) and even result in population extinctions (Oliver et al., 2015; Oliver & Morecroft, 2014). The threat of global change appears particularly strong for specialist species (Clavel et al., 2011), which thrive under specific habitat conditions that global changes can alter (Hämäläinen et al., 2018; Mosnier et al., 2008). Those conditions may change not only through variation in the occurrence and abundance of community members (e.g., Berteaux et al., 2018), but also in how members share space. Indeed, species-specific patterns of habitat selection can reduce the strength of direct and indirect interactions and be essential for species coexistence (Oliver et al., 2009).

Species coexistence and trophic interactions can thus depend both on how human activities reshape landscapes and on how individual community members respond to those changes. Spatiotemporal simulations of community dynamics are a powerful approach to gain a mechanistic understanding of how environmental changes can influence species interactions (Oliver et al., 2009; Tylianakis et al., 2008). Such community approaches are necessary as single-species studies often overlook biotic interactions (such as indirect food web interactions) that are critical for realistic projections (Heinle et al., 2021; Trainor & Schmitz, 2014). While most research has focused on how species distribution and population demography vary with abiotic conditions (Bonnot et al., 2018; Dainese et al., 2017; Zurell et al., 2018), recent work has demonstrated that accounting for biotic interactions (such as predation or competition) improves the projection of species responses to change (Heinle et al., 2021; Trainor & Schmitz, 2014). Yet, few studies have examined the combined effect of projected changes in land use and in climate on multispecies trophic interactions (Bossier et al., 2021). We addressed this research gap by combining a spatially explicit simulation model of forest landscapes (FLM; Scheller et al., 2007) with an individual-based model (IBM; Latombe et al., 2014) of multiple species enmeshed in a boreal food web.

We conducted spatially explicit simulations on a food web involving the threatened boreal caribou (*Rangifer tarandus caribou*), moose (*Alces alces*), and wolf (*Canis lupus*) in the boreal forests of northeastern Canada (Figure 1). Boreal caribou, a cornerstone of First Nations culture and history as well as an effective umbrella of Boreal biodiversity (Bichet et al., 2016), was designated as threatened in Canada in 2002 (COSEWIC, 2002). Boreal caribou are particularly well-adapted to low-productivity environments (Crête & Manseau, 1996), as they selectively feed on nutrient-poor lichens (Klein, 1982), while other ungulates largely browse nutrient-rich deciduous vegetation. Boreal caribou populations are declining across their distribution range largely because of disturbance-mediated apparent competition—an indirect food web interaction (Environment Canada, 2012). For example, deciduous vegetation growing in logged boreal forests provides high-quality food for moose that can increase their abundance, which in turn can trigger a numerical response of their predators with a subsequent increase in caribou mortality (Serrouya et al., 2021). Recent work suggests, however, that such strong effect of apparent competition may not occur over most of the northern limits of the boreal caribou range because postdisturbance growth of deciduous vegetation would be insufficient to trigger such numerical responses (e.g., DeMars et al., 2019; Neufeld et al., 2020). Global change could alter the situation by enhancing primary productivity and vegetation growth (resource availability) through increased temperature and disturbance rates (Boulanger & Pascual Puigdevall, 2021). Despite recent advances (Oksanen et al., 2020), identifying thresholds in resource availability that trigger such changes in food web dynamics remains unclear.

Our study explores the potential cascading effects of human disturbance and CC on the strength of trophic interactions and, ultimately, on caribou mortality. Our study relies on a process-driven, mechanistic approach that combines models of landscape forest changes with trophic interactions among caribou, moose, and wolves. First, we project land cover changes with changes in temperature, precipitation, and forest fire (Figure 2) under three future climate scenarios (e.g., baseline, representative concentration pathway [RCP] 4.5, and RCP 8.5; Van Vuuren et al., 2011), along with three levels of LUC through forest harvesting (no harvest < medium harvest < high harvest). Second, we used an IBM in which agents of the three species move following empirical movement rules within the simulated landscapes (Figure 2), and herbivore agents can die from predation (Figure 2). The combined models reveal how CC and LUC trigger numerical responses and reshape predator–prey encounter rates through indirect interactions in a way that, ultimately, intensifies top-down forces at the expense of already declining caribou populations (Figure 2). Because results were largely similar in summer and winter, we describe winter results and only point out the few differences observed between seasons.

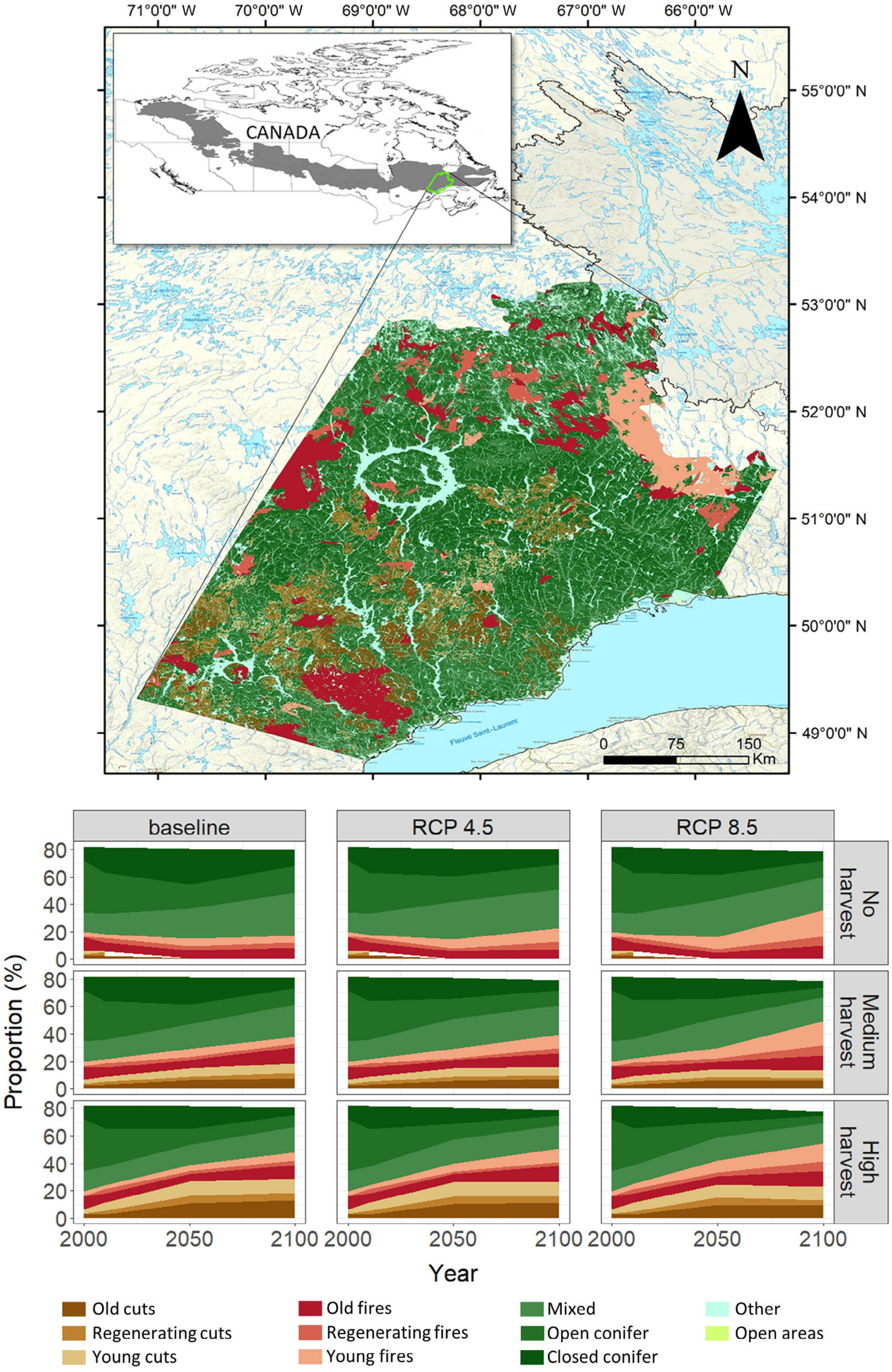

FIGURE 1 Study area in the province of Quebec, Canada, with delineation of the range of boreal woodland caribou in gray (top). Colors represent the different land covers in 2018. Trends in the proportion of cover classes (bottom) for each of the three land use scenarios under either the baseline, RCP 4.5, or RCP 8.5 climate scenario. Cover classes "open" and "other" are not shown. Note that under climate change, fire increase stands classified as regeneration (see Appendix S3: Figure S2). RCP, representative concentration pathway.

