Impacts des changements globaux sur les interactions trophiques du caribou forestier, une espèce parapluie de la forêt boréale

Thèse

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Résumé

Les changements globaux, induits par l'augmentation et le cumul des perturbations naturelles et anthropiques, modifient les caractéristiques environnementales, et par conséquent la répartition des espèces et la dynamique des réseaux trophiques. Les principaux objectifs de mon travail sont: 1) de caractériser, dans le contexte des changements globaux, les effets spécifiques et cumulés des perturbations naturelles et anthropiques sur les interactions prédateur-proie chez les grands mammifères, et 2) d'évaluer comment les changements globaux affecteraient la pertinence de la stratégie d'aménagement d'une espèce parapluie pour la conservation de la biodiversité régionale. Mon système d'étude est le caribou des bois (*Rangifer tarandus caribou*), écotype forestier, sujet à la prédation par les loups gris (*Canis lupus*) dans la région de la Côte-Nord (QC, Canada). Dans le Chapitre 1, j'évalue l'impact des épidémies de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana*) sur la répartition, la survie et les interactions trophiques du caribou. Pour cela, j'ai utilisé des relevés annuels de la sévérité des épidémies de tordeuse combinés avec les localisations des caribous et des loups munis de colliers GPS ainsi que des inventaires aériens d'orignaux (*Alces alces*). Pour considérer les effets de l'épidémie de tordeuse sur l'orignal, le loup et le caribou, j'ai utilisé des analyses de sélection d'habitat et de survie pour le caribou. J'ai démontré comment une épidémie d'insectes induit un enfeuillement, créant une augmentation de ressources pour les orignaux, résultant à une suite de réponses spatiales et démographiques chez l'orignal, le loup et le caribou. La réponse numérique de l'orignal et les réponses comportementales de l'orignal et du loup étaient fortement associées à une réponse négative chez le caribou. Le risque de mortalité du caribou était plus élevé pour les individus sélectionnant les peuplements forestiers les plus sévèrement affectés par la tordeuse, surtout si les peuplements étaient coupés après l'épidémie. Mes travaux indiquent une compétition apparente « retardée » entre l'orignal et le caribou médiée par la prédation des loups. En plus de l'impact des épidémies d'insectes, les feux de forêt et l'aménagement forestier menacent les caribous en modifiant également les interactions trophiques. Dans le Chapitre 2, j'ai évalué les effets cumulés de l'aménagement forestier et des changements climatiques sur la mortalité du caribou. En utilisant un modèle spatialement explicite centré sur l'individu (IBM), j'ai simulé le déplacement des animaux et les interactions interspécifiques dans des paysages virtuels, variant selon trois niveaux de coupes et trois scénarios de changement climatique. Je démontre que les changements induits par le climat et l'aménagement forestier influencent les interactions trophiques en exacerbant la compétition apparente, par une augmentation asymétrique de la disponibilité des ressources. Mon modèle prévoit un enfeuillement induit par les changements globaux, augmentant l'abondance des orignaux et des loups, avec des conséquences désastreuses pour le caribou. De plus, je démontre que les effets provenant de la réponse numérique prédominent par rapport à une réponse comportementale seule. Ainsi, les changements globaux devraient fondamentalement modifier la structure du réseau trophique, renforçant les interactions indirectes par la compétition apparente. Un autre résultat majeur souligne que l'impact de l'aménagement forestier devrait être plus précoce et trois fois plus élevé que l'impact des changements climatiques. Afin de préserver la biodiversité, ces résultats suggèrent de se concentrer d'abord sur la réduction des impacts négatifs de l'aménagement forestier. Enfin, dans le Chapitre 3, j'ai évalué l'impact des changements climatiques et de l'aménagement forestier sur le maintien de la biodiversité. Plus précisément, j'ai évalué l'efficacité et l'effet parapluie des stratégies d'aménagement de l'habitat du caribou forestier dans un contexte de changements globaux pour la conservation des oiseaux et des coléoptères. J'ai combiné des modèles mécanistes spatialement explicites pour prévoir l'efficacité des stratégies d'aménagement sur la survie du caribou, et des modèles prédictifs d'occurrence pour caractériser l'impact sur le maintien des assemblages d'espèces. Les paysages ont été simulés selon quatre aménagements forestiers, dont deux stratégies d'aménagement, et trois scénarios de changement climatique. Je démontre que les stratégies d'aménagement, conçues pour la conservation du caribou, devraient également maintenir les assemblages d'oiseaux et de coléoptères. Bien que j'ai détecté un effet plus important de l'aménagement forestier, l'effet parapluie des stratégies d'aménagement dépendraient également de la sévérité des changements climatiques. Les stratégies d'aménagement conçues pour une seule espèce pourraient donc avoir un important effet parapluie pour la biodiversité.

Abstract

Global change, through the increase and cumulative impacts of natural and anthropogenic disturbances, is predicted to modify species distributions and food-web dynamics, through changes in environmental characteristics. The main goals of my work are two-fold: 1) characterize, in the context of global change, the specific and cumulative effects of natural and anthropogenic disturbances on predator-prey interactions among large mammals, and 2) assess how global change is expected to impact the relevance of recovery strategy of an umbrella species for the conservation of regional biodiversity. My study system was the boreal ecotype of woodland caribou (*Rangifer tarandus caribou*), subject most notably to predation by gray wolves (*Canis lupus*) in the Côte-Nord region (QC, Canada). In Chapter 1, I assess the impact of spruce budworm (*Choristoneura fumiferana*) outbreaks on the distribution, survival and trophic interactions of boreal caribou. For this, I used annual surveys of spruce budworm outbreak severity, and combined these data with locations of GPS-collared caribou and wolves, and aerial inventories of moose (*Alces alces*). To account for comparative effects of spruce budworm outbreak on expected responses in moose, wolves, and caribou, I used a statistical habitat selection and survival analyses for boreal caribou. For the first time, I demonstrated how an insect outbreak triggers a flush of deciduous vegetation creating a resource pulse for herbivores, which then translates into a suite of spatial and demographic responses in moose, wolves, and boreal caribou. I show a numerical response in moose and behavioral responses in both moose and wolves that associated strongly with a negative response in caribou. Consistently, mortality risk of caribou was higher for individuals selecting forest stands most severely impacted by spruce budworm, especially if stands were logged post-outbreak. My work is indicative of “delayed” apparent competition between moose and caribou via wolf predation because wolves clearly showed selection to use impacted areas after post-outbreak logging that were of greatest risk to caribou. In addition to the impact of insect outbreaks, wildfires and forest harvesting threaten boreal caribou populations by also altering trophic interactions. Given the latest and harsh climate change projections, in Chapter 2, I assessed the cumulative impacts of forest harvesting and climate change on the mortality of boreal caribou. I use a spatially explicit individual-based model (IBM) to simulate animal movement and species interaction in virtual landscapes, varying in terms of three levels of forest management and three climate change scenarios. I demonstrate that climate- and land-use-induced changes influence trophic interactions by exacerbating apparent competition, through asymmetric increase in resource availability between the two herbivores species. My analysis forecasts how climate and land-use changes increase the proportion of deciduous vegetation, and show this bottom-up forcing increases moose and wolf abundance, with dire consequences for boreal caribou. Moreover, I partition the indirect effects on caribou into behavioral-numeric versus behavioral only interactions and show that numeric effects predominated. Thus, combined impacts of land-use and climate changes can fundamentally alter the food web structure, making indirect interactions stronger through apparent competition.

Another major result highlights that land-use impacts are predicted to be earlier and three times higher than climate change impacts. This has globally relevant and urgent implications for biodiversity conservation – focus first on reducing negative impacts of land-use change as an effective longer-term climate change biodiversity conservation strategy. Finally, in Chapter 3, I assessed the impact of global climate and land-use changes on biodiversity integrity. More specifically, I assessed the effectiveness and umbrella value of management strategies designed to meet the needs of the boreal caribou in a context of global change for conservation of birds and beetles. I combined mechanistic, spatially explicit models to forecast the impact of management strategies on the survival of boreal caribou, and predictive models of species occupancy to characterize concurrent impacts on bird and beetle diversity. Landscapes were simulated based on four forest management plans, including two management strategies, and three climate change scenarios. I found that strategies that best mitigate human impact on boreal caribou were also the best at maintaining bird and beetle assemblages. While I detected a stronger effect of land-use change compared to climate change, the umbrella value of the management strategies was also impacted by the severity of climate change. Single-species conservation actions may therefore have important umbrella biodiversity benefits.

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À ma famille et mes amis qui m’ont aidée à
écrire ce chapitre de ma vie.

“There is still a window of time.
Nature can win if we give her a chance.”
Dr. Jane Goodall

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Bonne lecture.

Avant-propos

Ce doctorat est présenté sous la forme d'une thèse comprenant trois articles scientifiques. La thèse inclut également une introduction et une conclusion générales qui lient l'ensemble des articles.

En tant qu'auteure principale des trois chapitres, j'ai élaboré les objectifs de recherche en collaboration avec mes directeurs, j'ai effectué toutes les analyses statistiques et j'ai rédigé la première version complète des articles. Mon directeur de thèse, Daniel Fortin, a largement contribué au développement des objectifs et aux révisions des manuscrits. Mon co-directeur, Mark Hebblewhite, a fortement contribué à la révision des manuscrits. Je dois également souligner la collaboration de Yan Boulanger, qui a réalisé les simulations des paysages en fonction de divers scénarios de changements climatiques et d'aménagement forestier utilisées dans les Chapitres 2 et 3. Les Chapitres 1, 2 et 3 sont rédigés sous forme d'article scientifiques.

Mon Chapitre 1, intitulé *Insect-mediated apparent competition between mammals in a boreal food web*, a été publié dans la revue *PNAS* en juin 2021, avec la collaboration de Philip D. McLoughlin, Mark Hebblewhite et Daniel Fortin. La version présentée est identique à celle publiée. Le Chapitre 2, intitulé *Global change risks a threatened species due to alteration of predator-prey dynamics*, a été soumis à *Ecological Monographs* avec Clément Hardy, Yan Boulanger, Virginie Vanlandeghem, Mark Hebblewhite et Daniel Fortin. Le Chapitre 3, intitulé *The umbrella value of caribou for biodiversity conservation in boreal forest under global change*, sera soumis à Ecological Applications. Il a été écrit en collaboration avec Ilhem Bouderbala, Yan Boulanger, Mark Hebblewhite et Daniel Fortin.

J'ai également contribué à deux autres articles scientifiques en dehors de mon travail de thèse. J'ai participé à l'élaboration des objectifs, à la création de cartes, à l'extraction de données spatiales et à la révision du manuscrit de l'article de Bouderbala et coll. (2022), qui a été soumis dans *Global Change Biology*, pour lequel je suis deuxième auteure. J'ai également contribué à la création de cartes, à l'extraction de données spatiales du deuxième manuscrit d'Ilhem Bouderbala. Un article est en cours de rédaction dans lequel je suis deuxième auteure. Ce dernier article sera soumis à *Plos Climate*.

Introduction générale

1. Global change impacts on the environment and ecological communities

1.1. Characteristics of global change

Global change is a complex process meaning changes in the global environment (U.S. Global Change Research Program 1990). This includes alterations in climate, water cycle, ocean, overfishing, land productivity, land-use, urbanization, pollution, population, food-webs, biological diversity, and more. I use the term 'global change' in my thesis to define more specifically the combine effects of climate and land-use changes within an ecosystem. Climate change considers the change in temperature and precipitation, and land-use change considers how anthropogenic activities affect ecosystems and their development. More specifically, I use the term 'land-use change' as a direct effect of human activities on landscape without a change in land-cover class, (e.g., changing natural forest to intensive production forestry) (Bürgi *et al.* 2017).

There is a broad consensus that the global climate is warming at a rate that is unprecedented in at least the last 2000 years (IPCC 2021). Future climate scenarios predict that the largest temperature increases will be in the upper latitudes of the Northern Hemisphere. General circulation model scenarios (GCMs) predict a temperature increase of 3 to 5°C, and a slight increase in annual mean precipitation by the end of the 21st century at high latitudes (IPCC 2013). Such changes in temperature and precipitation are expected to influence extreme events and natural disturbance regimes such as wildfire, drought and insect outbreaks at various spatial and temporal scales (Dale *et al.* 2001; Flannigan *et al.* 2006; Régnière *et al.* 2012; IPCC 2021). These projected changes in climate and natural disturbances may have critical ecological outcomes, including the negative impacts on ecosystem services and continued decline in global biodiversity (Pereira *et al.* 2010).

Climate change is not the only global environmental driver that is expected to alter ecological communities (Mendoza & Araújo 2019; Pacifici *et al.* 2020). Anthropogenic disturbances alter land covers (Gomes *et al.* 2019) and the resources that species depend on to survive (Feeley *et al.* 2020; Filazzola *et al.* 2020). Indeed, more than 80% of Earth's land surface are already influenced by Humans (Sanderson *et al.* 2002). By the end of the century, human population is expected to double its current size, and a portion of the planet could experience climatic and environmental conditions that have no modern analog (Sala *et al.* 2000; Williams *et al.* 2007; Blois *et al.* 2013). Anthropogenic disturbances, such as habitat destruction, habitat conversion and fragmentation, eutrophication, pollution, overexploitation, and the introduction of exotic species, threaten the environment and the ecological communities (Rands *et al.* 2010; Cardinale *et al.* 2012).

Climate and land-use changes are expected to influence each other (Cochrane 2001; Laurance 2004; Boulanger *et al.* 2019), potentially resulting in positive feedbacks (Laurance & Bruce Williamson 2001; Northrup *et al.* 2019). The effects of both drivers can occur at faster rates than expected in isolation (Laurance & Bruce Williamson 2001; Northrup *et al.* 2019). While evidence that global climate and land-use changes may ultimately lead to species extinction, community reorganization and biotic homogenization, we still lack information on how these two dominant drivers of global environmental changes interact to impact species (Mantyka-pringle *et al.* 2012; Sirami *et al.* 2017). For example, in the boreal forest, cumulative impacts of both climate and land-use changes can result in a net loss of biodiversity, while a net increase in biodiversity can be expected with the impact of climate change alone (Berteaux *et al.* 2010, 2014). Given this, understanding the response of species to the cumulative effects of climate and land-use changes is one of the most pressing issues facing biologists today, especially for determining adequate predictions of the impact of global change on ecological communities (Cahill *et al.* 2013).

1.2. Direct impacts of global change

Climate and land-use changes could profoundly impact species distribution, community structure and ecosystem functions by affecting the environment and individual organisms. Global change can directly impact a population through the influence of abiotic factors on the physiology and behavior of individuals (Gunderson *et al.* 2017). For instance, climate change is expected to have many direct effects on ecosystem functioning, some of which resulting from warmer temperatures, but others arising from changes in water availability and increases in atmospheric CO2 concentration. Such increase in CO2 concentration can have a direct effect on photosynthetic rates (Smith & Dukes 2013), and temperature effects on metabolic rates (Dillon *et al.* 2010). Other changes, such as phenology, are especially likely to alter trophic interactions (Matías & Jump 2012), resulting in trophic mismatches (Post & Forchhammer 2008) and community instability (Post 2013). For example, in arctic, plant phenology advances in response to climatic warming, resulting in a trophic mismatch with migratory herbivores, such as caribou (*Rangifer tarandus caribou*) (Post & Forchhammer 2008). Indeed, the timing of caribou parturition mainly depends on the photoperiod, whereas the plants are more temperature dependant. Climate change is already having a large direct impact on ecological communities by modifying environmental conditions (Wilmers & Getz 2005; Blois *et al.* 2013), which ultimately alter trophic interactions (Ullah *et al.* 2021). Furthermore, the impacts of climate change are expected to intensify and accelerate (Cox *et al.* 2000).

Anthropogenic activities have also some direct major effects on ecological communities. For example, in forest ecosystems, anthropogenic activities such as forest harvesting and oil and gas industries directly affect the composition, age structure and spatial configuration of forests (Baker 1995; Bergeron *et al.* 2006; Yamasaki *et al.* 2008). These environmental characteristics are major drivers of the distribution and persistence of species and biotic interactions could be indirectly modified by such landscape modifications (Thompson *et al.* 1998; Dawe *et al.* 2014; Tremblay *et al.* 2018). The impacts of anthropogenic activities can be combined with those from natural disturbances such as wildfires and insect outbreaks. For instance, climate and landscape changes cumulatively triggers the spatial decline of wolverine populations (*Gulo gulo*, Linnaeus, 1758) in the Canadian Rocky Mountains (Heim *et al.* 2017), by diminishing spring snow and changing mesopredator communities. As natural and anthropogenic disturbances increase (Diffenbaugh & Field 2013; Müller *et al.* 2019), there is an increasing urgency to understand the impact of habitat changes on individuals, and ultimately on their biotic interactions to correctly anticipate the impact of global change on the persistence of ecological communities.