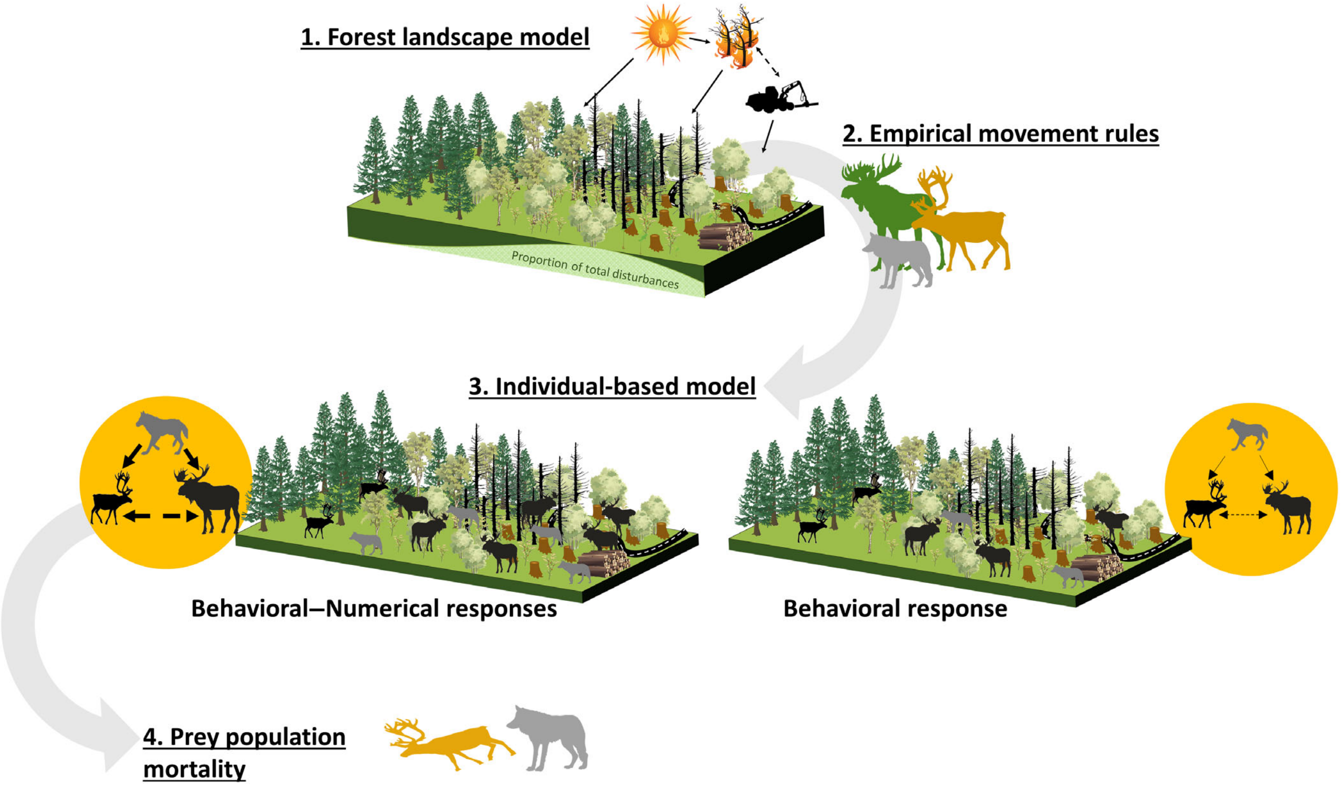

FIGURE 2 Schematic representation of the simulation design implemented in this study. (1) A forest landscape model was used to simulate stand- (i.e., individual tree establishment, growth, and mortality) and landscape-scale dynamics (seed dispersal, natural, and anthropogenic disturbances), allowing climate change (CC) and land use to differentially impact forest landscapes. We then combined the forest landscape simulation outputs with empirical movement rules from boreal caribou, moose, and wolves (2), to calibrate the individual-based model (3), and ultimately project prey mortalities (4) in landscapes developed from different land use change (logging) and CC (fire) scenarios. To isolate effects of behavior versus numerical responses indirectly induced by changing landscape, we created two sets of simulations: one with no change in species abundance (behavioral response) and the other with abundance being scaled to resource availability once accounting for the relationship between species abundance and the resource availability (behavioral–numerical responses). The contribution of the numerical response to caribou mortality rate was assessed from the difference between caribou mortalities in the behavioral–numerical response simulations and those in the behavioral response simulations. Tree symbols courtesy of UMCES (2021).

METHODS

Model overview

A description of the methods used to parameterize, calibrate, and validate the model is included in Appendices S1 and S2. Below, we outline the major model components and their behavior. Readers interested in the details of these components may also refer to Tremblay et al. (2018) and Vanlandeghem et al. (2021). Empirical movement rules were determined from empirical data collected from 2005 to 2018. We then validated the IBM with a bottom-up analysis strategy (Grimm & Railsback, 2005) by verifying that individual-level behaviors of agents were consistent with the empirical data under the same landscape conditions by using maps for the years 2005, 2007, 2009, 2011, 2013, 2015, and 2018. For the projections, the interactions among agents of the three species were assessed for three specific years (2000, 2050, and 2100), each representing expected landscape conditions at different times. We fixed caribou density in all simulations to 2996 individuals, whereas wolf and moose abundances were scaled to resource availability in the simulations related to behavioral–numerical responses (Appendix S2: Table S1).

Study area

The study area (48° N–54° N and 63° W–73° W) covers 115,470 km^2 and is located in the Côte-Nord region of Québec, Canada (Figure 1). Spruce budworm (SBW) (*Choristoneura fumiferana* [Clem.]) outbreaks recurring every 35–40 years and frequent wildfires (roughly 250–400 years fire return interval) are the major natural disturbances (Boucher et al., 2017; Labadie et al., 2021). The northern part of the study area belongs to the spruce-feathermoss domain, where black spruce and balsam fir dominate. The southern part of the study area belongs to the eastern balsam fir-white birch subdomain of the eastern boreal forest, mostly dominated by balsam fir and white spruce (*Picea glauca*, [Moench] Voss) mixed with white birch (*Betula papyrifera*, Marsh.). Forest harvesting has been the main source of forest disturbance since the late 1990s (Bouchard & Pothier, 2011). Historically, forest harvesting mostly occurred in the southern part of the study area and gradually extended northward, while fires occurred mostly in the north.

Spatially explicit forest simulation model

To estimate forest composition at each time step we used a forest landscape simulation model (Figure 2.1).

Climate scenarios

Future climate projections are based on two different radiative forcing scenarios known as RCPs (see van Vuuren et al., 2011, for more information). We obtained future climate projections from the Canadian Earth System Model version 2 (CanESM2; Arora et al., 2011), which ran under both RCP 4.5 and RCP 8.5. The ANUSPLIN method was used to downscale climate projections to a 10-km resolution. Future mean annual temperature is expected to increase between about 3°C (climate scenario RCP 4.5) and 7.5°C (RCP 8.5) in the study area by 2100 (compared with 2000), while average precipitation is projected to increase by 7% (RCP 8.5) to 10% (RCP 4.5) (Boulanger et al., 2018). Monthly time series for each climate scenario (CC, baseline, RCP 4.5, and RCP 8.5) were used to parameterize forest landscape simulations.

Forest landscape simulations with LANDIS-II

Forest landscape simulations were performed using LANDIS-II v7.0 (Scheller & Mladenoff, 2004). This model is a spatially explicit raster-based FLM that dynamically simulates key forest ecosystem processes at both the stand (e.g., tree competition, establishment, and growth) and landscape scales (e.g., disturbances and tree species dispersal) (Boulanger et al., 2018). It thus allows assessing interacting ecological processes at broad spatial and temporal scales (Boulanger et al., 2018). LANDIS-II captures forest succession across landscapes as an emergent property of both stand- and landscape-scale processes (Boulanger et al., 2018). Parameterization was conducted using the individual tree-based, forest patch model PICUS version 1.5 (Lexer & Hönninger, 2001; Taylor et al., 2017). Details can be found in Appendix S1: Section S1. Dynamic inputs were obtained for each combination of tree species, land type, time period (2000–2010, 2011–2040, 2041–2070, and 2071–2100), and climate scenario.