2. Trophic interactions and habitat heterogeneity

2.1. Trophic interactions

Understanding the consequences of indirect effects of global changes requires an understanding of species interactions and trophic dynamics (e.g., Trainor and Schmitz (2014)). The origin and maintenance of species diversity are determined by biotic interactions, which provide diverse ecosystem services such as primary productivity or nutrients cycles (Pereira *et al.* 2010). Indeed, ecological communities are defined on the basis of interactions among species and between species and the physical environment (Hairston *et al.* 1960). Subsequently, ecological interactions that influence one species also affects many others (Chapin III *et al.* 2000). Species interact with each other through multiple processes, such as predation, competition, pollination, herbivory or parasitism. More specifically, trophic interactions between consumers and their resources maintain the structure, function and stability of ecological communities (Bascompte *et al.* 2005; Ripple *et al.* 2014b; Schaum *et al.* 2018). In many systems, such as terrestrial, fresh water and marine systems, the presence of consumers can strongly influence the abundance, distribution and range limits of the resource species (Estes et al. 2011, Wisz et al. 2013). For instance, the restoration of wolf (*Canis lupus*) in Yellowstone National Park, USA, and the increase in ungulate predation resulted in an increase in willow (*Salix* spp.) growth, together with an increase in bird richness, abundance, and diversity (Baril *et al.* 2011).

According to the Exploitation Ecosystems Hypothesis (EEH, (Oksanen *et al.* 1981), an increase in plant abundance should result in more complex food webs (e.g., more trophic levels) with stronger direct and indirect interactions. Herbivores in unproductive environments tend to be under bottom-up control, while top-down control only occurs when plant production reaches sufficient levels (Aunapuu *et al.* 2008; Welti *et al.* 2020).The boreal forest, for example, is characterized as a relatively unproductive forest and is expected to have a higher proportion of deciduous vegetation induced by global change (Boulanger & Pascual Puigdevall 2021). Given prey habitat association, climate and land-use-induced changes on forest structure and composition (e.g., fire suppression, restoration, and timber extraction) alter the distribution and abundance of prey species, and subsequently influence predator space use and territory occupancy rates (Hobart *et al.* 2019). Moreover, these changes in environmental conditions, such as forest structure and composition following a disturbance, can result in the presence of new species, leading to new interactions and ecosystem changes. For example, white-tailed deer (*Odocoileus virginianus*) has recently been expanding into the boreal forest beyond its typical habitats, due to the increase in human disturbances (Côté *et al.* 2004; Latham *et al.* 2011). This increase in white-tailed deer result in a numerical response by wolves, and consequently higher predation on threatened boreal populations of woodland caribou (*Rangifer tarandus caribou*, hereafter boreal caribou) (Latham *et al.* 2011). Species invasions and habitat modification frequently occur in combination, and it can be hard to properly isolate the individual effects of each driver (Didham *et al.* 2007; Tylianakis *et al.* 2008). Evaluating and predicting the impact of global change can be puzzling, especially regarding trophic interactions, due to their sensitivity to the physiology, phenology, relative abundances and behavior of species (Suttle *et al.* 2007; Tylianakis *et al.* 2007, 2008). Quantifying the strength of the interactions between the consumers and their resources is thus crucial for understanding how ecological communities are organized and how they respond to any environmental changes (Bascompte *et al.* 2005).

2.2. Spatial heterogeneity

A landscape is considered heterogeneous when it is perceived by individuals as a set of patches, each comparatively uniform in its ecological characteristics and markedly separated from its neighbors (Dutilleul & Legendre 1993). The spatial heterogeneity comes from different factors including exogenous factors, such as climate, landscape composition and structure, resource fragmentation, and endogenous factors, such as developmental traits, behavior and dispersal (Vinatier *et al.* 2011), which are highly altered by global change (Pacifici *et al.* 2017; Hansen *et al.* 2019). The influence of spatial heterogeneity on species behaviors and their foraging activities has important consequences for population dynamics (Bonsall & Hassell 2007). For instance, predator behavioral decisions can lead to forage in a non-random way: predators may target areas rich in prey or in prey's food (Fortin *et al.* 2015). The way prey and predators distribute themselves across patches, move between patches, and exploit resources across heterogeneous environments have thus implications in the structure, function, and stability of ecological communities. Indeed, the heterogeneity of the habitat is a major factor that allow predators and prey to coexist (Holt 1984; Begon *et al.* 2006; Bonsall & Hassell 2007; Gorini *et al.* 2012), by impacting not only the encounter rate, but also the search efficiency, the success rate and even the predator consumption rate (Gorini *et al.* 2012). Spatial heterogeneity also provides prey refuges (Mason & Fortin 2017) and niche diversification among prey even if there is no competition for resources (Holt 1984). Ultimately, spatial heterogeneity impacts predator-prey interactions by introducing difference between the total prey population density and the proportion which predator has the possibility to kill and feed (Gorini *et al.* 2012). Consequently, the spatial structure and composition of the environment play an important role in the predator-prey dynamics. Considering the spatial heterogeneity is thus of great importance to understand the dynamics of populations, communities, and ecosystems under global change (Lovett *et al.* 2005).

Understanding the major role in spatial heterogeneity of species habitat is critical to assess global change effects at large spatial scales. For example, changes in land-use can modify how water vole (*Arvicola terrestris*) habitat patches are connected to surrounding rabbit (*Oryctolagus cuniculus*) habitat. Land-use change was associated with occurrence of 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). Although water voles and rabbits are largely spatially segregated due to differences in preferred habitat, they can still have an indirect effect on one another via their common predator, the mink, which uses both habitat types (Oliver *et al.* 2009). Understanding the role of spatial heterogeneity is thus crucial to establish reliable and robust recommendations for conservation and ecosystem management. For example, 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 zebra (*Equus burchelli*), thereby reducing hartebeest (*Alcelaphus bucelaphus lelwel*) predation rate by lions (*Panthera leo*). It is therefore important to assess the impacts of environmental changes and predict how it will modify the spatial heterogeneity in order to anticipate future changes in the use of the environment by individuals and to establish effective management plans to mitigate the effects on populations (Fahrig 2001; Doherty & Driscoll 2018). However, although essential, including the effects of spatial heterogeneity in community studies is challenging, because of the increasing number of indirect effects linking trophic levels (e.g., apparent competition, anti-predator behavior, hunting efficiency, Gorini et al. 2012).

3. Indirect impacts of global change and complex cascading effects

3.1. Specificity of indirect impacts

In a context of global change, population responses in time and space (e.g., range shifts and spatial distribution), community composition and dynamics (e.g., abundance, diversity and multitrophic interactions), and ecosystem responses (e.g., net primary productivity) can be unevenly impacted (Parmesan and Yohe 2003, Hickling et al. 2006, Newman et al. 2011, Price et al. 2013, Ullah et al. 2021). A review study showed that indirect impacts can have a greater effect than direct ones and are therefore essential to be considered (Ockendon *et al.* 2014). One of the most striking studied systems showing the importance of indirect effects is the reintroduction of wolf in Yellowstone National Park, USA (Fortin *et al.* 2005; Berger *et al.* 2008; Ripple *et al.* 2014a). In this system, the increase in predation pressure of elk (*Cervus elaphus*) by wolves had allowed the vegetation to return (Ripple & Beschta 2012) and, had even changed the morphology of the streams (Beschta & Ripple 2012), to ultimately change the entire associated ecosystem (Ripple *et al.* 2014b); a concept known as trophic cascade (Carpenter *et al.* 1985).

Global change can indirectly trigger trophic interactions locally through the change in resource availability, such as mast fruiting by trees and herbs (Schmidt & Ostfeld 2008; Grendelmeier *et al.* 2018; Czeszczewik *et al.* 2020), periodic irruption of palatable insects (Haney 1999; Venier & Holmes 2010), and transport of marine resources (e.g., whale carcasses) to terrestrial systems (Rose & Polis 1998; Nash *et al.* 2021) or of terrestrial resources (organic nitrogen or phosphorus) to aquatic systems (Burkholder *et al.* 1997; Larsen *et al.* 2016). Determining how the effects of resource pulses ricochet across food webs is a major challenge for community ecology (Ostfeld & Keesing 2000; Yang *et al.* 2008). In low productive or arid environments, the effect of climate on the availability of resources can have a significant impact on trophic interactions. Indeed, changes in rainfall regimes may affect predator-prey interactions from the bottom-up by increasing primary productivity and resource availability, and subsequently lead to the increase in the density of small mammals, such as deer mouse (*Peromyscus maniculatus elusus*) and their predator, the barn owl (*Tyto alba*) (Thomsen *et al.* 2018). In years of high abundance, owls eat more mice. After one to two years, when the density of the mice decreases following the reduction of the resource, the owls switch to the Scripps's murrelet (*Synthliboramphus scrippsi*), thus increasing their mortality rate (Thomsen *et al.* 2018). This change in mouse density that causes a change in the risk of Scripps's murrelet mortality from a shared predator is defined as apparent competition. This example highlights several essential points of trophic interactions. First, the temporal aspect as the indirect effect on Scripps's murrelet was delayed from the triggering event. Then, the spatial aspect, as the terrestrial and marine environments are indirectly connected by a shared predator in this example.

Apparent competition is a common indirect interaction increasingly reported in field studies (Holt 1977; Schmidt & Ostfeld 2008; Adams *et al.* 2010; Frost *et al.* 2016; Holt & Bonsall 2017). Two species are in apparent competition when the presence and abundance of one of the two prey species negatively affects the population of the second, by inducing a numerical response from the predator which, in turn, intensifies the predation pressure (Holt 1977). It has largely been characterized in the terrestrial system with human-induced change on resources (Bryant & Page 2005), prey or predator communities (Taylor 1979; Courchamp *et al.* 2000). Furthermore, apparent competition caused by resource modifications and introduced species has been frequently found to be the cause of species endangerment and declines (DeCesare *et al.* 2010). Yet little is known on how change in landscape composition and resource availability induced by global change would impact populations dynamics or how these effects will transfer through food chains (Martin & Maron 2012; Stoner *et al.* 2018; Ims *et al.* 2019).

3.2. Changes in species distribution and abundance

Global change is affecting species abundances (van der Putten *et al.* 2010) and is causing many species to shift their distributions poleward and towards higher altitudes to track changes in optimal habitat (Parmesan 2006; Chen *et al.* 2011). Shift in species distribution and abundance is related to changes in climatic regimes, often via species-specific physiological thresholds of temperature and precipitation tolerance and/or habitat changes (Aspinall & Matthews 1994; Parmesan 2006). When climatic envelope migrates faster than a species or species habitat, the species is expected to have difficulties with these non-optimal conditions and may be unable to survive (Warren *et al.* 2001). Habitat loss and fragmentation, through human activities, may also exacerbate these shifts (Guo *et al.* 2018; Northrup *et al.* 2019). Yet, species' responses are expected to vary greatly, mainly due to their sensitivity to climate or land-use changes (Parmesan & Yohe 2003). While numerous species are declining, there are also many increasing species (McKinney & Lockwood 1999; LaManna & Martin 2017; Cadieux *et al.* 2020), highlighting that species are not equally at risk under global change (Olden 2006). It is thus important to know which factors make a species vulnerable to guide further conservation efforts both for the same species and for ecologically similar species that might be threatened by extinction.

Changes in species distribution have already occurred across a wide range of geographical locations and taxonomic groups during the last century and are expected to intensify (Walther *et al.* 2002; Parmesan & Yohe 2003; Pecl *et al.* 2017). In general, birds may shift faster than most of organisms, such as mammals, insects, plants, or soil organisms (Berg *et al.* 2010; van der Putten *et al.* 2010). Species range shift and changes in species composition and structure are likely result in displacement of ecological niches and, consequently, in changes to the local biodiversity and species interactions (Tylianakis *et al.* 2008; van der Putten *et al.* 2010). When range shifts vary between species, or when prey and predator both shift ranges, species may not automatically interact in the new range as they did in the original one (Menéndez et al. 2008, van der Putten et al. 2010). For example, Brown Argus butterfly larvae (*Aricia agestis*) can partially escape from parasitism in newly colonised areas, even though the parasitoid species where already present (Menéndez *et al.* 2008). This is due to the presence of alternative host species and the ineffectiveness of the parasitoids at locating the new host (Menéndez *et al.* 2008). Therefore, changes in species distribution may result in decoupling of trophic interactions (van der Putten *et al.* 2010). This could be caused by the inability of predators and prey to interact in the new range or differences in dispersal rate (van der Putten *et al.* 2010). Moreover, the asynchronous speed of range shifts can create new interactions with new combinations of species and have major consequences for ecological communities (Gilman *et al.* 2010; Urban *et al.* 2013; Pecl *et al.* 2017). For example, the northward range shift of *Phidiana hiltoni*, a sea slug, caused the decline of other nudibranch species because of *P. hiltoni* predation and competition (Goddard *et al.* 2011). The decline of these species is directly caused by the range shift of a new species, and subsequently indirectly related to global change. Changes in herbivory, host-plant associations, predation dynamics, competition, and mutualisms can thus have repercussions through multiple members of the community, multiplying extinction risks and therefore have substantial impacts at the community level (Sorte *et al.* 2010; Zarnetske *et al.* 2012; Cahill *et al.* 2013).

In many ecosystems, disturbances play a fundamental role in defining vegetation composition (Crawford *et al.* 2001; Capitanio & Carcaillet 2008; Brice *et al.* 2020). Variations in species responses to global change can thus be exacerbated by natural and anthropogenic disturbances. For example, some ungulate species (e.g., elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*) and moose (*Alces alces*)) exhibited a positive association with bark beetle outbreaks, likely due to the growth of diverse and numerous assemblages of understory species providing an abundant food resource (Ivan *et al.* 2018). Moreover, the creation of road networks associated with human activities, impact not only the landscape structure and composition, but also animal behavior (Trombulak & Frissell 2001; Fortin *et al.* 2015). For some predators, such as wolves, roads make them move faster and farther (Dickie *et al.* 2017). Moreover, Courbin et al. (2014) found that wolves targeted the most highly connected patches, highlighting the critical role of roads. These effects can be mitigated by reducing road construction and increasing the restoration or removal of existing roads. The integration of the effects of natural and anthropogenic disturbances and environmental characteristics on the effects of global change on ecosystem dynamics are useful in guiding conservation planning with the determination of adequate disturbance threshold for maintaining sustainable populations.

3.3. Cumulative effects of climate and land-use changes

Global change acts on ecosystems through complex direct and indirect effects, and it is very challenging to consider all the drivers. While the vast majority of studies have investigated effects of a single global change driver on species and their interactions, the cumulative drivers of global change need to be further studied (Didham *et al.* 2007; Foster *et al.* 2016; Sirami *et al.* 2017). The multiple drivers can act synergistically, antagonistically, or additively on ecological communities (Sirami *et al.* 2017). A wide range of mechanisms induced by land-use and climate changes cumulative effects can affect different levels of biological organization and biodiversity, such as impacts on species diversity, population dynamics, and species' dispersal capacity (Fischer & Lindenmayer 2007; Bellard *et al.* 2015; Sirami *et al.* 2017). For example, Northrup et al. (2019) showed that climate and land-use changes act synergistically, leading to the declines of forest bird populations. Ferger et al. (2017) highlighted in their study that disregarding the cumulative effects of climate and land-use on biodiversity underestimates the joint effect. While the number of studies analyzing multiple drivers of global change on species range shifts and abundance have recently increased (Ferger *et al.* 2017; Sirami *et al.* 2017; Guo *et al.* 2018; Northrup *et al.* 2019), only few considered indirect effects on multi-species and changes in trophic interactions (Bossier *et al.* 2020). The restricted understanding of how drivers may interact and affect observed changes will likely hamper the ability to make robust projections and provide reliable conservation and management recommendations (Titeux *et al.* 2016; Sirami *et al.* 2017).

The management of ecosystems, particularly forests, after a natural disturbance often includes salvage logging, which represents a good case study of a cumulative impact of climate and land-use changes. Salvage logging –the removal of disturbance-affected trees– has become a widespread and a common practice to recover some of the economic value that would otherwise be lost (Lindenmayer *et al.* 2012). Salvage logging may occur after a wide variety of disturbances, such as wildfires, insect outbreaks, and windstorms (Schmiegelow *et al.* 2006; Lindenmayer *et al.* 2012). Initially, salvage logging could be seen as a favorable option as it mostly involves the disturbance of areas already disturbed, thereby keeping largely constant the disturbed area (except for the addition of roads). However, some studies found that the effects of harvesting disturbed forest differ from those of harvesting undisturbed forest (Lindenmayer *et al.* 2004; DellaSala *et al.* 2006; Lindenmayer & Noss 2006; Thorn *et al.* 2016), indicating that interactions between natural and anthropogenic disturbances can be expected. Moreover, it has been shown that salvage logging disrupts post-disturbance succession, removes biological legacies (e.g., snags), and reduces the value of wildlife habitat (Lindenmayer & Noss 2006; Norvez *et al.* 2013; Thorn *et al.* 2018; Thomas *et al.* 2019). In addition to removing standing trees, salvage logging involves the deployment of an extensive road network, which is well-known to increase the hunting efficiency of some predators, such as wolves (James & Stuart-Smith 2000; Whittington *et al.* 2011). Interactions between natural disturbances and logging imply that increasing disturbances, through global change, are expected to impact even more ecological communities, with unknown characteristics and consequences (Lindenmayer *et al.* 2012; Leverkus *et al.* 2018). Information is thus needed to understand how the responses of populations, communities and ecosystems to global change will generate new responsibilities, opportunities, and challenges for the conservation of biodiversity in regions highly impacted by cumulative disturbances. In order to address this important research gap, we need to study the relative and combined effects of land-use and climate changes on species occurrence, composition of ecological communities, and trophic interactions.

4. Approach for biodiversity conservation

4.1. Specialist and generalist species

There is a well-established hypothesis that specialist species are more vulnerable to environmental changes because of their specific habitat requirements and the reduced adaptability, as opposed to generalist species (Gilman *et al.* 2010; Clavel *et al.* 2011; Filazzola *et al.* 2020). More specially, the highly negative impacts of habitat fragmentation and habitat loss on specialist species render them less capable of adjusting their distribution to the rapidly changing landscape (Tuanmu *et al.* 2013; Walkup *et al.* 2017). Land-use or land-cover change may lead to changes in the occupancy of generalist and specialist species among sites, and consequently alter species coexistence (Kay et al. 2018). On the one hand, some species lose part of their habitat (Newbold *et al.* 2015; Ruffell *et al.* 2017; Kay *et al.* 2018), while other species (generalists or specialists of the new environmental conditions) arrive, colonize and exploit the new environment (Kay *et al.* 2018). In the case of habitat loss and fragmentation induced by natural or anthropogenic disturbances, the effect on generalist and specialist species may have very different consequences both for prey and for predators (Ryall & Fahrig 2006). For instance, the conversion of the environment can be advantageous for generalist predators (i.e., feeding on a variety of prey) since they can exploit more resources (Swihart *et al.* 2001; Gehring & Swihart 2003). Conversely, the capacity of habitat specialists to track climatic and environmental changes may be affected by habitat loss and fragmentation (Walther *et al.* 2002), with possible consequences for the mutualisms and antagonisms in which they are involved (Tylianakis *et al.* 2008).

Habitat modifications induced by climate and land-use changes are expected to decrease the number of specialist species confined to the declining habitat type, resulting in biological communities dominated by mobile and widespread habitat generalists (Warren *et al.* 2001; Devictor *et al.* 2008; Clavel *et al.* 2011). For instance, the loss of forest specialists may alter food webs and ecological functions, such as pest control and seed dispersal (Finke & Snyder 2008; Edwards *et al.* 2013; Galetti *et al.* 2013). The overall homogenisation of biodiversity induced by global change is likely to lead the ecological communities even more sensitive to disturbances (Newbold *et al.* 2019). Moreover, specialist species of low productive habitats are predicted to be more impacted by an increase of primary productivity occurring with climate change (Boisvenue & Running 2006) and change in land-use (Serrouya *et al.* 2021), which may increase predation risk (Creel *et al.* 2005; Attum *et al.* 2006; Thaker *et al.* 2011; Ims *et al.* 2019; Serrouya *et al.* 2021). It is thus necessary to develop and improve conservation management. Planning decision affect the proportion of land-cover within a landscape (urban or natural) and can thus influence the composition of both specialist and generalist species at landscape and local scales (Chace & Walsh 2006; Davison & Fitzpatrick 2010). Besides, habitat specialist species are more at risk to be placed on the national red-list (WallisDeVries 2014). Yet, the potential cascading effects of anthropogenic and climate change-driven modifications in landscape on the strength of trophic interactions associated with specialist species remain to be assessed.

4.2. Ecosystem-based management

The main goal of the ecosystem-based management is to protect and maintain regional biodiversity and the sustainability of ecosystems through the application of adapted management, while considering current social and economic needs (Elliott 2013; Laurila-Pant *et al.* 2015). It can be applied to marine (Ellis *et al.* 2011) or terrestrial (Gauthier *et al.* 2008) ecosystems. For instance, in forest ecosystems, ecosystem management is based on maintaining the rate and spatial extent of disturbance that occurs naturally (Gauthier *et al.* 2008). If human disturbances mimic natural disturbances, local biodiversity should be resilient to landscape changes. However, while each type of stand needs to be adequately represented at the landscape level to maintain the associated biodiversity, it is rarely the case (Mori *et al.* 2013).

Planning for the preservation of biodiversity in a changing world is challenging. While protected areas are created to maintain high quality habitat and the associated species, there is a global trend in species range shift (Parmesan & Yohe 2003). Yet, current protected areas and conservation managements are based on species' current distribution and environmental condition and could be rendered obsolete by global change. This highlights that static conservation planning has its limitations (Fuller *et al.* 2011; Dobrowski *et al.* 2021). Spatial conservation plans have been developed to consider global change, such as protecting every species in all its ranges – present and future, and increase habitat connectivity with various corridor (Fuller *et al.* 2011; Berteaux *et al.* 2014; Dobrowski *et al.* 2021). From an ecosystem-based management perspective, modelling techniques are essential to build predictions about future changes and evaluate the most effective conservation plans (Fuller *et al.* 2011; Mori *et al.* 2013; O'Higgins *et al.* 2020). It is therefore necessary to test and adopt flexible and robust management strategies that consider various scenarios, rather than opting for a single measure.

The projected impacts of global change on all levels of ecological communities mean that ecologists must provide scientific recommendations for the development and the improvement of conservation strategies (Pressey *et al.* 2007; Dawson *et al.* 2011; Bellard *et al.* 2014), and governments must implement them. Moreover, the large variation in species responses necessitates to be considered in ecosystem-based management to maintain all the biodiversity (i.e., threatened, rare, common, specialist and generalist species) and ecosystem services, while providing solutions for both ecological and human needs. The conservation strategy involved in ecosystem-based management imply two scales of filters: fine and coarse (Gauthier *et al.* 2008; Mori *et al.* 2013). A coarse filter approach entails maintaining a diversity of habitats representative of natural environments. The aim is to conserve most of the biodiversity. The fine filter approach targets more specific species such as rare or threatened species or species with special habitat requirements. A combination of coarse and fine filters can be used by focusing efforts on specific species – a surrogate – (fine filter) to evaluate the effects of environmental changes and use it for biodiversity conservation (coarse filter) (Brashares 2010).

4.3. Use of surrogates

Only a small proportion of species have been described on Earth, so recovery strategies are always based on species for which data are available and, hence, assumed favorable for the other unknown and sympatric species (Rodrigues & Brooks 2007). The use of surrogates is expected to save resources and time compared with more conventional methods and have attracted increasing interest among conservation practitioners and scientists (Forest 2017). Surrogates can be used as 'indicator surrogates" to provide information about ecological systems, or as 'management surrogates' (e.g., umbrella species) to facilitate achieving management goals, such as maintain biodiversity or increase ecosystem resilience (Hunter *et al.* 2016).

An umbrella species is a species with a large range of habitat, sensitive to human-induced habitat changes and typical of its ecosystem. From a manager's perspective, an umbrella species provides a convenient shortcut for managing ecosystems: if the population of the chosen umbrella species can be kept viable through protective measures, then the populations of many sympatric species are expected to be protected (Caro 2010). An effective umbrella species must represent the conservation needs of sympatric species and must provide protection from vertebrates to invertebrates, which are all an essential part of ecosystems (Rubinoff 2001). Despite being a very attractive concept, the use of umbrella species has often been questioned and criticized for their poor efficiency in maintaining biodiversity in managed landscapes (Andelman and Fagan 2000, Roberge and Angelstam 2004, Branton and Richardson 2010). Indeed, most studies consider only species or taxa requiring the same habitat characteristics than the umbrella species (Roberge & Angelstam 2004; Hurme *et al.* 2008; Roberge *et al.* 2008), leading to uncertainty in umbrella effectiveness. With global change, species assemblages could change to the point that an umbrella species is expected to no longer represent the same species assemblages than at present (Terrigeol *et al.* 2022). Few studies, however, have assessed what the consequences of global change will be on the relevance of using a given umbrella species for biodiversity conservation in a given biome. To anticipate the future consequences of changing environmental conditions induced by global change and to minimize the impacts on populations, it is important to have ecological models that can predict how the specific ecological system will be affected (Evans 2012).

5. Mechanistic approaches to predict future changes

5.1. Spatially explicit models

Landscapes are dynamic and change naturally. In the context of global change, changes in environmental conditions can directly affect the way individual use space (Koper & Manseau 2009; Garmendia *et al.* 2013; Beauchesne *et al.* 2014). The spatial organization of the environment have a key role on individual space-use, the resulting risk of predation, and therefore on the dynamics of the prey populations (Vanlandeghem *et al.* 2021). A spatially explicit approach allows to consider species populations or communities in specific places both in aquatic (Heinle *et al.* 2021), and terrestrial systems (Carroll 2007), associated with local conditions, such as spatial heterogeneities, and organism behaviors (DeAngelis & Yurek 2017). Spatially explicit models provide a unique opportunity to account for local conditions in the landscape while predicting fine-scale interactions in ecosystems (DeAngelis & Yurek 2017), especially those involving specialist species. Indeed, there is a tight relationship between habitat specialist species and spatial heterogeneity (Clavel *et al.* 2011), which provides an excellent opportunity to examine the potential cascading effects of global change-driven modification on the strength of trophic interactions associated with specialist species (Filazzola *et al.* 2020).

Predictive spatially explicit models are useful for species management or conservation under current and/or future conditions. Indeed, such models can assist managers in their decision-making to select the most appropriate strategy to achieve the management or conservation objective (Marley *et al.* 2017; Simon & Fortin 2020). For example, Bauduin et al. (2020) used spatially explicit models to define effective protected areas to implement in a regional network for the current and future conditions. They used an individual-based model (IBM), and simulated movements for the endangered Atlantic-Gaspésie caribou population (*Rangifer tarandus caribou*) to assess functional connectivity based on this large mammal. Predictive models of species distribution are also commonly used to evaluate potential species response to environmental changes and to guide conservation planning (Domisch *et al.* 2019; Maiorano *et al.* 2019). Species distribution models describe the multivariate structure of a species' niche and produce spatially explicit predictions of the probability of occurrence (Guisan *et al.* 2013). However, most of the predictions are based on environmental variables without incorporating the influence of biotic interactions (van der Putten *et al.* 2010) nor interactions between climate and land-use changes. Given the tight links between global change, community composition, species dispersal and biotic interactions, models evaluating only individualistic species-environmental condition relationships are thus not sufficient to predict future ecological changes (Blois et al. 2013, Wisz et al. 2013, Urban et al. 2013). Indeed, increasing evidence demonstrates the key role of biotic interactions in determining species distribution under global change (Wiens *et al.* 2011; Fordham *et al.* 2013; Wisz *et al.* 2013; Dormann *et al.* 2018) and their influence in improving the predictive accuracy of species distribution models (Araújo & Luoto 2007; Santos *et al.* 2019; Khosravi *et al.* 2021). For example, Hof et al. (2012) enhanced the accuracy of species distribution models of the arctic fox (*Alopex lagopus*) in Fennoscandia by including occurrences of interacting species (prey availability and predator pressure).

Most of the time, a combination of spatially explicit models is used to explore the interacting effects of climatic, landscape change, and life-history patterns on species distribution and population viability (Pearson & Dawson 2003). Prediction on future environmental conditions and the consequences on species and their suitable habitat under global change can thus be inferred (Tremblay *et al.* 2018). This can be possible with the combine use of landscape dynamics simulation (Pauli *et al.* 2015; Fullman *et al.* 2017; Cadieux *et al.* 2019), population dynamic (Carroll 2007; Fullman *et al.* 2017; Lyons *et al.* 2018; Davies *et al.* 2020), individual-based (Watkins *et al.* 2015), and species distribution (Domisch *et al.* 2019) models. Spatially explicit models have the possibility to include a large amount of parameters (e.g., soil characteristics, climate characteristics, natural and anthropogenic disturbances, and species characteristics), which allow to better anticipate future changes in the environment and in populations dynamics and to establish effective management plans to mitigate the effects on populations (Fahrig 2001; Doherty & Driscoll 2018).

5.2. Forest landscape models

Forest landscape models are spatially explicit raster-based forest landscape models that dynamically simulate 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) (Lexer & Hönninger 2001; Boulanger *et al.* 2018). Individual trees are modelled explicitly as a mixture of stochastic and deterministic processes for a number of small forest patches (Lexer & Hönninger 2001). For example, population dynamics processes are explicitly linked to environmental factors such as temperature and soil moisture (Lexer & Hönninger 2001). Global change highly impacts forest ecosystems, by affecting tree species distribution through changes in temperature and precipitation, and through the impact on disturbances like the frequency of forest fires and the level of forest harvesting (Iverson & Prasad 1998; Boulanger & Pascual Puigdevall 2021). Even though alterations of forest ecosystems are projected to be critical, the severity, nature and direction of the impacts are expected to be spatially heterogeneous. Forest landscape models can thus be a useful tool to predict the cumulated impacts of climate and land-use changes on forest ecosystems. Furthermore, as vegetation is a major factor in individual life history, such as shelter, foraging and breeding grounds (van Putten 2002), modeling the distribution and structure of vegetation is a key feature to understand how organisms may respond to global change.

Forest landscape models play an important role informing policy and management decision in forest ecosystems, by projecting the future consequences of human actions – in particular forestry activities – on the structure and the composition of the forest (Carpenter *et al.* 2009). Forest landscape models can be used to investigates the various impacts of human activities on wildlife over large areas and long-time frames. Insights gained from these models can thus inform stakeholders which important habitat attributes need to be conserved for wildlife. For example, Pauli et al. (2015) used a forest landscape model to simulate future forest conditions under different harvest models to determine the impact on suitable habitat for Indiana and northern long-eared bats (*Myotis sodalist* and *M. septentrionalis*, respectively). Their study highlights how habitat conservation for more than one species can be difficult, but simulations made with forest landscape models can help guide forest management. Indeed, they were able to determine the effects of the different intensities of forest harvesting on both species. In addition to compare forest management for the wildlife conservation, forest landscape models can also help to define effective protected areas (Carlson *et al.* 2019). Forest landscape models can thus provide decision support to forest resource managers with respect to global change issues.

5.3. Individual-based models

Animal population dynamics are driven by many factors, such as other interacting species, and environmental characteristics. Individual-based models (also called agent-based models) allow to consider both bottom-up and top-down processes by simulating individual movements and interactions between resources, prey and predators, thus simulating the complex dynamics of ecological systems (McLane *et al.* 2011). Indeed, individual-based models represent the dynamics of populations by the emergence of the behaviors of individuals interacting both with the environment and with each other (Schmitz & Booth 1997; McLane *et al.* 2011; Stillman *et al.* 2015). The movement rules established to reproduce individual behavior include to feed in locations in which food consumption rate is maximized and to minimize predation risk (Grimm & Railsback 2005). These models allow more biologically realistic predictions and better estimates of variability and uncertainty (Grimm & Railsback 2005; Semeniuk *et al.* 2011). Hybrid models, simulating the behavior of individuals at a fine scale and using spatially explicit virtual environments, offer the possibility of estimating emergent properties that are difficult to predict by observing individuals alone. Habitat conservation planning of endangered species and their management can thus be better conducted (Pressey *et al.* 2007). While we can apply individual-based models to any organism, mechanistic approaches often focus on a single species of conservation interest (e.g., rare or threatened species) (Piacenza *et al.* 2017; Grant *et al.* 2018; Kong *et al.* 2021) because methods used to collect detailed data on species physiology and behavior, which are essential to parameterize such models, are costly and time-consuming.

Individual-based models (IBM) provide a platform with which to study specific and temporal phenomena difficult to measure in the real system or to quantify empirically, such as the impact of global change, disturbance experiments, or conservation managements (DeAngelis & Mooij 2005). IBMs can also be useful to explore the potential outcomes of different management and intervention scenarios, and to predict the effect of changes and the configuration of the environment on the populations (Kong *et al.* 2021; Vanlandeghem *et al.* 2021). In the case of predator-prey dynamics, spatial and temporal components of the functional response of predators (i.e., encounters rate and time spent per prey) can be modeled and influenced by the individual heterogeneity in the landscape (Murrell 2005). Indeed, each individual interacts with the virtual environment, affecting the spatial dispersion and the mobility of species in the virtual community, resulting in differences between individuals. Consequently, two individuals may show different behaviors only due to the local constraints of their environment (Mason & Fortin 2017), which in turn affects the encounter rates between predators and prey and consequently alters the dynamics of species interactions (Lurgi *et al.* 2016; Vanlandeghem *et al.* 2021). Therefore, individual-based models can allow biologists to enhance the understanding of population dynamics and of direct and indirect trophic interactions among community members, under current and future environmental conditions.

6. Study model: The boreal caribou in the Canadian boreal forest

6.1. Flagship, umbrella species & cultural keystone species

Boreal caribou are considered threatened in Canada (COSEWIC 2014). Boreal caribou are well adapted to low productive environment and occupy old-growth conifer stands, which are typically avoided by other ungulates, such as moose (James *et al.* 2004; McLoughlin *et al.* 2005). Boreal caribou are considered as a keystone cultural species in Canada, as the species become embedded in people's cultural traditions, identity and is an integral part of the Canadian heritage (Hummel & Ray 2008). Moreover, as a threatened species sensitive to human activities and generating conservation interest, funding and public support, boreal caribou acts as a symbol (i.e., a flagship species) for the protection of old-growth forests (Festa-Bianchet *et al.* 2011). Since the creation of conservation plans, and with their life history requirements (i.e., large annual home range, sensitive to human-induced habitat changes, and specific habitat requirements), boreal caribou have also been identified as an effective umbrella species (Bichet *et al.* 2016; Drever *et al.* 2019).