Natural disturbances

Fire and SBW outbreaks were considered in LANDIS-II simulations. Fire simulations were conducted using the LANDIS-II Base Fire Extension v4.0, which simulates stochastic fire events dependent upon fire ignition, initiation, and spread, which vary with climate scenarios according to projections available in Boulanger et al. (2017). Outbreaks of SBW were simulated using the Biological Disturbance Agent extension (Sturtevant et al., 2004), which is specifically designed to simulate host tree mortality following insect outbreaks. Forest composition and structure resulting from SBW outbreaks (i.e., the increase in mixed stands) were tracked.

Forest harvesting and roads

To determine the impact of forest disturbance levels on caribou mortality, we simulated three harvesting scenarios (i.e., LUC scenarios) according to a gradient of forest harvesting, from no harvesting (no harvest), to medium-intensity clearcutting similar to half of the mean rate of the current forest harvesting in the study region (medium harvest—applied to 4% of the harvestable upland area per 10 years), to 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). Then, roads were created with the Forest Roads Simulation (FRS) module, which allows to create roads to cells that are harvested while reducing the costs of construction of roads as much as possible (Hardy, 2021). Hence, the road networks varied among forest harvesting scenarios. The Biomass Harvest extension (v5.0; Gustafson et al., 2000) was used to simulate forest harvest. Only stands that included tree cohorts older than 60 years were allowed to be harvested. Mean harvested patch size varied from 40 to 150 km^2, 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.

Simulation design

Forest landscape simulations with LANDIS-II were run for 100 years, starting in the year 2000, under each radiative forcing and forest harvesting scenario using a 10-year time step. Because fire regime projections were only available for

30-year periods, and because producing yearly dynamic input parameters with PICUS would have been too computer intensive as it would involve three times the number of PICUS simulations, we updated the dynamic parameters (i.e., [1] species establishment probabilities [SEP], [2] maximum possible aboveground net primary productivity [maxANPP], and [3] maximum aboveground biomass [maxAGB]) only at the time step beginning in 2011, 2041, and 2071. Consequently, except for scenarios involving the baseline climate, climate-sensitive parameters were allowed to change for three different 30-year periods, according to the average climate corresponding to each forcing scenario obtained from CanESM2 (Boulanger & Pascual Puigdevall, 2021). While FLMs provide a range of useful information on vegetation types and disturbances, and the IBM provides information on predator–prey interactions, it would have been impossible to simulate 100 years with both models. Indeed, to run all the simulations at 1-year timestep, it would have taken 385,440 core days (i.e., measurement of computational time indicating the number of days needed to run all the simulations with one CPU). For the next steps of the analysis, we thus used landscapes resulting from LANDIS-II models for three years: 2000, 2050, and 2100. These simulated landscapes were used to temporally assess the cumulative impact of anthropogenic disturbances and CC on caribou mortality in the IBM analysis.

Habitat characteristics for simulated landscapes

To estimate forest composition and create the final maps to use with the IBM, we used the relative proportions of species groups (conifer and deciduous species) from the LANDIS-II biomass outputs. Using species group and predicted crown closure detailed in Appendix S1: Section S1, we created five land cover classes from the Earth Observation for Sustainable Development of Forests Land Cover Classification Legend (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 nontreed ≥ vegetation treed), and other (nonvegetation ≥50%). Land cover maps were then updated by adding roads, recent (≤10 years), regenerating (11–20 years), and old (21–50 years) cutblocks/burned areas that LANDIS-II simulated at each 10-year time step.

Analysis of the structure and composition of the landscape

To determine changes in landscape composition, we calculated the proportion of anthropogenic and natural disturbances and the proportion of deciduous land cover from LANDIS-II outputs. Following Environment Canada's (2011) approach, the levels of disturbance were calculated as the percentage of the landscape that consisted of the nonoverlapping surfaces of burns, roads, and cuts, the latter two buffered by 500 m. Environment Canada (2011) found that the decrease in caribou recruitment was more strongly associated with human disturbance when also considering this 500-m buffer. The proportion of total disturbances and burned areas associated with each simulation is represented in Appendix S3: Figure S1. The proportion of deciduous vegetation for each simulation was represented in Appendix S3: Table S1.

Configuration metrics resulting from LANDIS-II simulations were calculated using "landscapemetrics" package in R (Hesselbarth et al., 2019). Two metrics that reflect complementary aspects of landscape structure and potentially mediate individual responses to LUC and CC were selected. At the patch level (i.e., neighboring cells belonging to the same land cover class), we calculated the mean "isolation index" (calculated as 1 − "cohesion index"), characterized as the connectedness of patches belonging to a land cover class (Hesselbarth et al., 2019). If the value of the "isolation index" was close to 0, patches of the same class were aggregated, while an increase in the value indicated that patches became isolated (Appendix S3: Table S1). At the landscape level, we calculated the "homogenization index" (calculated as 1/"conditional entropy," characterized as the complexity of a landscape pattern configuration) (Hesselbarth et al., 2019; Nowosad & Stepinski, 2019). If the value of the "homogenization index" is small, cells of one category are adjacent to cells of many different categories. On the other hand, high "homogenization index" values show that cells of one category are predominantly adjacent to only one other category of cells (Appendix S3: Table S1).

Movement rules derived from radio tracking caribou, moose, and wolves

To identify species-specific movement rules that were implemented in the IBM, we used empirical data collected for caribou, moose, and wolves over the study area (Figure 2.2).

Briefly, we used 68 GPS-collared adult female caribou, 16 wolves, and 15 moose monitored between March 2005 and December 2018. We focused our investigation on winter and late summer, two periods of relatively high caribou mortality in the study area (Basille et al., 2013). To test predictions based on whether individuals change their movement behavior relative to environmental characteristics, we used step selection functions (SSFs; Fortin et al., 2005). SSFs were estimated from data for the real animals and provide the relative probability of selection among a set of options based on the comparison of observed and random steps (i.e., the linear segment between successive locations at an 8-h interval) using conditional logistic regression (Appendix S1: Section S2) (Fortin et al., 2005). Details on GPS data and SSF models can be found in Appendix S1: Section S2.

Habitat was characterized from 2005 to 2018 using the Canadian National Forest Inventory (CNFI) forest cover maps (Beaudoin et al., 2014). To estimate forest composition, we used the relative proportions of species groups (conifer and deciduous species), treed land, and tree crown closure maps from these NFI data. We created five land cover classes as detailed in *Habitat characteristics for simulated landscapes*. Land cover maps were updated every year by adding actual roads, recent (≤10 years), regenerating (11–20 years), and old (21–50 years) cutblocks/burned areas based on information provided annually (from 2005 to 2018) by local forestry companies (Ministère des Forêts de la Faune et des Parcs, 2019a) and from the Canadian National Fire Database (Canadian Forest Service, 2019).

Individual-based model

A complete description of the model and how it was parameterized and validated can be found in Appendices S1 and S2 (Figure 2.3). Below we outline the major model components.

We compared the simulated caribou mortality predicted by the IBM as an emergent outcome of the interactions between prey and predators under each forest management and climate scenario (Appendix S1: Section S3). Briefly, the IBM simulations were conducted in a spatially explicit representation of the Côte-Nord region using maps from 2005 to 2018 for the calibration and with simulated landscapes created from the FLM for projections. To integrate the effect of the distance to roads, we superimposed a landscape with a raster of distance-to-road. Movements and predation events depended on species and landscape characteristics (Appendix S1: Section S3). Indeed, spatial configuration of landscape composition is likely to influence differently the spatial game that wolves play with caribou and moose (Fortin et al., 2015; Vanlandeghem et al., 2021). The three species react differently to landscape features, such as cuts and roads (Fortin et al., 2013, 2015; Gagné et al., 2016), which generates differences in the land cover types where each prey species is most likely to encounter a predator (Courbin et al., 2009, 2013). Empirical movement rules were determined using SSFs (Appendix S1: Section S2) specific for each species. To do so, we used SSFs (described above; Fortin et al., 2005) determined from field observations for each species and each season. When individual agents moved, 21 random steps were drawn within a buffer around their current location. Each agent then moved to the location with the highest SSF score. The maximum length that an individual of a given species could move in one step corresponded to the 99th percentile of the empirical step length (SL) distribution (Dickie et al., 2017) of that species (Appendix S1: Table S1). Given that SSFs consider SL and ln(SL), the distance that the agent actually moves would generally be much shorter than the maximum length, as observed with real animals. Prey could only die from predation, and they were then removed from the simulation.

Model calibration

To calibrate the IBM, simulations were run for the years 2005, 2007, 2009, 2011, 2013, 2015, and 2018, three times for each year and each season (42 simulations).

SSF scores

To calibrate and validate the model, we first compared the relative probabilities of selection of the different land cover types by virtual agents and radio-collared boreal caribou, moose, and wolves tracked in the Côte-Nord region. We used GPS data of individuals associated with the random steps used for the SSFs, and we summarized the relative probability of selection of land cover types by species and season defined:

$$\frac{\dfrac{\text{Number of realized (used) steps within the landscape } i}{\text{Total number of realized steps}}}{\dfrac{\text{Number of random steps within the landscape } i}{\text{Total number of random steps}}}. \qquad (1)$$

For simulated data, each step (i.e., simulated) was paired with 20 random steps (availability) where an animal could have moved in the simulation. The SLs and turning angles (TAs) of random steps were drawn within a radius of the 99th percentile maximum SL based on the observed distribution determined from GPS collar data for each individual in each season. We also summarized the relative probability of selection by season for each species.

Memory

We calibrated virtual individuals' movements by adding a memory effect that is intended to avoid individuals getting artificially trapped in large patches of disturbances. This parameter added a weight based on the memory of the polygons last visited by the animal. Those weights only affected the probability of choosing a patch. The weight is multiplied by the number of time steps since the last time this animal was on the polygon. Each visited patch was recorded for 4 days. The weights were −2, −0.7, and −3 for caribou, moose, and wolves, respectively. When the agent of a given species first arrives in a polygon, the initial weight was −2 for caribou, −0.7 for moose, and −3 for wolves. In other words, as the agent remains within a polygon, the weight becomes increasingly negative, and the agent becomes progressively more likely to leave that polygon.

Parameters for hunting a prey

The distance that wolves could move depended on their movement modes; they could either be in hunting mode when actively searching for prey or they could be in stationary mode when consuming a prey and resting after the kill (Mech & Boitani, 2003). Accordingly, we considered mode-dependent SL distributions to draw random steps (Appendix S1: Table S1). Finally, we adjusted the probability of hunting a chosen prey to reach the mortality risk similar to the one observed in the study area. We calibrated the probability that wolves attack a prey located in their vicinity because this parameter is difficult to evaluate in the field. We ran the 42 simulations and adjusted the attack probability until the model yielded a mortality risk similar to the one observed in the study area (i.e., 10% for boreal caribou and moose; Crête & Courtois, 1997; Équipe de rétablissement du caribou forestier du Québec, 2013). Our results showed that an encounter probability of 25% could best match the mortality rates observed in the field. Wolves went into stationary mode for 24 h (i.e., handling time) after a caribou kill and for 72 h after a moose kill (Hayes et al., 2000). They could not kill another prey while in stationary mode. For simulations with wolf and moose numerical responses, parameters for hunting a prey did not change. However, the increase in wolf abundance would increase the probability of predator–prey co-occurrences and thus prey mortality.

Moose and wolf numerical responses

To consider the response of moose to food availability and the subsequent increase in wolf density, we adjusted the number of moose to the proportion of deciduous vegetation available in simulated landscapes. We used data from aerial surveys of moose conducted in 2006 in hunting zone 18, in the Côte-Nord region of Québec (Ministère des Forêts de la Faune et des Parcs, 2019b). The double sampling method (Courtois, 1991) has been applied for the aerial survey of 72 plots of 60 km^2 in 2006. We considered all survey plots that overlapped the study area, delimited by radio-collared caribou and wolves. A total of 48 plots of the 72 surveyed were in the study area. Based on those 48 plots, we estimated moose density while considering a visibility rate of 0.68 (Ministère des Forêts de la Faune et des Parcs, 2019b). For each survey plot, we extracted the percent cover of deciduous vegetation from CNFI forest cover maps (Beaudoin et al., 2014). To test our predictions that moose density increased with deciduous vegetation, we evaluated the importance of vegetation characteristics on moose densities in 2006 by building a log-transformed regression with the proportion of deciduous vegetation.

From the aerial surveys of moose conducted in 2006 (Ministère des Forêts de la Faune et des Parcs, 2019b), we found that moose occurred at a density of 0.60 individual/10 km^2 (95% confidence intervals [CI]: 0.36–0.83) in 2006. The linear model indicated that moose density was positively related to the proportion of deciduous vegetation ($\text{moose density} = \log[0.936 + 0.006 \times \text{proportion}_{\text{deciduous}}]$; $R^2 = 0.24$, $p < 0.001$, $n = 48$). We used this relationship to determine the future density of moose in function of the forecasted proportion of deciduous vegetation within the study area (Appendix S2: Table S1). We then adjusted the number of wolf packs to moose density based on Messier (1984). Values of moose and wolf pack densities used in the simulations are included in Appendix S2: Table S1.

Validation of the IBM

To validate the IBM, we verified that individual-level behaviors of agents were consistent with the empirical data. Considering that we ran simulations in a virtual landscape with the same characteristics as the landscape where empirical data was collected, the different land cover types should be selected or avoided similarly by agents and radio-collared individuals. To do so, we ran the simulations in the study area from 2005 to 2018, corresponding to the period and the location where GPS-collared individuals of all three species were monitored. We ran simulations with 2194 caribou, 4965 moose, and 91 wolf packs, in accordance with the mean density of these three species observed over this study area. Simulations were run for the years 2005, 2007, 2009, 2011, 2013, 2015, and 2018, three times for each year and each season (3 replicates × 7 years × 2 seasons = 42 simulations). We then compared the relative probability of selection of land cover types and SL distributions between empirical data and the output of the simulations conducted under the same landscape conditions. We incorporated minor adjustments on IBM inputs to reproduce adequately the behaviors of the actual radio-collared animals (Appendix S2: Table S2). Each time we changed a coefficient, the 42 simulations were run to verify the relative probability of selection of land cover. All SSF coefficients and their adjustments were presented in Appendix S2: Table S2. We observed that virtual agents selected or avoided land cover types similarly to radio-collared boreal caribou, moose, and wolves in the different seasons (Appendix S2: Figures S1–S3, respectively). Differences between simulated and empirical selection probabilities could be expected for two principal reasons. First, when simulated agents were in a large forest stand, they can remain stationary for a few time steps until the memory parameter forced them to leave. Although the memory parameter was necessary to simulate more realistic behavior from agents, it also generated an increase in the relative probability of selection for simulated agents compared to radio-collared individuals, especially for disturbed stands. Then, for each simulated step, 21 random steps were drawn, and the agent then moved to the location with the highest SSF score. This method allowed the agents to move in environments that would not be chosen by individuals in reality if the random points were all drawn in non-optimal land cover types. Simulated agents may thus have higher probability of selection for some land cover types compared to radio-collared individuals. While there were some differences, we were careful to ensure (i.e., with minor adjustments on IBM inputs) that the main pattern of selection or avoidance was maintained between radio-collared individuals and agents to obtain realistic responses of each species.

We also compared the distribution of SLs between agent individuals and radio-collared individuals (Appendix S2: Figures S4 and S5). We observed that virtual agents and radio-collared individuals had a similar SL distribution.

Model projections

To model wolf, moose, and caribou movements and estimate wolf predation rate under the different scenarios, we ran the IBM for 1 year in the years 2000, 2050, and 2100, with 10 replicates. We thus ran a total of 380 simulations per season, that is, 760 simulations. We used one output of LANDIS-II simulation model per combination of CC and LUC scenarios because we were more interested in the uncertainty of the IBM than that of the FLM. Moreover, stochasticity-induced variation in forest landscapes yielded from LANDIS-II is generally rather small at the spatial extent of the study area (Boulanger et al., 2018).

Analysis of IBM's outputs

The validation of the IBM can be found in Appendix S2.

Analysis of prey mortality

The cumulative impact of anthropogenic disturbance and CC was assessed by comparing the temporal trends of the simulated caribou and moose mortalities predicted by the IBM in various CC and LUC scenarios (Figure 2.4).

First, to explore how changes in forest structure and composition impacted the proportion of caribou killed (number of caribou killed/total number of caribou), we used a generalized linear mixed model with a binomial distribution to relate the proportion of caribou mortalities to the proportion of areas disturbed by cuts and roads, burned areas, and landscape characteristics, such as the proportion of deciduous vegetation, landscape homogenization, and isolation of mature conifer stands. We created a factor from the combination of CC, LUC, and years (i.e., CC × LUC × Year) that was used as a random effect. We considered a logit link and binomially distributed errors. Disturbance covariates were correlated to other landscape characteristics. Thus, to evaluate the additive effect these landscape characteristics had on prey mortality without facing multicollinearity issue, we used residual values of these covariates from the relationship they shared with the proportion of burned areas and cuts associated with roads (hereafter "Residuals for proportion of deciduous," "Residuals for isolation of mature conifer stands," and "Residuals for landscape homogenization"). We conducted this analysis for the two sets of simulations, considering the behavioral response and the behavioral–numerical responses, to explore how changes in species densities impacted trophic interaction.