The use of umbrella species can be valuable 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 & Wildlife Service 1973, Government of Canada 2002). In addition, the degree of popularity of a species with the public is an asset that makes it a flagship species for conservation actions (Roberge & Angelstam 2004). Integrated the social perception is important in improving legitimacy in management decisions through effective solutions that avert conflicts (Ernoul *et al.* 2021). Such species that benefit from governmental action plans may thus serve as a catalyst for research to inform approaches for biodiversity conservation. Moreover, boreal caribou, as a flagship, umbrella, and cultural keystone species sensitive to habitat disturbances, are used by the Forest stewardship council (FSC) for the certification of forest managements (Dzus *et al.* 2010). This certification indicates that forest products come from responsibly managed forests and, in the case of boreal caribou, that forestry practices are aimed, as much as possible, at the conservation of their habitat (Dzus *et al.* 2010). Boreal caribou are therefore a useful study case to determine whether ecosystem-based management would mitigate the impacts of forestry on biodiversity.

The loss, fragmentation, and modification of boreal caribou habitat by human activities are the main causes of their current decline (Environment Canada 2011) and largely result from human disturbance-mediated apparent competition with other herbivores (Environment Canada 2012; Serrouya *et al.* 2017, 2019). Disturbed areas provide high-quality food for deciduous-browsing species, such as moose and deer (*Odocoileus* spp.*).* The subsequent increases in these prey populations triggers a numerical response in wolves, exacerbating predation risk to boreal caribou which select for old-growth forests to avoid predation (Serrouya *et al.* 2017). Boreal caribou can also be affected by the construction of linear corridors, such as roads and trails, as these features can steepen the functional response of wolves to prey density (i.e., increase prey detection/hunting efficiency) (James & Stuart-Smith 2000; Whittington *et al.* 2011). Collectively, such environmental changes affect the spatial dynamics and hence interaction rates of predators and their prey (Fortin *et al.* 2015; Gagné *et al.* 2016).

6.2. Future consequences of climate and land-use changes

The use of boreal caribou as a model species offers an opportunity to study the cumulative effects of anthropogenic and natural disturbances on trophic interactions because climate change is expected to have a great impact on disturbances affecting old forest stands, a key habitat component for this species (Fortin *et al.* 2008a). Wildfire regimes are known to influence the forest structure by affecting the density and composition of tree species (Johnstone & Chapin III 2006; Remy *et al.* 2017). Moreover, large spatial and temporal variations in the Canadian boreal forest are expected due to longer fire seasons (Wotton & Flannigan 1993), and more severe (Flannigan & Van Wagner 1991; Stocks *et al.* 1998) and frequent fires (Bergeron & Flannigan 1995; Boulanger *et al.* 2014). The species composition of the forest is further impacted by insect outbreaks, which are themselves also being exacerbated by climate change - an example of a relevant biotic interaction. For example, Régnière et al. (2012) predicted that the distribution of spruce budworm (*Choristoneura fumiferana*, Clem.) outbreaks, a tortricid moth that defoliates fir (*Abies* spp.) and spruce (*Picea* spp.), is expected to shift northward in response to climate change. Pureswaran et al. (2015) argued that, due to early budburst as a result of warmer temperatures, there will be a possible increase in synchrony between emergence of larvae of spruce budworm and budburst of black spruce (*Picea mariana* (Mill.) BSP). This potential increase in synchrony could increase the severity of outbreaks for more northerly distributed conifer and change ecosystem trajectories depending on ecosystem productivity and the cumulative impact of other disturbances.

Changes in disturbance regimes, cumulated with anthropogenic disturbances, alter the landscape mosaic by compromising ecological succession (Couillard *et al.* 2013). Indeed, over two-thirds of Canada's 5 million square kilometers of boreal forest is now considered as managed forest, much of which includes industrial wood production (Gauthier *et al.* 2015). Depending on the intensity and the cumulative number of disturbances, the forest species composition may partially change, if disturbances are not cumulated, but completely differ if the area is highly disturbed (Payette *et al.* 2000). For example, old forests are expected to decline under high disturbance, while fire-adapted species (e.g., trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.)) will tend to expand, replacing those that lack resilience to fire (e.g., white spruce (*Picea glauca* (Moench) Voss), cedar, and firs (Thompson et al. 1998, Bernhardt et al. 2011, Price et al. 2013). Besides, recent northward expansion of the range of many species has been documented and attributed to climate change in the Canadian boreal forest (Schneider *et al.* 2009; Boisvert-Marsh *et al.* 2014; Dawe & Boutin 2016). These changes in the distribution of tree species, in fact, vary across a north-south climatic gradient (Schneider *et al.* 2009; Périé & de Blois 2016), with the colonization of tundra ecosystems by forest species in the north (Johnston *et al.* 2009) and the replacement of species in the south by more temperate species (Boulanger *et al.* 2016). However, the northward range shift of forest species into tundra ecosystem could be counteracted by the increase in disturbances and the resulting expansion of lichen woodlands (Girard *et al.* 2008). Furthermore, these changes in the distribution of tree species are expected to be exacerbated by land-use changes (Boulanger & Pascual Puigdevall 2021). These projections on future boreal forest changes should provide more high-quality food for moose that would increase their abundance, which in turn would trigger a numerical response of their predators, with a subsequent increase in caribou mortality (Serrouya *et al.* 2021). Despite recent advances (Oksanen *et al.* 2020b), identifying thresholds in resource availability that trigger such change in food web dynamics remains unclear.

The expected northward range shifts and changes in species composition and structure of the boreal forest (Boulanger *et al.* 2016; Schneider *et al.* 2016) will likely result in displacement of ecological niches and, consequently, in changes to the local biodiversity and species interactions (Kerr & Packer 1998; van Putten 2002; Morin & Thuiller 2009). For example, in the boreal forest, Berteaux et al. (2010, 2014) studied the effect of climate change on multiple taxa and showed that biodiversity might increase in the northern ecosystems of Quebec. This general range shift of all living organisms is not occurring at the same pace because of lags in biological response (Svenning & Sandel 2013; Wu *et al.* 2015), due to, for example, different dispersal capabilities. Indeed, species associated with deciduous vegetation may disperse northward faster than species associated with old forest because of the increase prevalence of deciduous species and their relatively rapid expansion to the north in the boreal forest (Warren *et al.* 2001). In the case of the Canadian boreal forest, there is a need to understand if northern regions will become future refuges for biodiversity expanding or shifting their range northward to elaborate effective conservation plans. This is particularly critical for species associated with old forest, which are expected to be further impacted by disturbances (Stralberg *et al.* 2020). Studying change in biodiversity is essential to evaluate the effectiveness of boreal caribou recovery strategy to maintain regional biodiversity in the future.

6.3. Recovery measures

All Canadian provinces have established forest management plans to protect caribou's habitat (Environment Canada 2012). The 2012 Recovery Strategy set a threshold of 65% of undisturbed habitat as a critical component of habitat for the species, because it is expected to provide a 60% probability that a local population will be self-sustaining (Environment Canada 2012). In 2017, only 19 of the 51 caribou ranges in Canada included a 65% or greater proportion of undisturbed habitat, with only one in Quebec (Environment and Climate Change Canada 2017). In Quebec, forestry is the major anthropogenic disturbance impacting boreal caribou populations (Équipe de rétablissement du caribou forestier du Québec 2013). With the expected increase in wildfires, achieving this threshold will require a further decrease in human activities or a change in the spatial configuration of cut-blocks to maintain this threshold of 65% (Environment Canada 2012). Furthermore, the impact of insect outbreaks on this limit is unknown.

In the face of such global changes, recovery and management strategies need to consider future changes in natural disturbance regimes and in habitat characteristics. The current recovery strategy for the boreal caribou suggests measures that ensure a constant renewal of suitable habitat for caribou, while also maintaining human activities (Environment and Climate Change Canada 2018). In light of all of the knowledge gained from the past decades, and with a consensus within the scientific communities, new guidelines on boreal caribou habitat management were developed in the province of Quebec (Équipe de rétablissement du Caribou Forestier 2013). For example, the Government of Quebec plans to create two protected areas covering 20 000 km² within the distribution area of boreal caribou (Équipe de rétablissement du Caribou Forestier 2020). These measures have the objective to preserve species of all successional stages, including those unused by boreal caribou, justifying the use of this species as an umbrella species. Moreover, the predicted northward shift of species and the changes in local biodiversity, under global change, would result in overlap changes with boreal caribou home range. The management measures implemented to help protect caribou habitat are thus expected to also influence local biodiversity, and subsequently the umbrella value of the action plan. It is thus necessary to determine how the level of disturbances and habitat changes are expected to impact boreal caribou and species assemblages given land-use and climate changes and how management measures are predicted to act as umbrella for maintaining sufficient high-quality habitat for cooccurring species.

7. General objective and thesis structure

The main goals of my dissertation build on these conceptual topics in the boreal forests of Quebec are two-fold: 1) to characterize, in the context of global change, the specific and cumulative effects of natural and anthropogenic disturbances on predator-prey interactions among large mammals, and 2) to assess how global change is expected to impact the relevance of an umbrella species for the conservation of boreal biodiversity. My doctoral research investigates the cascading effects of global change on large-mammal relationships in human-altered ecosystems, through the change in landscape characteristics. By choosing boreal caribou as a study model, and thus boreal forest as a study area, global change can be characterized through three main disturbances: insect outbreaks, wildfires, and forest harvesting. Moreover, in the context of global change, my study aimed to assess the relevance of a management strategy for the conservation of a single species in maintaining regional biodiversity. To fulfill this goal, I undertake three specific objectives.

Chapter 1. Wildfires and forest harvesting threaten boreal caribou populations by altering trophic interactions. Disturbed areas are colonized by deciduous vegetation that provides high-quality food for moose

(Potvin & Courtois 2004). The subsequent increase in moose numbers triggers a numerical response of wolf (Messier 1985), which intensifies predation risk for boreal caribou (Wittmer *et al.* 2007; Serrouya *et al.* 2021). While the effect of fire and logging on caribou's food-web have been repeatedly demonstrated, other factors can also generate such secondary succession. Insect outbreaks disturb larger areas than wildfires and logging combined (Ressources naturelles Canada 2018); yet little information exists on how insect outbreaks impact boreal caribou. The objective of this chapter is to determine the impact of spruce budworm (*Choristoneura fumiferana,* SBW) outbreaks on the distribution, survival, and trophic interactions of boreal caribou. While the main objective of the thesis is on the future impact of global change, it is not possible to predict the effect of insect outbreaks on boreal caribou as the current impact is unknown. That is why this first chapter's focus is on the current outbreak of spruce budworm in Quebec, Canada.

Chapter 2. Given the latest and significant climate change projections, cumulated with current anthropogenic activities, the structure and the composition of boreal forest is expected to be highly impacted, which in turn should impact ecological communities by influencing species interactions. However, few studies have examined the combined effect of projected land-use and climate changes on multiple species and the impacts on their trophic interactions (Bossier *et al.* 2021). By using an approach based on behavioral landscape ecology (Schmitz *et al.* 2017), we addressed this research gap in the current study by combining two mechanistic models, a spatially explicit forest landscape model landscapes (Scheller *et al.* 2007) and an individual-based model (Latombe *et al.* 2014). Such a combination of mechanistic approaches enables direct and indirect effects of biotic interactions to be modelled depending on specific behavior and numerical response associated with simulated environmental changes. As oppose to single-species studies (Trainor & Schmitz 2014; Heinle *et al.* 2021), integrating a community perspective with a temporally and spatially explicit approach would thus allow a more mechanistic understanding of the ecological consequences of rapid environmental change (i.e., forest structure and composition) (Tylianakis *et al.* 2008; Tylianakis & Morris 2017; Stireman & Singer 2018). Therefore, my objective in this chapter was to test the potential cascading effects of human disturbances and climate change on the strength of trophic interactions and, ultimately, on caribou mortality.

Chapter 3. In this chapter, my objective was to evaluate the umbrella value of management strategies designed around the needs of a single species (i.e., boreal caribou) in a context of global change in the boreal forest of Canada. Natural and anthropogenic disturbances are increasingly linked and are predicted to increased (IPCC 2021). The boreal forest is thus expected to be more fragmented or disturbed with great changes in forest composition (Boulanger & Pascual Puigdevall 2021) and structure, and subsequently in biodiversity (Berteaux *et al.* 2014). I used the same modeling approach as Chapter 2 to address these questions with the same land-use and climate scenarios. In addition, a management strategy planed by the Ministère des Forêts, de la Faune et des Parcs in the province of Quebec was tested to determine to what extent protected areas would succeed in protecting high-quality habitats and populations under global changes. I linked landscape simulation model with individual-based model of caribou, moose and wolf agents and empirical models of bird and beetle species distribution to (1) Evaluate the effectiveness of management strategies and their landscape characteristics, through four scenarios of forest management, combined with three scenarios of climate change (2) Compare how species occurrences differ between land-use and climate changes scenarios; (3) Contrast land-use scenarios on biodiversity integrity; and (4) Evaluate if management measures aiming at maintaining caribou populations would also benefit biodiversity following global change.

Chapitre 1. Insect-mediated apparent competition between mammals in a boreal food web

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1.1. Résumé

Alors que le rôle des interactions médiées par les animaux dans la restructuration « top-down » des communautés végétales est bien documenté, leurs répercussions aux niveaux trophiques supérieurs sont moins bien connues. Nous démontrons comment une épidémie d'un insecte ravageur cyclique et commun de la forêt boréale, la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana*), a modulé une interaction trophique indirecte en initiant une croissance de la végétation décidue qui a profité à l'orignal (*Alces alces*). Cela a renforcé la compétition apparente entre l'orignal et le caribou forestier (*Rangifer tarandus caribou*), une espèce menacée, par la prédation du loup (*Canis lupus*). La prédation du caribou après l’épidémie a été significativement exacerbée par l'activité humaine (coupe de récupération). Bien que nos découvertes ici puissent être nouvelles, nous pensons que les interactions consommateur-producteur-consommateur à grande échelle sont susceptibles d'être communes dans la nature.

1.2. Abstract

While the role of animal-mediated interactions in the top-down restructuring of plant communities is well documented, less is known of their ensuing repercussions at higher trophic levels. We demonstrate how typically decoupled ecological interactions may become intertwined such that the impact of an insect pest on forest structure and composition alters predator-prey interactions among large mammals. Specifically, we show how irruptions in a common, cyclic insect pest of the boreal forest, the spruce budworm (*Choristoneura fumiferana*), modulated an indirect trophic interaction by initiating a flush in deciduous vegetation that benefited moose (*Alces alces*), in turn strengthening apparent competition between moose and threatened boreal caribou (*Rangifer tarandus caribou*) via wolf (*Canis lupus*) predation. Critically, predation on caribou post-outbreak was exacerbated by human activity (salvage logging). While our findings here may be novel, we believe our observations of significant, large-scale reverberating consumer-producer-consumer interactions are likely to be common in nature.

1.3. Introduction

Community and population ecology have been first and foremost studied through direct resource-consumer interactions. There is growing recognition, however, that indirect effects of species interactions can shape ecosystems as much as direct effects (Wootton 2002), and sometimes in surprising ways. The loss of top predators, for example, can not only cascade down to impact bird, mammal, invertebrate, and plant abundance or richness, but predator removal can trigger a wave of resource-consumer changes that can even ultimately alter stream morphology (Ripple *et al.* 2014b). The risk that human-induced or natural changes in community composition have rippling effects on seemingly independent components of the environment has strong relevance to management and conservation planning.

Apparent competition is one common indirect interaction increasingly reported in field studies; it occurs between two prey species through a common, shared enemy (e.g., predator or pathogen) (Holt 1977). Apparent competition pervades many natural ecosystems (Frost *et al.* 2016; Holt & Bonsall 2017), and it can impact ecological communities to the extent that local prey populations may disappear (Holt & Bonsall 2017). Various factors can trigger apparent competition, notably species introductions or loss (Schmitz *et al.* 2000; Dunn *et al.* 2012; Frost *et al.* 2016) and pulses in resource availability (Ostfeld & Keesing 2000; Adams *et al.* 2010). For example, masting seed crops can exert apparent competition among songbird populations, mediated through generalist predator populations (Schmidt & Ostfeld 2008). Resource pulses can also be linked to the life cycle of animal species. Spawning Pacific salmon (*Oncorhyncus* spp.) provides wolves (*Canis lupus*) with a seasonal increase in food abundance that can support the predator at densities sufficient to maintain local ungulate populations at relatively low numbers (Adams *et al.* 2010). Wolves feed only a portion of the year on salmon, and the fish completes its life cycle with very limited interaction with wolves; yet this interaction has a strong impact on the terrestrial food-web involving several primary consumers.

Insect outbreaks are also recurrent events but with multi-year cycles (Cooke *et al.* 2021). Despite their relatively long cycles, these events can be the dominant disturbance agent of ecosystems, especially in temperate forests (FAO 2020). Insects have been recognized as ecosystem engineers (Jacobsen *et al.* 2015) because their impact on trees generates resources for various organisms (e.g., other insects, small mammals, birds, (Saab *et al.* 2014)). However, the influence of insect infestations goes much beyond the addition of new resources, as they can modulate energy flow across food webs (Ivan *et al.* 2018). Changes in canopy cover due to insect defoliation alter abiotic conditions (e.g., solar radiation at ground level) in a way that promotes the growth of understory shrubs and herbaceous vegetation (Bouchard *et al.* 2006). This tends to benefit biodiversity associated with early seral vegetation at the expense of species dwelling in mature forests (Ivan *et al.* 2018). For example, positive responses of elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) have been reported a few years following Mountain pine beetle (*Dendroctonus ponderosae*) outbreaks (Saab *et al.* 2014;

Ivan *et al.* 2018). Although the reaction of species to insect outbreaks can be diverse, the potential impact on ecosystem structure and function is undeniable. What remains unclear is how the impact of these cyclic events might reverberate into higher trophic levels to modulate both direct and indirect food-web interactions. Clarifying these effects on population and community dynamics is likely to be critical, however, to conservation and management especially when species of concern are involved. Here we provide rare empirical evidence that a forest insect pest can trigger apparent competition in a boreal food web between large mammals—one of which is a Threatened species—via a shared predator.