Second, to explore the relative contributions of CC versus LUC on the proportion of caribou killed by wolves, we used generalized linear models with binomial distribution. We only considered simulation results from 2050 to 2100 to evaluate how the effects of CC and LUC vary temporally. The model fit was assessed qualitatively, from the distribution of residual versus fitted values, and quantitatively, by comparing the Akaike information criterion (AIC) values of all the competing models (Appendix S3: Table S2; Appendix S4: Table S2). Differences in AIC values (ΔAIC) between the best and second-best models were reported for all tests. For relationships with $p < 0.05$, we conducted a post hoc Tukey's test using the "glht" function in the "multicomp" package in R. We performed post hoc Tukey's pairwise comparisons using one variable representing all combinations between CC and LUC scenarios to compare the cumulative effects of CC and LUC.

RESULTS

Structure and composition of the landscape

LUC (logging) and CC changed the composition and the structure of boreal landscapes (Figures 1 and 3).

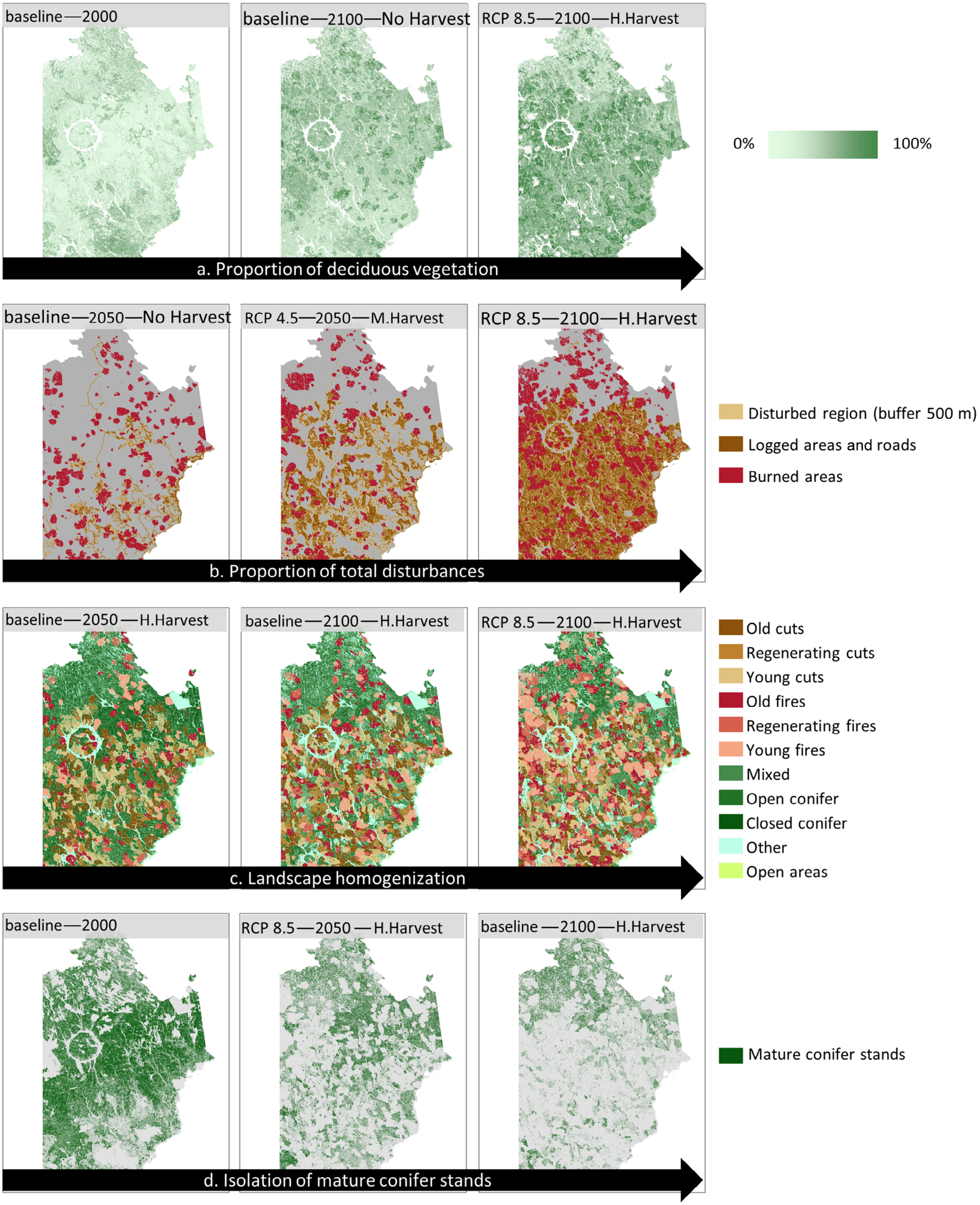

FIGURE 3 Maps showing (a) the proportion of deciduous vegetation, (b) the proportion of total disturbances, (c) the homogenization of the landscape, and (d) the isolation of mature conifer stands in the study area as a function of land use change (no harvest, high harvest [H.Harvest], and medium harvest [M.Harvest]) and climate change (baseline, RCP 4.5, and RCP 8.5). For each forest attribute, we illustrated scenarios that maximized the gradient of variation. RCP, representative concentration pathway.

Increased LUC and CC initiated widespread secondary succession (Figure 1) and subsequently increased the proportion of pioneer, deciduous vegetation (Figure 3a; Appendix S3: Figure S2). This shift to deciduous and younger vegetation was highlighted by the increase in mixed stands, burned areas, and in regenerating cuts (Figure 1). Forest disturbance levels (i.e., proportion of cuts and roads, and burned areas) increased with intensification of LUC and CC (Figure 3b). Moreover, LUC and CC altered the spatial configuration of the landscape by homogenizing it and by increasing the isolation of mature conifer stands (index of fragmentation and loss of mature conifer patches) (Figure 3c,d). Indeed, landscape complexity strongly declined with increasing proportion of burned areas along with CC through time (Pearson's correlation $r = -0.62$ in 2050 and $r = -0.91$ in 2100). Changes in natural and anthropogenic disturbances also led to a major loss of mature conifer stands (Figure 1), which reduced landscape complexity (Figure 3d).

Prey mortality

Results of the two sets of simulations in the IBM showed that land-use- and climate-induced changes in the forest stand mosaic influenced caribou mortality rates in the same way (Table 1a,b; Figure 4). Indeed, caribou mortality increased along with the proportion of natural and anthropogenic disturbances as well as in deciduous vegetation (Table 1a,b; Figure 4a,b). Landscape homogenization by disturbance further exacerbated the negative effect of such disturbances on caribou mortality (Table 1a,b; Figure 4c). This is shown by the residual values of the landscape homogenization covariate showing a significant positive effect on the proportion of caribou killed (Table 1a,b). Increased isolation of mature conifer stands with increasing levels of LUC and CC had a minor or no change in the proportion of caribou killed per se (Table 1a,b). Caribou mortality increased with the level of isolation of mature conifer stands (Figure 4d), a relationship that also reflected the impact of total disturbances as the isolation of mature conifer stands increased with total disturbances (Pearson's correlation $r = 0.75$ in 2050 and $r = 0.87$ in 2100). The impact of changes in landscape composition and structure on caribou mortality increased over time (Figures 4 and 5).

By 2100, under the most severe CC and LUC scenarios, the proportion of caribou killed was three times higher for simulations considering the behavioral–numerical responses compared to simulations including only the behavioral response (Figures 4 and 5). Consistently, the comparison of regression coefficients showed that the effect of increased proportion of cuts and roads was 5.5 times (i.e., 0.787/0.143) higher when simulations included both the behavioral and numerical responses than when they only considered the behavioral response (Table 1c).

LUC and CC had an additive effect in winter (Appendix S3: Table S2), but an interactive effect in summer (Appendix S4: Table S3). Regardless, LUC consistently had a stronger impact than CC on caribou mortality (Figure 6). Indeed, when averaging all climate scenarios, the high harvest scenario increased caribou mortality by 31% compared with simulations with no harvest in 2100 (Figure 5). By contrast, simulations conducted under the RCP 8.5 scenario resulted, on average, in a 12% increase in caribou mortality in 2100 compared with caribou mortality simulated under the baseline scenario (Figure 5).

The negative effects of CC and LUC on caribou survival both increased over time (positive "CC × year" and "LUC × year" interaction terms). For example, in 2050, CC still had no detectable effect on predator–prey interactions ($p > 0.1$; Tukey honestly significant

TABLE 1 Model results of forest attribute changes on the proportion of caribou killed.

Variable	(a) Behavioral response	(b) Behavioral–numerical responses	(c) |Effect ratio|
Proportion of cuts and roads	0.143 (0.038)***	0.787 (0.072)***	5.503
Proportion of burned areas	0.202 (0.104)NS	1.964 (0.194)***	9.723
Residuals for proportion of deciduous	−0.003 (0.002)	0.046 (0.005)***	4.870
Residuals for isolation of mature conifer stands	0.031 (0.010)**	−0.027 (0.019)	0.871
Residuals for landscape homogenization	3.840 (0.752)***	3.111 (1.402)*	0.810

Note: Coefficients (with SEs in parentheses) of generalized linear mixed models relating the proportion of caribou killed by wolves in winter as a function of the proportion of disturbances (roads and cuts with 500-m buffer and burned areas) and residual values of the proportion of deciduous vegetation, the isolation of mature conifer stands and the landscape homogenization from the relationship they shared with the proportion of burned areas and cuts associated with roads. Because the response was the proportion of caribou killed by wolf, we considered a logit link and binomially distributed errors. The proportion of caribou killed was the consequence of land use change and climate change indirect effects resulting in the change in (a) behavioral or (b) behavioral and numerical responses of species to changing landscape conditions. Summer results can be found in Appendix S4: Table S1.

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; NS, $p < 0.10$.

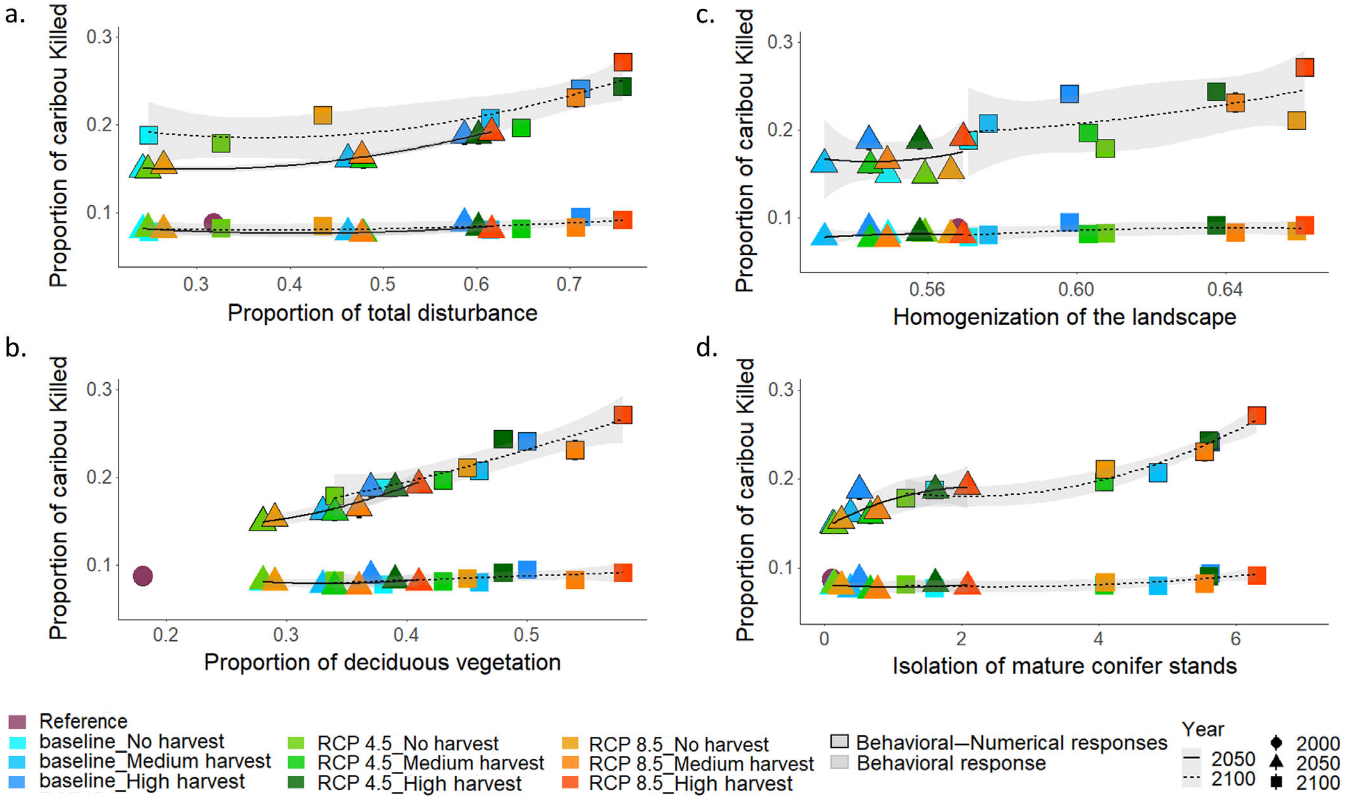

FIGURE 4 Proportion of caribou killed in 2000 (point in purple, determined as the reference), 2050, and 2100 in winter as a function of (a) the proportion of total disturbances, (b) the proportion of deciduous vegetation, (c) the homogenization of the landscape (as measured by conditional entropy metric), and (d) the isolation of mature conifer stands. In each panel, average mortalities (represented by points, triangles, and squares) and their standard errors of simulations ($n = 10$) are represented for each simulation: the three different colors represent the three climate scenarios: baseline (blue), RCP 4.5 (green), and RCP 8.5 (orange) with a gradation representing the different three levels of land use: no harvest (light), medium harvest (medium), and high harvest (dark). Shapes with the colored edge represent the behavioral response, while shapes with black edge represent the behavioral–numerical responses of moose and wolf to emergent changes in forest landscape composition. Summer results can be found in Appendix S4: Figure S1. RCP, representative concentration pathway.

difference [HSD]; Appendix S3: Table S4), and LUC was the only factor increasing the number of caribou killed by wolves ($p < 0.001$; Tukey HSD). We also did not detect a difference in caribou mortality between RCP 4.5 and baseline conditions ($p = 0.87$; Tukey HSD).

DISCUSSION

Structure and composition of the landscape

CC altered landscape composition mostly through an important surge in area burned from CC-induced forest fires. The proportion of deciduous vegetation in the landscape was mainly driven by disturbance induced (both anthropogenic and climate induced) increases in boreal, co-occurring deciduous species (e.g., trembling aspen, *Populus tremuloides*) rather than through a climate-induced northward expansion of deciduous thermophilous species. The land cover changes we report are broadly consistent with those expected under CC and concomitant changes in disturbance regimes (Boulanger & Pascual Puigdevall, 2021). In particular, the increase in deciduous vegetation is consistent with observations following increasing forest harvest rates in eastern Canada (Boucher et al., 2014) and increased fire disturbance rates in western North America (Wang et al., 2020). Such climate-mediated changes in forest composition have already been shown as deleterious for caribou populations using species distribution models (SDMs) (Masood et al., 2017). While SDMs bring information on species occurrence, our approach using combined models improves projections of the indirect effects of global changes by including biotic interactions, changes to forest composition, alterations to disturbance regimes (e.g., fire), and the interactions between CC and LUC. Our approach can reveal the relative contribution of behavioral response alone and behavioral–numerical responses of species combined. LUC- and CC-induced predicted increase in resource availability for moose (i.e., deciduous vegetation) will strongly impact predator–prey interactions, through their