Boreal populations of woodland caribou (*Rangifer tarandus caribou*) are classed as Threatened across most of their range in Canada (Goverment of Canada 2018), with well-known population declines resulting from apparent competition with other herbivores (Environment Canada 2012; Serrouya *et al.* 2017, 2019). Wildfire and logging are the dominant factors threatening boreal caribou by driving the observed apparent competition, which is principally mediated by wolves. Disturbed areas provide high-quality food for deciduous-browsing moose (*Alces alces*) and deer (*Odocoileus* spp.), and subsequent increases in these prey populations triggers a numerical response in wolves. This increase in wolf numbers intensifies predation risk to boreal caribou which select for old-growth forests and displace to the latter to avoid predation (Serrouya *et al.* 2017). The construction of linear corridors such as roads and trails can also impact caribou as these features can steepen the functional response of wolves to prey density (i.e., increase prey detection/hunting efficiency) (James & Stuart-Smith 2000; Whittington *et al.* 2011). Collectively, such habitat changes alter the spatial dynamics and hence interaction rates of predators and apparent competitors (Fortin *et al.* 2015; Gagné *et al.* 2016). Because the main agents of caribou declines are habitat-driven, much attention is currently devoted to the role of fire and anthropogenic disturbance in the process. However, a cyclic insect outbreak can also generate secondary succession in forests. Although insect outbreaks often disturb larger areas than wildfires and logging in Boreal forests (Ressources naturelles Canada 2018), little information exists on how outbreaks might impact on survival of boreal caribou through direct and indirect food-web interactions.

We assessed the impact of the common spruce budworm (SBW, *Choristoneura fumiferana*) on the distribution, survival, and trophic interactions of boreal caribou in an area subject to current outbreak of budworm. The SBW is one of the most damaging outbreaking insects in the boreal and sub-boreal forests of North America, with irruptions recurring every 30–35 years resulting in tree mortality after 5–6 years of defoliation (Bouchard *et al.* 2006; Bouchard & Pothier 2010). SBW-damaged stands are often salvage-logged following disturbance (Lindenmayer *et al.* 2012), which serves to expand resource extraction road networks (Fortin *et al.* 2013). With climate change and a northerly expansion of SBW distribution, boreal caribou ranges are also at risk of experiencing increasing SBW outbreaks. Building on the hypothesis of disturbance-mediated apparent competition (Seip 1992; Serrouya *et al.* 2015), and taking advantage of detailed data on SBW outbreaks, forest succession, and multiple mammal populations in Québec, Canada, we predicted that outbreaks of SBW would induce apparent competition between caribou and moose through their common predator, the wolf (links L1–L5, **Figure 1.1**). We predicted that reductions in canopy cover in conifer stands caused by relatively severe outbreaks would stimulate growth in deciduous vegetation (L1, blue vs. green links, **Figure 1.1**). Deciduous vegetation is prime food to moose, whereas boreal caribou focus much more on lichens and graminoids (Thompson *et al.* 2015). We further expected the latter to result in a detectable numerical response in moose (L2), thereby increasing local prey available to wolves. Mortality risk for caribou was therefore expected to be higher in forest stands most severely impacted by SBW (L5), especially if the infected stands enhanced predator-prey encounter rates (i.e., both wolves and caribou selectively using those stands, L3 and L4). Finally, we assessed the effect that salvage logging of SBW infested stands (SBW_{cut} hereafter) could exacerbate apparent competition (yellow links) by providing additional deciduous vegetation that attracts more moose (thereby wolves) and increases predation risk for boreal caribou (Figure 1.1, larger arrows).

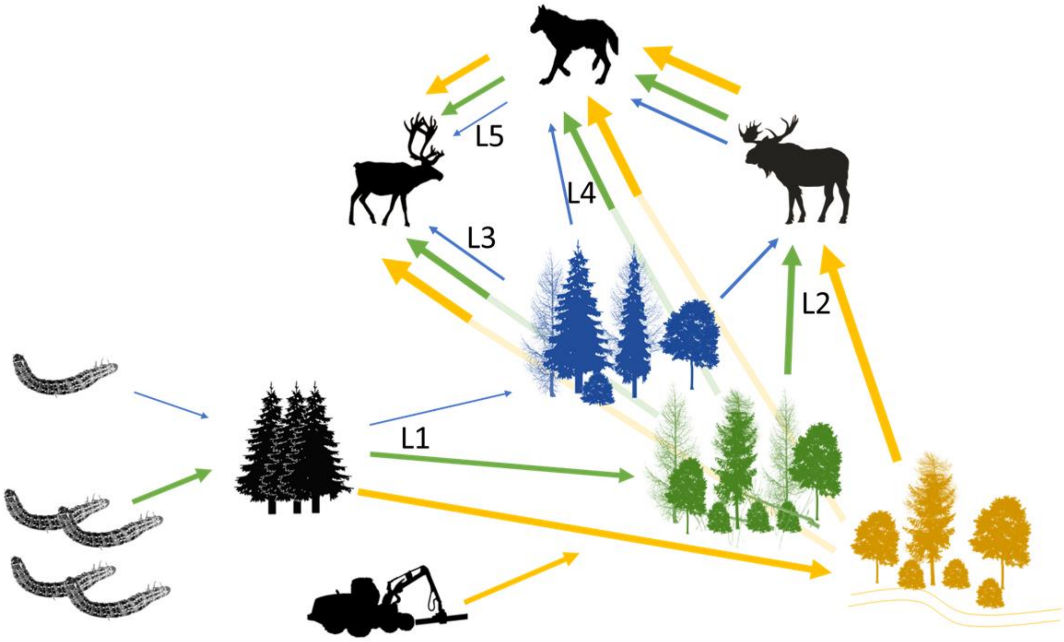

Figure 1.1. Simplified schematic of a boreal caribou-wolf-moose system illustrating the indirect effects of a spruce budworm outbreak on trophic interactions. Links L1–L5 are described by arrows. Blue arrows indicate effects for an early or less-impacted stage of spruce budworm outbreak (e.g., 3 years of defoliation) and green arrows indicate effects at a later or more severe outbreak stage (e.g.,10 years of defoliation). Yellow arrows represent effects of salvage logging inclusive of the associated road network introduced by logging.

1.4. Materials and methods

Study area

The 92 000-km² study area (48°N-54°N, 63°W-73°W) covering was located in the Côte-Nord region of Québec, Canada (**Figure 1.2**). The northern part of the study area is part of the spruce-moss domain, and is dominated by black spruce, with balsam fir. Insect outbreaks and wildfires are the major natural disturbances (Boucher *et al.* 2017). The southern part of the study area belongs to the eastern spruce-moss 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). This southern part is subject to SBW outbreaks, a forest insect (Lepidoptera: Tortricidae) that undergoes periodic population-level increases and causes widespread defoliation of host trees over large areas. Salvage logging during these insect outbreaks has become a usual practice to recover some of the economic value that would otherwise be lost (Lindenmayer *et al.* 2012). Measures have been established, including preventive harvesting, adapted silvicultural interventions as well as aerial organic insecticide sprays. The latest SBW outbreak in the study area started in 2006 and remains ongoing. The insect first impacted the southern part of the study area, before the outbreak gradually progressed northward (**Figure 1.2**).

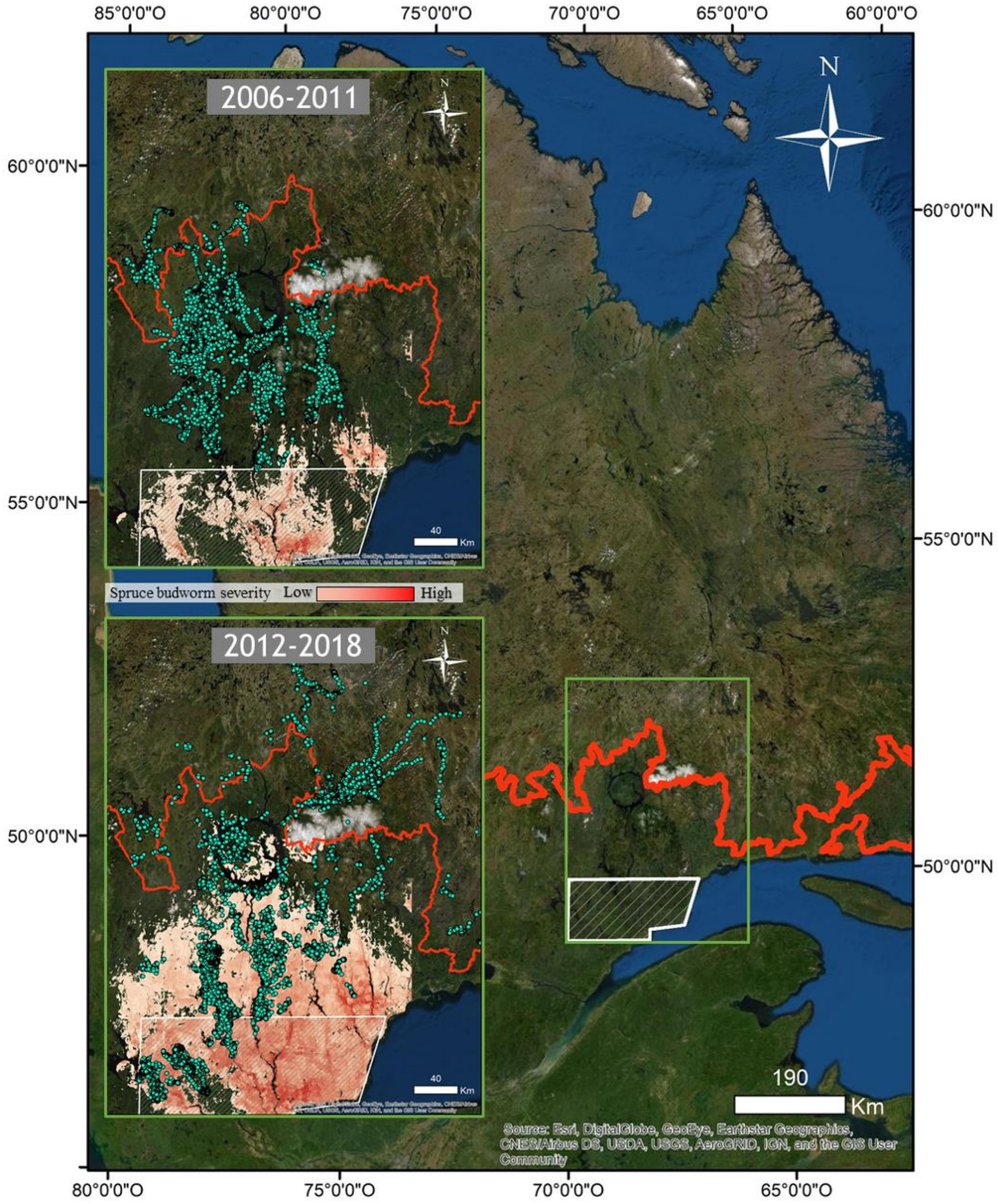

Figure 1.2. Study area in the province of Québec, Canada. Green boxes represent maps of the distribution and defoliation severity based on aerial survey data of the spruce budworm outbreak (Ministère des Forêts de la Faune et des Parcs (QMFFP) 2018) in 2011 (top) and 2018 (bottom) within the study area. Blue dots represent the distribution of GPS radiocollared caribou in 2006-2011, and 2012-2018 used in the analyses. Red line represents the northern limit for forest management activities. The hatched area defines Hunting Area 18 in Côte-Nord region within the study area.

Habitat characteristics

We characterized the study area using the Canadian National Forest Inventory (NFI) forest cover maps (Beaudoin *et al.* 2014), corresponding to L1 in **Figure 1.1**. These maps are a k-nearest neighbour interpolation at a 250-m resolution of the NFI photograph plot data acquired in 2001 (see Beaudoin et al. (2014)). To estimate forest composition, we used the relative proportions of species groups (needle-leaved and broad-leaved species), treed land and tree crown closure maps from these NFI data. We created five land cover classes based on the Earth Observation for Sustainable Development of Forests (EOSD) Land Cover Classification Legend (Beaubien *et al.* 1999): closed-canopy conifer forest (Needleleaf > 75% and crown closure > 60%), open-canopy mature conifer forest (Needleleaf > 75%, and crown closure ≤ 60%), mixed forest (Needleleaf > 25% and Deciduous > 25%), open area (Vegetation > 50% and Vegetation non-treed ≥ Vegetation treed) and other (Non-Vegetation ≥ 50%). Land cover maps were updated every year by adding roads, recent (< 5 years), regenerating (6–20 years) and old (21–50 years) cutblocks/fires based on information provided annually by local forestry companies (Ministère des Forêts de la Faune et des Parcs 2019a) and from the Canadian National Fire Database (CNFDB,(Canadian Forest Service 2019).

SBW outbreaks were mapped annually based on aerial surveys characterizing damages caused by SBW since 2006 (Ministère des Forêts de la Faune et des Parcs (QMFFP) 2018). In-flight surveyors delineated polygons of insect damage using topographic maps and assign a severity class to an estimate of current-year defoliation to each polygon. Defoliation severity classes were recorded as low (1–35%), medium (36–70%), and high (71–100%). We quantified the cumulative severity of the outbreak by summing the estimated severity for each year (2006–2018) and created maps with 250-m resolution (corresponding to blue and green links of L1 in **Figure 1.1**). We also determined a covariate “SBW_{cut}” that corresponded to pixels infested by SBW for at least 1 year and then cut (yellow link, L1, **Figure 1.1**).

Post-SBW outbreak vegetation growth

To evaluate the availability of deciduous vegetation in stands impacted by the SBW outbreak and test our prediction that the reduction in canopy cover caused by SBW in coniferous stands would result in greater deciduous vegetation (blue and green links L1, **Figure 1.1**), we used the map of cumulative outbreak severity calculated in 2018. We visited 26 of those 250-m pixels in fall 2019 (18 September to 23 September) to validate the relationship between SBW cumulative severity and the percentage cover of deciduous vegetation of two height strata ([0-1m] and [1-3m] classes). September was the best period to record the maximum defoliation severity of the year, once larvae have finished feeding (from May to July). Within each pixel, we visually estimated the percentage (based on 10% cover classes) of deciduous vegetation in five circular (10-m radius) plots. The plot centers were located at 250 m of the road, and the other plots were located in each of the four cardinal directions, 50 m from the central plot. Average values were used in subsequent analysis.

Moose density

We assessed the influence of SBW outbreak on moose abundance (L2 in **Figure 1.1**) by comparing moose densities before and during SBW outbreak. We used data from aerial surveys of moose conducted in 2006 and in 2018, 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-km² in 2006 and 62 plots in 2018. For analyses, we considered all survey plots that overlapped the study area, delimited with radio-collared caribou and wolves (**Figure 1.2**). A total of 48 plots of the 72 surveyed in 2006 and 44 of the 62 plots surveyed in 2018 were in the study area. Based on those 92 (48 + 44) plots, we estimated moose density while considering a visibility rate of 0.68 in 2006 and 0.70 in 2018 (Ministère des Forêts de la Faune et des Parcs 2019b). We compared moose density using Poisson Generalized Linear Models (GLM), but we detected model overdispersion and thereby corrected the standard errors using a quasi-Poisson GLM model (Zuur *et al.* 2009). For each survey plot, we extracted the mean cumulative severity of SBW and the percent cover of SBW_{cut} from the map of the cumulative severity of SBW outbreak in 2018 and deciduous vegetation from Canadian National Forest Inventory (CNFI) forest cover maps (Beaudoin *et al.* 2014). To test our predictions that SBW outbreak triggers apparent competition, corresponding to L2 in **Figure 1.1**, we evaluate the importance of vegetation characteristics on moose densities in 2018, by building a multiple regression to better understand if the cumulative severity of SBW and the proportion of deciduous vegetation could explain change in moose densities. Finally, we used the Mann-Whitney U test to compare moose density in plots with low (≤ 20%) and high (> 20%) percent covers of SBW_{cut} in 2018 to test our hypothesis that moose densities would be higher in plots with high cover of cuts which would increase the availability of deciduous vegetation.

Telemetry

A total of 133 GPS-collared adult female caribou were monitored from March 2005 to December 2018, with each individual being followed for an average of 23.1 months (range: < 1–56 months). Animal capture and handling protocols adhered to guidelines under the Canadian Council on Animal Care and were approved by Université Laval animal protection committee. The GPS collars were programmed to collect a location every 1, 2, 3, 4, 8 or 16 h, depending upon collar type and year. For wolves, 16 adults (8 females and 8 males) were followed from March 2005 to December 2018, with each individual being tracked for an average of 19.6 months (range: < 1–49 months). The collars were programmed to acquire a location every 1, 4, 6 or 10 h. Statistical analysis accounted for the differences in sampling intensity (see section Caribou and wolf habitat selection, below). We focused our investigation on winter (January-mid-May). Although caribou mortalities can occur year-round, our study focuses on winter because: (1) most mortalities occurred during winter in our study area (38 mortalities including 23 from predation, 2 from natural death and 13 from unidentified causes), (2) winter is the only season when we observed enough mortality events to investigate the impacts of disturbances on survival (38 mortalities in winter vs 19 mortalities in the three other seasons), and (3) winter is recognised as a critical mortality season for ungulates (Gaillard *et al.* 2000). Mortality sites were visited to identify the cause of death using standard diagnostic methods (i.e., predation, natural or unidentified (Alt & Eckert 2017)). We kept for our study only caribou which survived during the monitoring period in addition to caribou which died from predation. Consequently, we kept 118 caribou for analyses.

Caribou and wolf habitat selection

We developed Resource Selection Functions (RSFs, (Boyce & McDonald 1999)) for caribou and wolves to assess habitat selection and test our predictions related to L3–5 (**Figure 1.1**). RSFs compare resource characteristics of observed (scored 1) and random (scored 0) locations (Manly *et al.* 2002). To delineate the annual winter home range of each animal, we used the 100% minimum convex polygon (MCP) for each radio-collared caribou, whereas for wolves, we drew 95% MCP of all radio-collared members of its pack. This latter approach excluded extraterritorial excursions (McLoughlin *et al.* 2004; Courbin *et al.* 2009). GPS locations (i.e., observed locations) were then paired with random locations (5 times the number of observed locations) to define resource availability within the MCP for each individual (caribou) and pack (wolf). Although the MCP should exceed the home range of an individual (Burgman & Fox 2003), our intent was not to determine the actual home range, but rather to delineate an area that could be considered broadly available to the individual in winter. Such broad-scale assessment was deemed necessary here because disturbances can influence animal movements over several kilometers (Environment Canada 2012), and the MCP provided a satisfactory overview of resource selection by including landscape at the edge of their seasonal home ranges. RSFs were implemented using mixed-effects logistic regression expressed as:

$$\mathrm{w}(\mathbf{x}) = \exp\left(\beta_0 + \left(\beta_1 + \gamma_{1jk}\right)\mathrm{x}_{1ij} + \cdots + (\beta_n + \gamma_{njk})\mathrm{x}_{nij} + \gamma_{0jk}\right)$$

where $\mathrm{w}(\mathbf{x})$ represents the RSF scores (relative probability of selection, or odds ratio), β_0 is the fixed intercept, β_n is the selection coefficient for the nth variable, x_{nij} is the value of the nth variable for the ith location for the jth individual, γ_{0jk} is the random intercept specific to the jth individual at year k, and γ_{njk} is the random slope for the nth variable specific to the jth individual at year k (only for caribou model). For caribou RSFs, we included a random intercept for individuals and for the year and a random slope associated with SBW covariates to take into account the non-independence among an individual's locations within a given year and the different collar schedules (Gillies et al. 2006). For wolves, we used a random intercept for individuals within pack and year because a given pack could include more than one collared wolf (Gillies *et al.* 2006; Hebblewhite & Merrill 2008). We fitted the weighted logistic regression model (using W = 5,000) with fixed intercept variance at 10^6 to ensure the convergence of the models, following procedures outlined in Muff et al. (2020),

To assess the overall effect of SBW outbreak on the use of boreal caribou and wolves in managed forests, we created a model that accounted for both natural and anthropogenic disturbances, together with land cover types. Closed-canopy conifer forest, open-canopy mature conifer forest, mixed forest, open area, SBW_{cut}, recent (< 5 years), regenerating (6–20 years) and old (21–50 years) cutblocks/fires and other land covers were represented by categorical covariates. SBW outbreak severity was centered and scaled. Wolves displayed such broad scale avoidance of old cuts that this land cover type was almost never available among observed or random locations and, therefore, could not be included in the analysis. We could not directly consider the behavioral response of radio-collared wolves and caribou to spatial patterns in moose density because moose surveys were only conducted in southern portion of the study area, whereas radio-collared individuals were tracked throughout the area. This is why we did not directly test the link between wolf and moose in **Figure 1.1**. Instead, we indirectly tested this link by assessing the response of caribou and wolves to SBW-impacted forests (links L3 and L4). We did not detect multicollinearity issues, given that variance inflation factors of all covariates were < 4 (Graham 2003) for both species.

We evaluated model robustness using k-fold cross-validation, by developing RSFs with 80% of the locations (training set), and then by testing the predictive power of these RSFs with the 20% withheld locations (testing set). To evaluate the predictive success of the RSF model we used the R package IndRSA (Bastille-Rousseau 2018) using 10 repetitions of 5-fold cross-validation with 10 bins of equal size and calculated the averaged Spearman's rank correlation coefficient ($\overline{r_s}$) (Siegel 1956).

Consequences of habitat selection and use to caribou survival

First, to link SBW covariates with caribou mortality in the RSF model, we identified factors linked to caribou mortality (link L5, **Figure 1.1**) by adding interaction terms between mortality status (remained alive throughout the study = 0, died = 1) and SBW-related covariates. Then, we used a Cox-proportional hazards regression model (Cox 1972) to evaluate whether the proportion of natural and anthropogenic disturbances within winter home range had an effect on the mortality risk of caribou. We calculated the 95% Brownian bridge movement kernel (Horne *et al.* 2007) of each individual from its winter locations, which provides an estimate of use intensity across its home-range (Worton 1989; Horne *et al.* 2007). We used these kernels to estimate more specifically the percent cover of landscape variables used by individuals. It reflected habitat features in the immediate vicinity of caribou at the time of surveys by removing outliers and ensuring that only core areas of use were compared.

We considered the percent cover of forest that had been cut 0–5 years or 6–20 years ago, the percent cover of burned area and the percent cover of SBW_{cut} for caribou survival analysis. To test the effect of the cumulative severity of the SBW outbreak on mortality risk, we calculated the mean cumulative severity of defoliation (SBW_{ms}) within individual caribou winter home ranges. Survival analysis considered 'year' as a random effect by using random intercept to account for potential temporal variability because the cumulative defoliation in areas affected by the SBW outbreak increased over years. We included random coefficients for SBW covariates to consider variation in individual-level responses. The Cox model is especially suited to situations like ours whereby individuals are followed, and die or survive, over different time intervals. For the survival analysis we only used characteristics of the home range from the previous winter when an individual was followed over more than one winter, and time was defined as the total period of monitoring for that individual (from the first day of survey to the last day). We did not detect any multicollinearity issues, given that variance inflation factors were < 4 (Graham 2003) for all covariates. The proportional hazard assumption of our model (excluding the random factors) was not violated according to the Schoenfeld test ($P > 0.30$) (Grambsch & Therneau 1994). All analyses were conducted in program R using the packages survival (Therneau 2018b), coxme (Therneau 2018a), MuMIn (Barton 2018), IndRSA (Bastille-Rousseau 2018), glmmTMB (Brooks *et al.* 2017) and lme4 (Bates *et al.* 2012).

1.5. Results

Link 1: Post-SBW outbreak vegetation growth

Our field sampling confirmed that stands, within the 0.063 km^2 plots, impacted by higher cumulative severity of SBW outbreak were covered by a greater proportion of deciduous vegetation at two different heights (strata: [0-1 m] and [1-3 m]) of vegetation of differing availability to large herbivores in this system (**Figure 1.3**). Both height strata were positively correlated (Pearson's correlation = 0.72, $P < 0.01$).

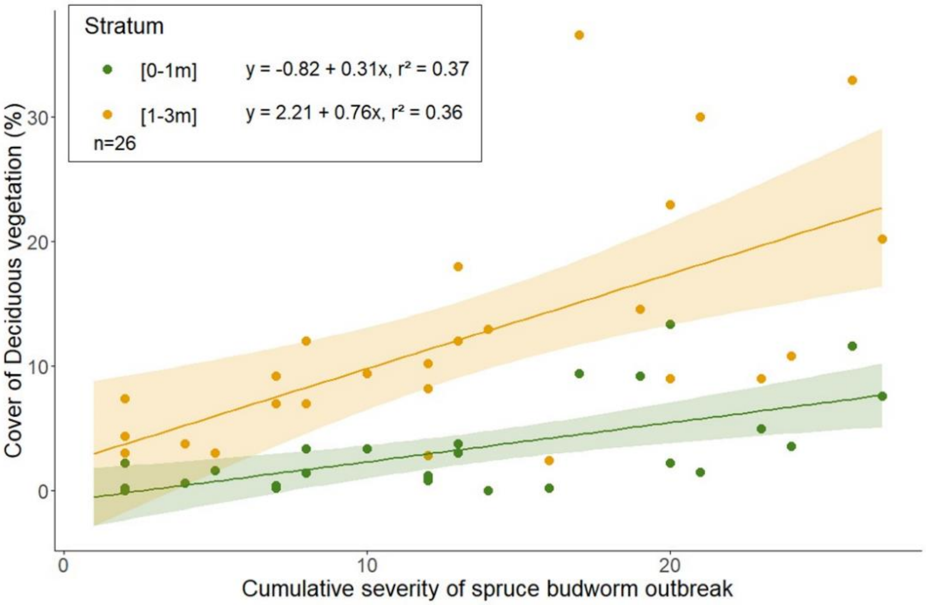

Figure 1.3. Observed percentage cover of available deciduous vegetation in spruce budworm-infested forest stands in relation to an index of budworm cumulative severity in 2018 (Côte-Nord region, Québec, Canada). Points represent raw values and coloured ribbons indicate 95% confidence intervals.

Link 2: Moose density

Moose occurred at a density of 0.60 individual/10 km^2 (95% confidence intervals [CI]: 0.36–-0.83) when the SBW infestation started in 2006, and then rose to 1.01 individual/10 km^2 (95% CI: 0.59–1.43) in 2018 during the infestation, i.e., a 70% increase in moose density over 13 years ($P = 0.07$). In 2006, when the outbreak began, moose density was positively related to the proportion of deciduous vegetation ($R^2 = 0.24$, $P < 0.001$, n = 48). In 2018, areas (60-km2 plots) with high availability of deciduous-dominated stands tended to have low mean cumulative severity of SBW (Pearson’s correlation = -0.54, $P < 0.01$, n = 44). In this spatial context, multiple regression showed that moose density simply remained positively associated with the proportion of deciduous vegetation in the area ($R^2 = 0.17$, $P = 0.02$), without an independent link to the mean cumulative severity of the ongoing SBW outbreak ($P = 0.51$). A connection between moose density and SBW became apparent, however, when considering stands that were impacted by SBW and then logged (SBW_{cut}). Indeed, moose density in 2018 was higher in areas with proportion of $SBW_{cut} > 20\%$ than areas with $SBW_{cut} \leq 20\%$ ($U = 76.5$, $P = 0.04$; **Figure 1.4**). The difference reflected local increases in moose density, because moose density increased (though marginally) between 2006 and 2018 ($U = 18.0$, $P = 0.09$) in areas that became characterized by a high proportion of SBW_{cut} [> 20%] in 2018 (**Figure 1.4**). Thus, it was the proportion of deciduous vegetation itself that influenced moose, which did increase moose density especially in areas characterized by a high proportion of SBW_{cut}.

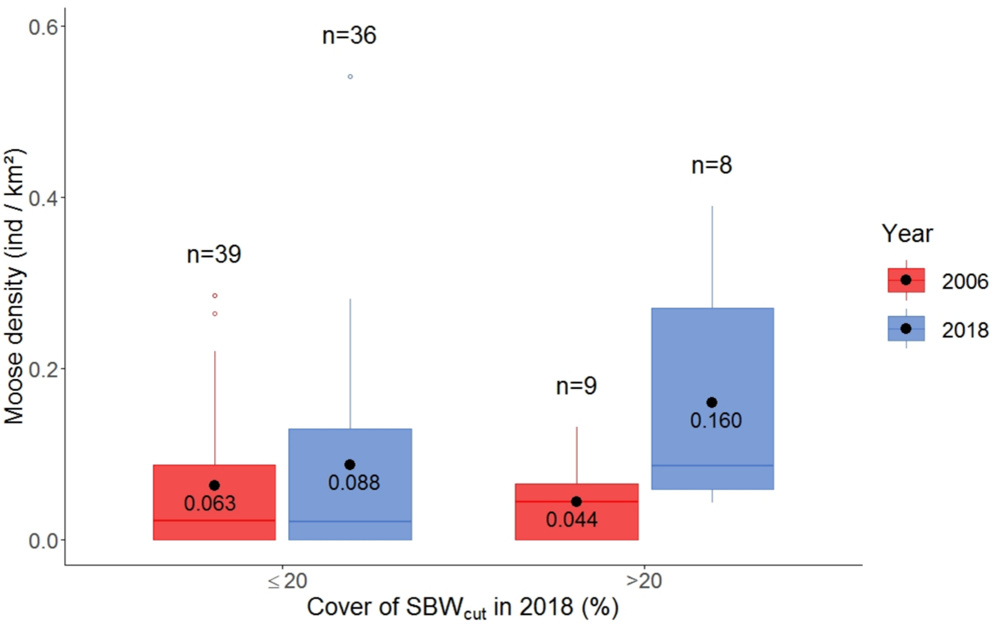

Figure 1.4. Relationship between moose density and percentage cover of salvage-logged forest stands (Côte-Nord region, Québec, Canada). We compared moose density before and after spruce budworm outbreak (2006 vs 2018) within areas that were subject to salvage logging, with a spatial reference where salvage logging was low (< 20%), conforming to a before-after-control-impact (BACI) design. Boxplots describe moose density in 2006 and in 2018 in relation to the percent cover of areas infested by spruce budworm for at least 1 year and then cut (SBW_{cut}) within plots (each 60 km^2) characterized by a low (< 20%) or a high (> 20%) percent cover of SBW_{cut} in 2018. Black points correspond to the mean density of moose, the center value is the median, edges of the box are 25th and 75th percentiles, and whiskers represent ± 1.5 the inter-quartile range.

Links 3, 4: Caribou and wolf habitat selection models

Resource selection functions (RSFs) during the winter monitoring period showed that relative to open-conifer forests (the reference category), caribou selected mixed forests and open areas whereas they avoided burned stands and cuts (**Table 1.1**). Wolves selected mixed forests, dense conifer forests, burned stands < 20 years old whereas they avoided older burned stands. While accounting for these basic habitat selection patterns, the analysis revealed that caribou (L3, **Figure 1.1**) and wolves (L4, **Figure 1.1**) both responded to the impact of SBW on habitat features. Specifically, caribou avoided areas with high SBW cumulative severity (**Table 1.1**), while most (but see Caribou survival below) also avoided SBW_{cut} more than cuts of all age classes and burned stands > 5 years (**Table 1.1**). Wolves selected SBW_{cut}, whereas they avoided young cuts (< 20 years old) that had not been impacted by SBW.

Table 1.1. Summary of the habitat selection models. Mixed-effects logistic regression models of habitat selection of 16 wolves and 118 caribou during the winter period in the Côte-Nord region, Québec (Canada), with their selection coefficients (β); standard error (SE) and P value. Reference category is open conifer forest. SBW_{cut} represents areas infested by spruce budworm for at least 1 year and then cut. Mortality status indicates if individuals remained alive throughout the study (0) or died (1). Models were robust to cross-validation, as indicated by high mean Spearman rank correlations ($\bar{r}_s$).

	Caribou			**Wolf**		
Variables	**β**	**SE**	***P* value**	**β**	**SE**	***P* value**
Conifer dense	-0.212	0.009	< 0.001	0.225	0.033	< 0.001
Mixed	0.070	0.009	< 0.001	0.494	0.023	< 0.001
Open area	0.143	0.011	< 0.001	-0.066	0.038	0.084
Other	-1.268	0.010	< 0.001	-0.385	0.031	< 0.001
Burned (< 5 years old)	-2.868	0.091	< 0.001	0.747	0.041	< 0.001
Burned (6-20 years old)	-1.453	0.054	< 0.001	0.520	0.034	< 0.001
Burned (≥ 21 years old)	-0.407	0.016	< 0.001	-0.513	0.057	< 0.001
Cut (< 5 years old)	-0.719	0.026	< 0.001	-0.531	0.048	< 0.001
Cut (6-20 years old)	-1.152	0.031	< 0.001	-0.377	0.034	< 0.001
Cut (≥ 21 years old)	-0.339	0.047	< 0.001			
Distance to road	0.587	0.004	< 0.001	-0.146	0.013	< 0.001
Spruce budworm cumulative severity	-1.505	0.534	0.005	-0.019	0.016	0.252
SBW_{cut}	-2.429	0.462	< 0.001	0.359	0.076	< 0.001
Mortality status × Spruce budworm cumulative severity	2.119	1.250	0.090			
Mortality status × SBW_{cut}	0.505	0.904	0.576			
Random effects for caribou	**Variance**	**95% CI**				
Spruce budworm cumulative severity	16.580	(10.758, 25.563)				
SBW_{cut}	6.103	(3.648, 10.208)				
k-fold: $\bar{r}_s$	0.697			0.852		

Link 5: Consequences of habitat selection and use to caribou survival

Concurrent resource selection of wolves and caribou revealed consequences for the survival of caribou consistent with predictions. Of the 118 female boreal caribou monitored from 2005 to 2018, 23 (19%) died from predation in winter during the monitoring period. Individuals that died displayed a similar level of avoidance of SBW_{cut} ($P = 0.58$, **Table 1.1**), but marginally stronger selection ($P = 0.09$, **Table 1.1**) of areas with higher spruce budworm cumulative severity. The difference in habitat selection strategies (*sensu* Fortin et al. (2008b)) became particularly evident when contrasting individual RSFs developed depending on caribou's fate (Annexe A, **Table A 1**). Individuals that remained alive avoided areas with high spruce budworm cumulative severity (β = -1.682; SE = 0.621, Annexe A, **Table A 1a**), whereas caribou that died did not, and even tended to select severely impacted stands (β = +0.585, SE = 0.366, Annexe A, **Table A 1b**). Furthermore, the survival analysis indicates that mortality risk increased with the use of areas strongly impacted by the insect and then harvested (SBW_{cut}, **Table 1.2**).