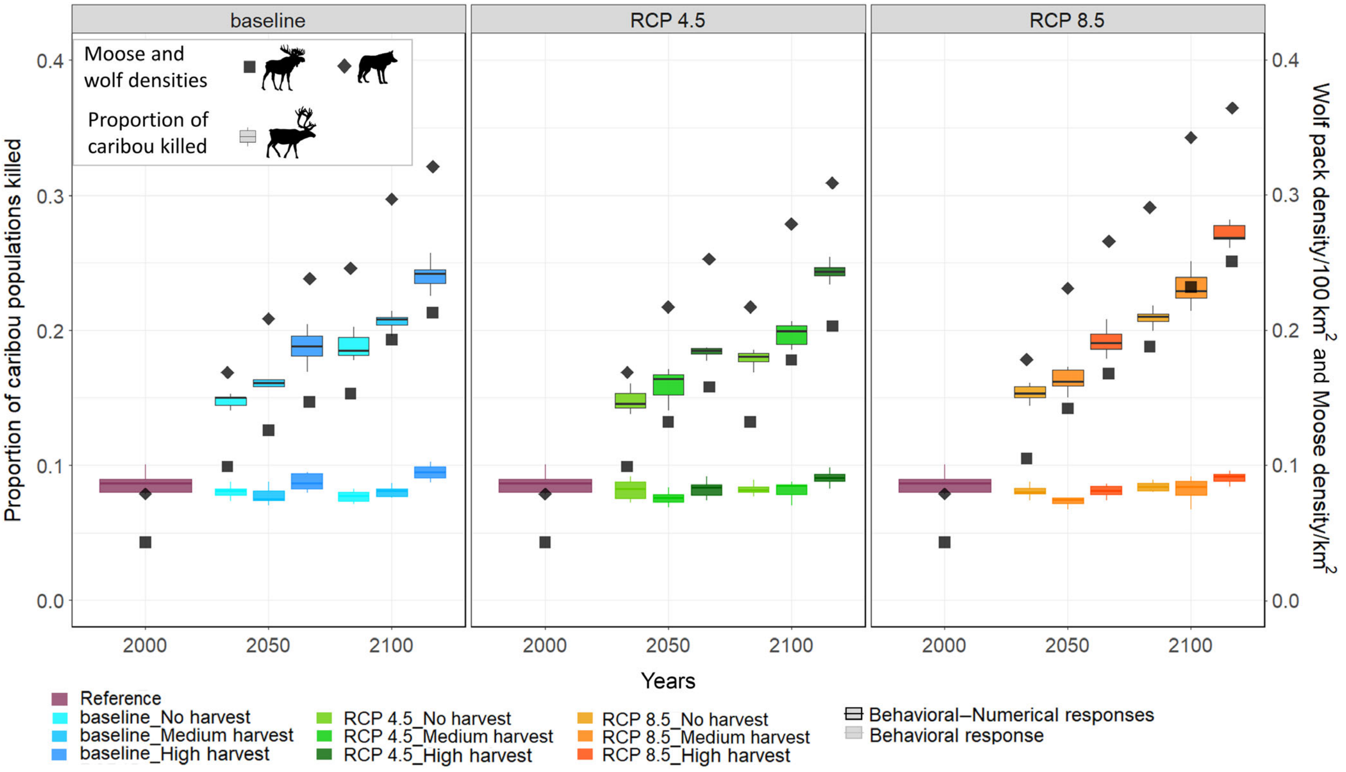

FIGURE 5 Proportion of caribou killed by wolves in winter under three climate scenarios (baseline in blue, RCP 4.5 in green, and RCP 8.5 in orange) and three levels of land use (no harvest in light, medium harvest in medium, and high harvest in dark color) in 2050 and 2100. Results of simulations for the reference year (2000) are represented in purple. Boxplots with the colored edge represent the behavioral response, while boxplots with black edge represent the behavioral–numerical responses of moose and wolf to emergent changes in forest landscape composition, with squares and diamonds representing moose and wolf pack density, respectively. The center value is the median, edges of the box are 25th and 75th percentiles, and whiskers represent ±1.5 of the interquartile range. Summer results can be found in Appendix S4: Figure S2. RCP, representative concentration pathway.

bottom-up cascading effects on moose and wolf numerical responses (Serrouya et al., 2021).

Prey mortality

We fixed caribou density in all simulations (a conservative assumption) to explore the relative contribution of behavioral response and behavioral–numerical responses under changing landscape conditions on caribou mortality rate. Thus, an increase in caribou mortality between scenarios necessarily implied an increase in the wolf–caribou encounter rate. This increase in encounters is due to a difference in landscape structure and composition that favor predator–prey encounters given species-specific movement rules (behavioral response) and/or an increase in wolf density (numerical response). Our simulations showed that the numerical response of moose, and then the numerical response of wolf triggered by LUC and CC, was the dominant process controlling caribou mortality.

The strong role of the numerical response was further evident from the decrease in the number of caribou that each wolf killed when the number of moose increased (Figure 7). Wolf–moose encounter rate increased with moose density, such that each wolf spent more time handling moose and less time attacking caribou. Although such a dilution effect is typical of a type II or III functional response (Huggard, 1993), an increased caribou mortality rate per wolf could have been observed if the response of wolf and caribou to landscape changes had strongly increased their encounter rate. This was not the case here. Our simulations thus indicate that the overall increase in caribou mortalities with increasing moose density comes mostly from the associated numerical response of wolves. Consequently, the asymmetry of the indirect interaction of apparent competition was mainly triggered by the numerical response of wolves, not their behavioral response to changes in landscape structure and composition. These results are in accordance with previous studies demonstrating the primacy of the indirect food web interaction and the predator numeric response in driving apparent competition in systems as diverse as the Channel Island Fox (*Urocyon littoralis*), feral pig (*Sus scrofa*), and golden eagle (*Aquila chrysaetos*)

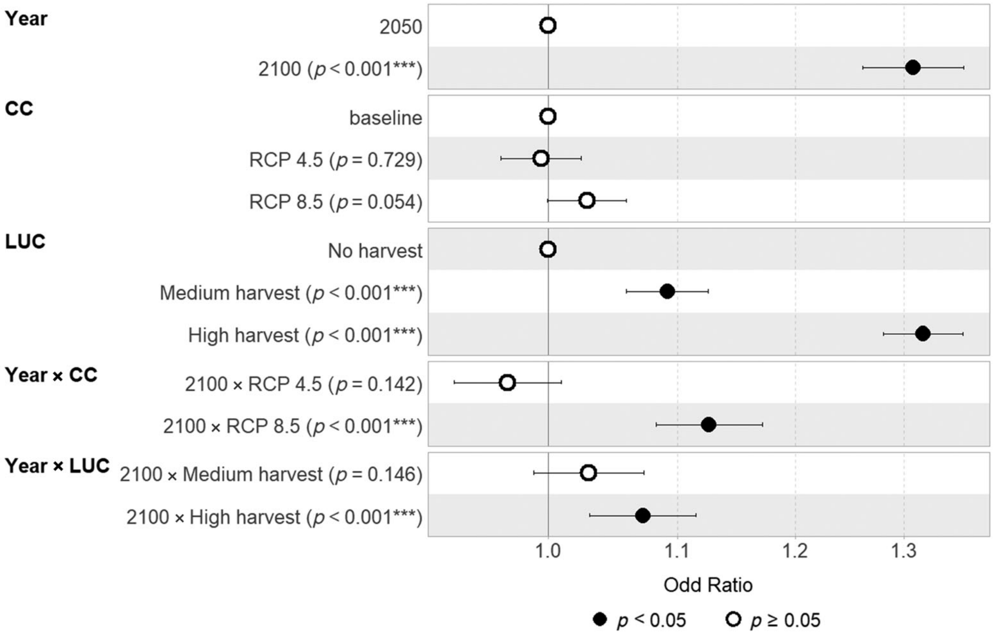

FIGURE 6 Impacts of land use change (LUC) and climate change (CC) on caribou survival in 2050 and 2100. The odds ratio is the exponential of beta coefficients of the selected logistic-binomial generalized linear model (see candidate models in Appendix S3: Table S2). The intercept for the fixed effects is the logit estimate for the year 2050, baseline, and no harvest. An odds ratio = 1 corresponds to the absence of effects of LUC, CC, and the year. The points and horizontal bars indicate the means and their 95% confidence intervals (CIs), respectively. CIs that do not overlap 1 are highlighted using black points, while CIs that overlap 1 are shown with white points. Values below 1 indicate that the likely CC and LUC outcomes for caribou survival will be positive (less mortalities), whereas values above 1 suggest a negative outcome. Results are shown for the behavioral–numerical response model. Numerical values are reported in Appendix S3: Table S3. RCP, representative concentration pathway.

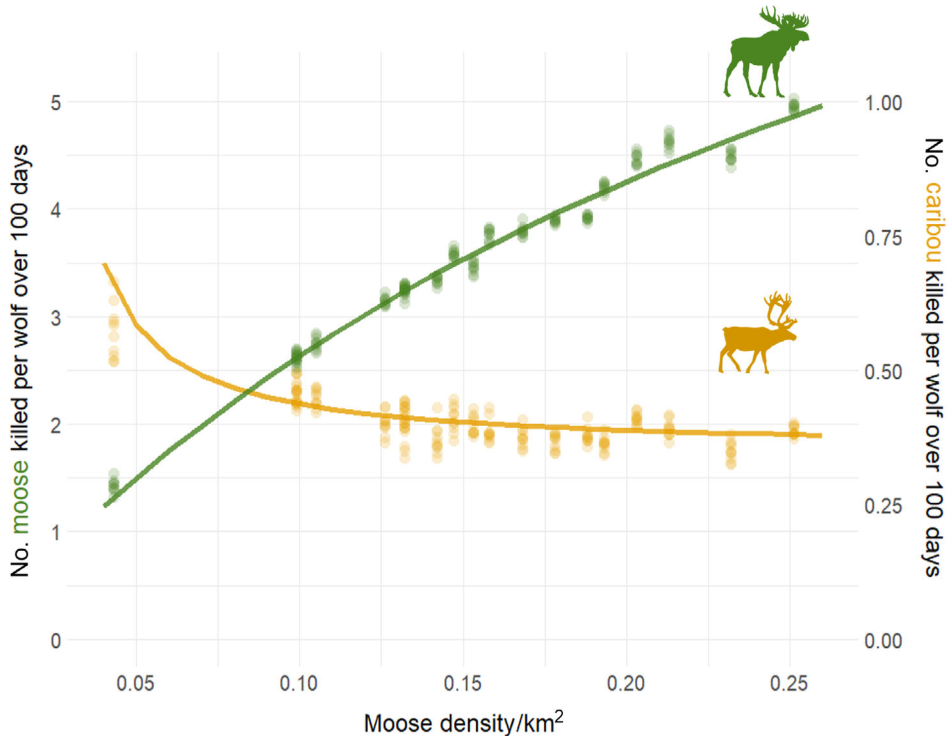

FIGURE 7 Number of prey killed per wolf over 100 days as a function of moose density. The number of moose killed by each wolf is represented in green on the left *y*-axis, while the number of caribou is represented in yellow on the right *y*-axis. Each point represent one replicate of a simulation.

(DeCesare et al., 2010; Roemer et al., 2002). Taken together, this suggests that future CC and LUC impacts could be tightly coupled by the biotic process of predation through indirect food web effects on predator abundance.

We provide strong evidence that a key indirect effect, the wolf–moose numerical response, is the main determinant of caribou mortality rates. We show that this process will strengthen over time, first under changing landscape conditions and then under a changing climate. As a result, projected changes in deciduous vegetation, whether caused by climate or anthropogenic disturbances, will strongly alter species interactions. Through a complementary approach, we modeled the relative impact of CC and LUC over time on predator–prey encounters by focusing on IBM simulations that included the behavioral and numerical responses. Results showed that LUC had a stronger impact than CC on caribou mortality. The size of the cumulated effect of CC and LUC was related to the availability of deciduous vegetation, such that the scenario with high resource input (i.e., deciduous vegetation and the associated increase in moose density) exerted a stronger indirect effect on predator–prey interactions.

We showed that if the numerical response of moose and wolves is not interrupted by unforeseen factors (e.g., management), then LUC will have a very strong immediate and long-term impact, while CC will have an impact in the long term. The negative effects of CC and LUC on caribou survival both increased over time. We also did not detect a difference in caribou mortality between the optimistic CC (i.e., RCP 4.5) and baseline conditions. This was because the proportion of deciduous vegetation (from burned and nonimpacted areas) was nearly the same under these two climate scenarios. Consequently, the species-specific numerical responses of moose and wolves remained similar between scenarios. The effect of CC was noticeable only in 2100 under the RCP 8.5 scenario (Figure 6), revealing a nonlinear effect of CC on trophic interactions. Those results highlighted that CC impacts would be noticeable after a certain time lag and need to be severe enough to impact predator–prey interactions. This is linked to the proportion of burned areas, which increased slowly from 13% to 16% between 2000 and 2050 under RCP 8.5 and then reached a maximum of 36% in 2100 (Figure 1). Our conservative approach, however, likely underestimates extirpation risk of caribou in Canada's boreal forest. Considering that most (>60%) of eastern Canada's boreal caribou populations are already declining, largely due to LUC-induced apparent competition (Environment Canada, 2012), the mortality rates we predict suggest caribou will struggle to survive long enough in the boreal forest to experience CC impacts. But our research also suggests the importance of prioritizing short-term management actions aimed to weaken the strength of indirect interactions of the wolf–moose numerical responses.

Our research adds to a growing body of evidence that specialist species of low productive environment may be vulnerable to landscape structure that affects the distribution of predation risk (Ims et al., 2019; Vanlandeghem et al., 2021). Empirical studies showed that wolves hunt by targeting areas rich in moose food, including disturbed areas where early-seral vegetation has emerged (Fortin et al., 2015; Labadie et al., 2021). Although the behavioral response had significant but minor effects on mortality per se, our findings are consistent with previous studies reporting that the increased disturbance rates (Labadie et al., 2021; Wittmer et al., 2007), resource availability (Ims et al., 2019; Serrouya et al., 2021; Thomsen et al., 2018), and changes in landscape structure (Oliver et al., 2009; Vanlandeghem et al., 2021) altered predator–prey interactions in many systems. For example, changes in land use can modify how water vole (*Arvicola terrestris*) habitat patch was connected to surrounding rabbit (*Oryctolagus cuniculus*) habitat, triggering apparent competition between the two prey species through a shared predator, the American mink (*Neovison vison*), with subsequent negative effects on the probability of water vole habitat patch occupancy (Oliver et al., 2009). In accordance with previous field studies, degraded habitats reduced complexity and showed more extreme environmental conditions than intact forest habitats, and these conditions were generally unsuitable for undisturbed forest specialist species (Mair et al., 2018).

We showed that increased LUC and climate-induced habitat fragmentation and loss (i.e., isolation index) will further imperil specialist species with an anti-predator strategy to segregate from predators as they did in their evolutionary history (Peters et al., 2013). This suggests that strategies enhancing habitat complexity and reducing the isolation of high-quality habitat can potentially buffer against the cumulated negative effects of CC and LUC and could be an effective conservation strategy for such specialist species of low productive ecosystems. Our study thus indicates that top-down control on an ungulate of conservation concern can be reduced simply by altering landscape configuration, as also demonstrated by Vanlandeghem et al. (2021), without resorting to lethal control of their most important predator, or alternative prey. Consistently, Ng'weno et al. (2019) demonstrated how the placement of livestock corrals in a savanna ecosystem, can be used to manipulate the spatial distribution of primary prey (zebra, *Equus burchelli*), thereby reducing apparent competition suffered by hartebeest (*Alcelaphus bucelaphus lelwel*). However, for some systems, species affected by disturbance-mediated apparent competition require simultaneous control of alternative prey and predators combined with reductions in habitat alteration that led to increased prey (Serrouya et al., 2019; Wittmer et al., 2013). For example, removal of predators and alternate prey increased survival of the endangered island fox in California (USA), leading to their recovery (Roemer & Donlan, 2004). However, control of predators and alternative prey is a short-term solution that must be combined with land use management such as promoting protected areas, natural restoration, and reducing road networks (Robichaud & Knopff, 2015).

In conclusion, our study highlights the large potential of indirect impacts CC and LUC can have on trophic interaction and food web functioning. The cascading and cumulative effects of LUC and CC on boreal ecosystems will alter predator–prey encounter rates, largely because of numerical responses of alternative prey and predators. CC and LUC can thus lead to significant declines of species through changes in landscape characteristics. In such context, complementary modeling approaches are indispensable to assess CC and LUC impacts on predator–prey dynamics. While our focus was on caribou–moose–wolf boreal systems, IBMs are a powerful tool to apply across species and systems. We suggested that such combined and indirect impacts of CC and LUC could be widespread in the future in low productive systems with similar trophic interactions, such as in semiarid island (Roemer et al., 2002; Thomsen et al., 2018), Arctic (Lamarre et al., 2017), or savanna ecosystems (Ng'weno et al., 2019). Indeed, CC and LUC impacts seem to be tightly coupled to predation in low-productivity environments where apparent competition can be a primary mechanism of species decline. Our study provided guidance to conservation strategies by clarifying mechanisms through which CC and LUC threaten species and their trophic interactions.

AUTHOR CONTRIBUTIONS

Guillemette Labadie and Daniel Fortin conceived the project. Clément Hardy developed the Forest Roads Simulation module for the forest simulation model, and Yan Boulanger simulated landscapes with the forest simulation model. Guillemette Labadie and Virginie Vanlandeghem calibrated the individual-based model. Guillemette Labadie analyzed the data and produced results. Guillemette Labadie, Daniel Fortin, Mark Hebblewhite, and Yan Boulanger wrote the paper. All authors discussed the analyses and results, edited the manuscript text, and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Labadie et al., 2023) are available from Dryad: https://doi.org/10.5061/dryad.ht76hdrkt. All other study data are included in the article and/or appendices.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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