Table 1.2. Summary of caribou hazard analysis. Coefficient (β), Standard error (SE) and P value of the Cox-proportional hazards model evaluating female boreal caribou survival, between 2005 and 2018. % Cut and % Burned represent the percent cover of the variable; % SBW_{cut} represents the percent cover of areas infested by spruce budworm for at least 1 year and then cut, and SBW_{ms} represents the mean cumulative severity of the spruce budworm outbreak within individual winter home range.

Variables	**β**	**SE**	***P* value**
% Burned	-10.646	9.235	0.250
% Cut (< 5 years old)	-3.016	14.506	0.840
% Cut (6-20 years old)	26.538	5.677	< 0.001
% SBW_{cut}	20.619	8.500	0.015
SBW_{ms}	-0.048	0.092	0.600

Random effects	**Variance**
% SBW_{cut}	$0.633\ x10^{-1}$
SBW_{ms}	$0.764x10^{-5}$

1.6. Discussion

We show that the impact of SBW on boreal forests can resonate broadly across the community by triggering an important indirect effect, apparent competition between two large herbivores. Increases in availability of deciduous vegetation as a result of SBW infestation of conifer stands generated a suite of spatial and demographic responses in moose, wolves, and caribou indicative of disturbance-mediated apparent competition (Seip 1992; Serrouya *et al.* 2015). Critically, however, salvage logging of conifer stands post-SBW outbreak in our study area facilitated an increase in predation mortality risk for boreal caribou, an ungulate Threatened with extinction (COSEWIC 2014). More generally, our study demonstrates that typically independent food webs (conifer–insect vs vegetation–moose–caribou–wolf) may interact such that the impact of an insect pest on forest structure and composition alters predator-prey interactions among large mammals. We draw this conclusion by providing quantitative support to predictions of three key processes involved in insect-driven apparent competition for our study area (**Figure 1.1**).

First, the outbreak of SBW increased the abundance of deciduous vegetation in coniferous stands (L1, **Figure 1.1**). For this to happen, outbreaks need to be sufficiently severe and last long enough for the old-growth canopy to open up and for pioneer, shade-intolerant plant species (i.e., deciduous, hardwood vegetation) to proliferate (Bouchard *et al.* 2006). The impact of an insect outbreak thus depends on the duration and severity of its infestation (Ivan *et al.* 2018), as we observed from our SBW cumulative severity index.

Second, the increase in deciduous vegetation we documented reflected a numerical response of moose (L2, **Figure 1.1**), with the population density of moose using the same survey methods increasing by 70% over a 13-year period post SBW-outbreak. Covariation between moose density and availability of deciduous (hardwood) vegetation is well established (Crête 1989). Moose, which are hardwood browsers (Gagné *et al.* 2016), are most abundant in early to mid-seral stages of boreal forest succession (Rempel *et al.* 1997; Fortin *et al.* 2017) where hardwood trees and deciduous shrubs are generally high in palatable biomass (Hodson *et al.* 2011). Moose did not alter their overall distribution following the outbreak, as they generally remained most closely associated with forest stands rich in deciduous vegetation. Such close affinity with food-rich areas is a basic expectation from ideal-free distribution principles (Fretwell & Lucas 1969). That said, we observed moose density to become especially high in areas largely comprised of deciduous stands and of stands first infested by SBW but then also logged. Outbreak-modified habitat selection patterns for moose are not unique to SBW, as Ivan et al. (Ivan *et al.* 2018) recently outlined a positive association between bark beetle (*Dendroctonus* spp.) outbreaks and the distribution of various ungulates, including moose.

Third, mortality rate of caribou was higher in areas impacted by SBW (L5, **Figure 1.1**). While the insect could have altered the hunting efficiency of wolves, it is unclear whether the overall outcome would be positive for the predator. On one hand, severe SBW infestations generally occur in forest stands with complex vegetation structure and high lateral cover (Cotton-Gagnon *et al.* 2018) and result in forest stands with more abundant dead wood (Norvez *et al.* 2013), which might reduce hunting efficiency especially of cursorial predators. On the other hand, salvage logging of SBW-impacted stands removes standing trees and requires deployment of a road network that is known to increase the search efficiency of wolves (James & Stuart-Smith 2000; Whittington *et al.* 2011; DeCesare 2012). Without excluding this possibility, our study was designed to evaluate the notion that the increase in caribou mortality could be indirectly linked to the response of moose to landscape changes. The tight link between wolf abundance and ungulate density, especially moose density (Serrouya *et al.* 2017), is well documented. Although no longitudinal data exists on the demographic response of wolves to prey availability in our study area, the expected numerical response of wolves to increased moose density during the SBW outbreak explains the increased risk of caribou mortality.

Apparent competition can also be driven by behavioral traits (Holt & Bonsall 2017). This would be the case, for example, when adjustments in the predator's search for a given prey results in more frequent encounters with another. Prey species with large home ranges and site fidelity, such as boreal caribou (Faille *et al.* 2010; Lafontaine *et al.* 2017), should be particularly prone to trait-mediated apparent competition. Wolves hunt by targeting areas rich in moose's food, including deciduous or mixed stands and disturbed areas where early-seral vegetation has emerged (Courbin *et al.* 2014; Fortin *et al.* 2015; Gagné *et al.* 2016). Accordingly, we found not only moose that were particularly abundant in areas characterized by a high proportion of SBW_{cut}, but also that wolves made selective used of these stands. This attraction of wolves for SBW_{cut} impacted a segment of the caribou population, with individuals avoiding less strongly (**Table 1.1**) or using more intensively SBW_{cut} (**Table 1.2**) more likely to die from predation. Our study provides the first demonstration that the strength of apparent competition between caribou and moose in a caribou-moose-wolf system can also depend on the indirect effects of an insect, SBW, on the availability of deciduous vegetation.

Given that caribou-moose-wolf interactions have evolved in environments shaped by a recurrence of insect outbreaks, including SBW irruption, we might expect that caribou populations would cope with enhanced predation risk resulting from asymmetrical apparent competition. What is most concerning, however, is that mortality rates following SBW infestation in our study area were clearly exacerbated by post-outbreak logging. Salvage logging during insect outbreaks has become a common practice across the boreal forest in North America (Lindenmayer *et al.* 2012). With climate change SBW infestations are expected to spread northward (Régnière *et al.* 2012), which should increase the spatial overlap between SBW outbreaks and caribou distribution in areas where most of the unlogged, primitive forests (Schaefer 2003; Fortin *et al.* 2008a; Drever *et al.* 2019) that can be subjected to salvage logging occur. In fact, the current outbreak is expanding northward, and is impacting areas that had not been previously affected by outbreaks (Pureswaran *et al.* 2015). By the end of our study, the SBW infestation overlapped with half the radio-collared caribou (Figure 1.2). Our study provides a textbook example of cumulative effects (Riffell *et al.* 1996) between natural and anthropogenic disturbance on food web properties, albeit in the context of an interaction that has thus far been missed by researchers and is new to the literature on boreal caribou conservation.

Our findings also expose potential risks involved with the current paradigm for boreal caribou management for habitat, notwithstanding the risk of ignoring the additive or interactive impacts of climate change on forest-insect outbreaks in caribou range. Current recommendations are largely based on the limitation of total disturbance (fire and anthropogenic) of caribou habitat to 35% (Environment Canada 2012). At first glance, salvage logging could be seen as a favorable option in this context as it mostly involves the disturbance of areas already mapped under a disturbance footprint (Beguin *et al.* 2015), thereby keeping the disturbed area largely constant (excepting the addition of haul roads). Our study underscores that salvage logging of SBW-impacted forests is not compensatory to natural disturbance, but highly likely to exacerbate the mortality risk of caribou. Moreover, salvage logging can disrupt post-disturbance succession (Leverkus *et al.* 2021), removes biological legacies (e.g., snags), and reduces the value of wildlife habitat (Lindenmayer & Noss 2006; Norvez *et al.* 2013; Thorn *et al.* 2018). There is a real danger that SBW outbreaks cumulative with post-outbreak salvage logging will present additive and not compensatory risk to the persistence probability of boreal caribou populations. Whether this finding also applies to other scenarios of salvage-logging, from fire or other insect outbreaks (e.g., from bark beetle), is plausible but unknown. Still, with the ongoing global changes in boreal ecosystems, there is a risk that pest insects become an indirect driving force behind the northward range recession of boreal caribou.

The impact we observed of SBW on large-mammal interactions occurred via forest-structure transformation and a subsequent pulse in resources for large herbivores. Previous studies have underscored the far-reaching consequences of resource pulses, including cascading effects across food webs (Chesson *et al.* 2004; Yang *et al.* 2008, 2010). For example, suitable weather conditions can result in a vegetation pulse of acorns (mast event) triggering a numerical response of rodents and then of predatory birds, with subsequent negative demographic effects on other bird species (Schmidt & Ostfeld 2008; Grendelmeier *et al.* 2018; Thomsen *et al.* 2018). Trophic cascades have also been initiated with the input of food and nutrients from the ocean by seabirds, providing nutrients for terrestrial plants as well as food for terrestrial consumers (Anderson & Polis 1998; Bartz & Naiman 2005; Fukami *et al.* 2006) in correlation with pulses in fish stocks (Bartz & Naiman 2005; Hocking & Reimchen 2009). Predation has been shown to modulate such effects, for example with introduced predators like foxes preying on birds reducing nutrient transport from ocean to land, and negatively affecting soil fertility (Croll *et al.* 2005; Maron *et al.* 2006). While predator-mediated apparent competition is also known from island systems (Roemer *et al.* 2002) and, more recently, in the context of abiotic (rainfall) limitation

(Thomsen *et al.* 2018), the relationships we show here is novel in that we link the former to a resource pulse initiated by a consumer (SBW), itself likely limited by abiotic conditions.

Our findings are relevant at large ecological scales in both space and time. The SBW is a common forest pest of the boreal forest, and SBW outbreaks occur in the periodically every 30–40 years (Boulanger & Arseneault 2004) or longer (Bouchard & Pothier 2010). However, with generation times ≤ 10 years (Gaillard 2007; COSEWIC 2014; Mech *et al.* 2016) and a typical longevity < 20 years (Mech 1988; Ericsson & Wallin 2001; COSEWIC 2014) for the three mammal species we considered in this study, multiple cohorts of individuals are expected to experience little to no SBW infestations during their lifetimes. This means that SBW-forest interactions and that of moose-wolf-caribou may generally operate independently at low levels of SBW. But when an outbreak occurs its impact on forests are likely to couple these otherwise independent interactions, ricocheting across the large-mammal food web. SBW therefore acts as an ecological engineer with its actions on forest structure and composition ultimately leading to enhanced apparent competition (*sensu* Schmidt and Ostfeld (2008)) between boreal caribou and moose. Furthermore, human activities, such as salvage logging, strengthened the strength of interactions between SBW-forest and plant-caribou-moose-wolf systems. Including humans as an additional species which might manipulate trophic interactions may be particularly important in human-impacted ecosystems.

In conclusion, we provide empirical evidence that ecosystem engineering by a common insect (SBW) can ricochet along a chain of ecological interactions to be felt by an apex mammalian predator before bouncing back down to impact an ungulate via apparent competition. Our study demonstrates that the cascading effects of SBW in boreal ecosystems can ultimately increase the mortality rate of a threatened ungulates, especially when human activities further disturb the system. Such insights are particularly critical in the context of global change, given evidence suggesting that both anthropogenic disturbances and climate change have the potential to disturb top-down and bottom-up control mechanisms that regulate ecological communities (Barton *et al.* 2009; Muhly *et al.* 2013). By integrating the spatiotemporal dimension and severity of forest-insect outbreaks simultaneously with other natural and anthropogenic disturbances, our study highlights how multiple disturbances can act on a boreal system by altering species densities and higher-trophic level interactions. Our finding of an insect-mediated interaction strong enough to bounce back into higher-trophic level apparent competition highlights the far-reaching role of multi-level indirect interactions on food-web dynamics.

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Data Availability: Information on animal distribution data have been de- posited in Dryad (https://doi.org/10.5061/dryad.j3tx95xds). All other study data are included in the article and/or Annexe A: Supplementary results in Chapter 1 on caribou habitat selection.

Chapitre 2. Global change risks a threatened species due to alteration of predator-prey dynamics

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2.1. Résumé

Les modifications du paysage induites par les changements globaux affectent l'ensemble des réseaux trophiques. Nous avons simulé la dynamique forestière et les déplacements d'espèces en interaction, paramétrés à partir d'observations réelles, pour prévoir les conséquences des changements globaux sur un réseau trophique de grands mammifères dans la forêt boréale. Nous démontrons que les changements induits par le climat et l'aménagement forestier dans les paysages exacerbent la compétition apparente entre les orignaux et les caribous, une espèce menacée, par la prédation des loups. Alors que l'augmentation de la mortalité des proies provenait à la fois des réponses comportementales et numériques, les effets des réponses numériques étaient plus importants. La mortalité des caribous était exacerbée par les effets cumulés de l'aménagement forestier et des changements climatiques, avec un impact plus élevé de l'aménagement forestier. Les interactions trophiques indirectes sont essentielles pour comprendre la dynamique des communautés face aux changements globaux.

2.2. 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 on 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 boreal forest. We demonstrate that climate- and land use-induced changes of forest landscapes exacerbate asymmetrical apparent competition between moose and threatened caribou populations, through wolf predation. While 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.

2.3. 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 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 producers to induce cascading effects across ecosystems (Rosenblatt & Schmitz 2016; Stoner *et al.* 2018). CC thus can exacerbate the well-known impacts of anthropogenic disturbances (e.g., land-use change, harvesting) on food webs (Brook *et al.* 2008), and even result in population extinctions (Oliver & Morecroft 2014; Oliver *et al.* 2015). The threat of global changes appears particularly strong for specialist species (Clavel *et al.* 2011), which thrive under specific habitat conditions that global changes can alter (Mosnier *et al.* 2008; Hämäläinen *et al.* 2018). 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 (Tylianakis *et al.* 2008; Oliver *et al.* 2009). 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 (Trainor & Schmitz 2014; Heinle *et al.* 2021). While most research has focused on how species distribution and population demography vary with abiotic conditions (Dainese *et al.* 2017; Bonnot *et al.* 2018; Zurell *et al.* 2018), recent work demonstrated that accounting for biotic interactions (such as predation or competition) improves the projection of species responses to change (Trainor & Schmitz 2014; Heinle *et al.* 2021). Yet, few studies have examined the combined effect of projected changes in land use and in climate on multi-species trophic interactions (Bossier *et al.* 2021). We addressed this research gap by combining a spatially explicit simulation model of forest landscapes (Scheller *et al.* 2007) and 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 2.1**). 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 post-disturbance growth of deciduous vegetation would be insufficient to trigger such numerical responses (e.g., DeMars et al. (2019), and Neufeld et al. (2021)). 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.* 2020b), identifying thresholds in resource availability that trigger such change in food web dynamics remains unclear.

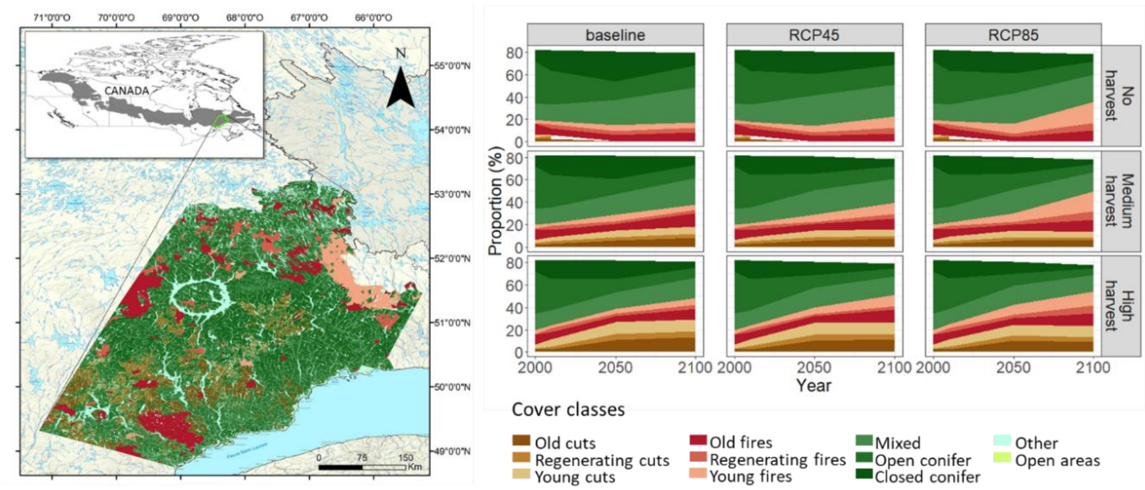

Figure 2.1. Study area and changes in land cover. Study area in the province of Quebec, Canada, with delineation of the range of boreal woodland caribou in grey (left). Colors represent the different land covers in 2018. Trends in the proportion of cover classes (right) for each of the three land-use 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, fires increase stands classified as regeneration (see Annexe B, **Figure B 1**).

Our study tests the potential cascading effects of human disturbance and climate change 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 2.2.1**) under three future climate scenarios (e.g., Baseline, RCP4.5 and RCP8.5 (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 2.2.2, 2.2.3**), and herbivore agents can die from predation (**Figure 2.2.4**). 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 2.2.3, 2.2.4**). Because results were largely similar in summer and winter, we describe winter results and only point out the few differences observed between seasons.

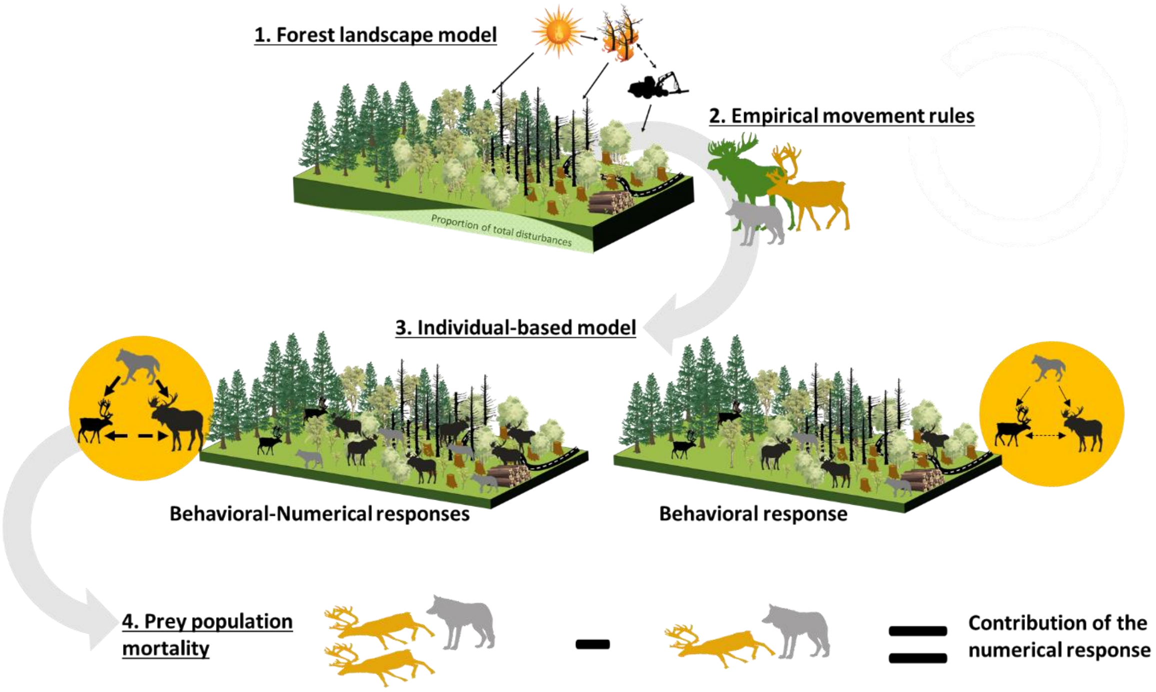

Figure 2.2. Schematic representation of the simulation design implemented in this study. (1) A forest landscape model was used to simulate stand-(i.e., individual tree establishment, growth and mortality) and landscape-scale dynamics (seed dispersal, natural and anthropogenic disturbances), allowing climate change and land use to differentially impact forest landscapes. We then combined the forest landscape simulation outputs with empirical movements rules from boreal caribou, moose and wolves (2) to calibrate the individual based model (IBM – 3), and ultimately project prey mortalities (4) in landscapes developed from different land-use change (LUC, logging) and climate change (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 once accounting for the relationship between species abundance and the resource availability (Behavioral-Numerical responses). Tree symbols courtesy of (UMCES 2021).

2.4. Materials and Methods

Model overview

A description of the methods used to parameterize, calibrate, and validate the model, are included in the Annexe C: Data partitioning in Chapter 2 and 3. and Annexe D: Details of the calibration and validation of IBM in Chapter 2 and 3. 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).

Study area

The study area (48°N-54°N, 63°W-73°W) covers 115 470 km² and is located in the Côte-Nord region of Québec, Canada (**Figure 2.1**). 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 (Figure 2.2.1)

Climate scenarios

Future climate projections are based on two different radiative forcing scenarios, known as Representative Concentration Pathways (RCP, see Van Vuuren et al. (Van Vuuren *et al.* 2011) for more information). We obtained future climate projections from the Canadian Earth System Model version 2 (CanESM2) ran under both RCP 4.5 and RCP 8.5. The ANUSPLIN method was used to downscale climate projection to a 10-km resolution. Future mean annual temperatures are 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 between 7% and 10% under RCP 8.5 and RCP 4.5 respectively (Boulanger *et al.* 2018). Monthly time series for each climate scenario (CC, baseline, RCP 4.5, RCP 8.5) were used to parameterize forest landscape simulations.

Forest landscapes 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 forest landscape model that dynamically simulate 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 to 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). Each cell is assigned to a 'land type' (*sensu* Scheller and Mladenoff (2004)) which are assumed to have homogeneous soil and climate conditions; therefore, these land types may be used as spatial units in which various sub-models are parameterized. We used the LANDIS-II Biomass Succession extension v5 to simulate forest succession in each cell. This extension simulates modifications in cohort aboveground biomass (AGB) over time by taking into consideration tree species' cohort age, life-history traits, and species-specific land type responses. We parameterized and calibrated three sets of dynamics growth and regeneration inputs sensitive to soil and climate conditions that are necessary in Biomass Succession, i.e., (i) species establishment probabilities (*SEP*), (ii) maximum annual aboveground net primary productivity (*maxANPP*), and (iii) maximum aboveground biomass (*maxAGB*). Parameterization was conducted using the individual tree-based, forest patch model PICUS version 1.5 (Lexer & Hönninger 2001; Taylor *et al.* 2017). PICUS simulates the dynamics of individual trees on 10 x 10 m patches across forest stand areas and accounts for spatially explicit interactions among patches via a 3D light module. PICUS simulates the effects of climate and soil properties on tree population dynamics (Lexer & Hönninger 2001). A complete description of the model and how it was parameterized and validated can be found in Taylor et al. (2017). Simulated forest succession trajectories and the distribution of the parameter values derived from Picus outputs among land types for maxANPP, maxAGB, and SEP were represented in Annexe B, **Figure B 2** - **Figure B** *6*. Dynamic inputs were obtained for each combination of tree species, land type, time period (2000-2010, 2011-2040, 2041-2070, 2071-2100) and climate scenario. LANDIS-II simulations were run for 100 years, starting in 2000, using a 10-yr time step and a 250-m resolution.

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., land-use change scenarios, LUC) 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 FRS (Forest Roads Simulation) module which allows to create roads to cells that are harvested, while reducing the costs of construction of roads as much as possible (Hardy C, Messier C, Filotas E, Valeria O (2022), in preparation). 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 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.

Simulation design

Forest landscapes 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 steps. Except for scenarios involving the baseline climate, climate-sensitive parameters were allowed to change in 2010, 2040 and 2070, according to the climate corresponding to each forcing scenario (Boulanger & Pascual Puigdevall 2021). For the next steps of the analysis, we used landscapes resulting from LANDIS-II models for the years 2000, 2050 and 2100.

Habitat characteristics for simulated landscapes

To estimate forest composition and create the final maps to use with the individual-based model, we used the relative proportions of species groups (conifer and deciduous species) from the LANDIS-II biomass outputs. As LANDIS-II does not directly output crown closure, we built a random forest model to predict crown closure covariate by using Canadian National Forest Inventory (NFI) forest attribute maps (Beaudoin *et al.* 2014). These maps are a k-Nearest Neighbours interpolation of the NFI photoplot data acquired in 2001 and are depicting over 130 forest attributes including species-specific biomass, stand age and crown closure at a 250-m resolution (see Beaudoin et al. (2014)). We therefore build a random forest model predicting cell-level crown closure in NFI product from NFI species-specific biomass as well as stand age. This model had very high goodness of fit ($R^2 = 0.86$). The model was then applied on LANDIS-II outputs to predict crown closure all along the simulation, for each cell by using simulated species-specific biomass and stand age. Using species group and predicted crown closure, we created five land cover classes from the Earth Observation for Sustainable Development of Forests (EOSD) 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 non-treed ≥ Vegetation treed) and other (Non-Vegetation ≥ 50%). Land cover maps were updated every year by adding roads, recent (≤10 years), regenerating (11-20 years) and old (21-50 years) cutblocks/burned areas that LANDIS-II simulated.

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 of the nonoverlapping surface of burns, roads, and cuts, the latter two buffered by 500 m. The proportion of total disturbances and burned areas associated for each simulation was represented in Annexe B, **Figure B 7**. The proportion of deciduous vegetation for each simulation was represented in Annexe B, **Table B 4**.

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, we calculated the mean 'isolation index' (calculated as 1-'cohesion index'), characterised as the connectedness of patches belonging to a land cover class. 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 (Annexe B, **Table B 4**). At the landscape level, we calculated the 'homogenization index' (calculated as 1/'conditional entropy', characterised as the complexity of a landscape pattern configuration). 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 (Annexe B, **Table B 4**).

Movement rules derived from radio-tracking caribou, moose and wolves (Figure 2.2.2)

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.

Telemetry

A total of 68 GPS-collared adult female caribou were monitored between March 2005 and December 2018, with each individual being followed for an average of 23.1 months (range: < 1 to 56 months). Animal capture and handling protocols for all species adhered to guidelines under the Canadian Council on Animal Care and were approved by Université Laval animal protection committee. For wolves, 16 adults (8 females and 8 males) were followed between March 2005 and December 2018, with each individual being tracked for an average of 19.6 months (range: < 1 to 49 months). Fifteen female moose were followed with GPS collars between March 2005 and March 2009. Following Basille et al. (2013), we defined three periods by merging caribou and moose biological seasons: pre-calving/calving season (mid-May through late July, which covers the calving season of both boreal caribou and moose), late summer (early August to the end of September), and winter (October to mid-May). Wolf locations were also separated according to the same periods. We focused our investigation on winter and late-summer, a period a relatively high caribou mortality in the study area (Basille *et al.* 2013).

Habitat characteristics

We characterized the study area, from 2005 to 2018, using the Canadian NFI 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 roads, recent (≤ 10 years), regenerating (11-20 years) and old (21-50 years) cutblocks/burned areas based on information provided annually 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).

Statistical analysis of empirical movement rules

To test predictions based on whether individuals change their movement behaviour relative to environmental characteristics, we used step selection functions (SSFs; (Fortin *et al.* 2005)). This approach assumes that landscape characteristics along and/or at the end of the step can influence the probability of an animal taking that step, i.e., that the characteristics of the environment between the start and end points of the step influence animal movements (Fortin *et al.* 2005). The SSFs were estimated from data for the real animals based the comparison between each 8-hours observed step of the individuals. Each step (i.e., used) was paired with 20 random steps (availability) where an animal could have moved. The step lengths (SL) and turning angles (i.e., the direction of the current step relative to the direction of the previous step, TA) of random steps were drawn within a disc of radius equal to the 99th percentile of step length distribution based on the observed distribution determined from GPS collar data for all individual of a given species within a given season. We estimated SSF parameters using conditional logistic regression:

$$w(\mathbf{x}) = \exp\left(\beta_{\ln SL} \times \ln(SL_x) + \beta_{SL} \times SL_x + \beta_{TA} \times TA_x + \beta_{LC} \times LC_x + \beta_{DR} \times DR_x\right)$$

where w(**x**) represents the SSF score of the step described by the vector $\mathbf{x}$ of variables x_i (i.e., SL, TA, LC and DR) with associated coefficient $\beta_{lnSL}, \beta_{SL}, \beta_{TA}, \beta_{LC}$,and β_{DR}. The term LC (land cover type) corresponds to a set of 11 dichotomous covariables described in *Habitat characteristics*. The term DR is a set of 5 dichotomous covariables representing the classes of distance to the nearest road (i.e., 1) ≤250 m, 2) 251–500 m, 3) 501–1000 m, 4) 1001–1500 m and 5) >1500 m as the reference category). The model includes both the natural logarithm of step length ln (SL) and step length SL (Annexe D, **Table D 1**), as recommended by Nicosia et al.

(2017). Higher values of w(**x**) indicated greater odds of being chosen by an individual. We did not detect multicollinearity issues, given that variance inflation factors of all covariates were ≤ 4 (Chatterjee *et al.* 2000). We assessed the robustness of SSF models of all species with k-fold cross validation using 100 repetitions of 5-fold cross-validation with 10 bins of equal size and calculated the averaged Spearman's rank correlation coefficient ($\overline{r}$s) (Fortin *et al.* 2009). A detailed description of model fitting is available in Annexe C: Data partitioning in Chapter 2 and 3..

Individual-based model (IBM) (Figure 2.2.3)

Simulation setup and initial conditions

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 forest landscape model for projections. To integrate the effect of the distance to roads, we superimposed a landscape with a raster of distance-to-road.

The IBM simulated individual movements and interactions between prey and predators. The IBM started with the initialization of agents. Each caribou and moose virtual agent represented a single individual, whereas a wolf agent represented a wolf pack (i.e., meta-individual) (similarly to Latombe (2013)). Caribou, moose, and wolf packs were initially randomly distributed across the landscape. To simulate wolf territoriality, we subdivide the map into sectors of equal areas and set one pack in each sector. Agents had the same initial positions in all simulations. Movements and predation depended on step length, turning angle, and landscape characteristics. To do so, we used step selection functions (SSFs; described above (Fortin *et al.* 2005)) specific for each species and season determined from field observations. The probability to choose one step over another was proportional to 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 distribution (Dickie *et al.* 2017) of that species (Annexe B, **Table B 5**). The distance that wolves could move in one step further depended on their movement modes; they could either be in hunting mode when actively searching for prey or they can be in stationary mode when consuming a prey and resting after the kill (Mech & Boitani 2003). Accordingly, we considered mode-dependent step length distributions to draw random steps (Annexe B, **Table B 5**). Wolf agent were able to detect prey only when in hunting mode and when the prey was within 1 km (Mech & Boitani 2003), in which case, they had a 25% probability of launching an attack (details of the calibration are included in Annexe D: Details of the calibration and validation of IBM in Chapter 2 and 3). Following an attack, they had a 20% probability of killing the prey (Latombe 2013; Mech *et al.* 2015). If wolves detected both caribou and moose within their vicinity, they went for moose (Mech & Boitani 2003). Wolves went into stationary mode for 24 hours after a caribou kill and for 72 hours after a moose kill (Hayes *et al.* 2000). They could not kill another prey while in stationary mode. Prey could only die from predation, and they were then removed from the simulation.

Moose and wolf numerical response

To consider 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-km² in 2006. We considered all survey plots that overlapped the study area, delimited with 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 Canadian National Forest Inventory (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. We then adjusted the number of wolf packs to moose density based on Messier(1994). Details of moose and wolf pack densities used in the simulations are included in Annexe D: Details of the calibration and validation of IBM in Chapter 2 and 3.

Simulation design

To model wolf, moose and caribou movements, and estimate wolf predation rate under the different scenarios, we ran the IBM for 1 year in years 2000, 2050 and 2100, with ten replicates. We thus ran a total of 380 simulations per season, i.e., 760 simulations. We used one output of LANDIS-II simulation model per combination of CC and LUC scenario because we were more interested by the uncertainty of the IBM than of the forest landscape model. 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 (Figure 2.2.4)

The validation of the IBM can be found in Annexe D: Details of the calibration and validation of IBM in Chapter 2 and 3.

Analysis of prey mortality

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

First, to test 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 used all years (2000,2050 and 2100) and we used the combination of all CC and LUC scenarios, and years as a random effect. Disturbance covariates were correlated to other landscape characteristics. Thus, to evaluate the additive effect of these landscape characteristics had on prey mortality without facing multicollinearity issue, we used residuals 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 test how changes in species densities impacted trophic interaction.

Second, to test 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 and 2100, to evaluate how the effect of CC and LUC vary temporally. The model fit was assessed qualitatively, from the distribution of residual versus fitted values, and quantitatively, by comparing Akaike information criterion (AIC) values of all the competing models (Annexe B, **Table B 1**, Annexe E, **Table E 2**). 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 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.

2.5. Results and Discussion

LUC (logging) and CC changed the composition and the structure of boreal landscapes (**Figure 2.1**, **Figure 2.3**). Increased LUC and CC initiated widespread secondary succession (**Figure 2.1**), and subsequently increased the proportion of pioneer, deciduous vegetation (**Figure 2.3a**, Annexe B, **Figure B 1Erreur ! Source du renvoi introuvable.**). CC altered landscape composition mostly through an important surge in area burned from climate changed 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. This shift to deciduous and younger vegetation was highlighted by the increase in mixed stands, burned areas and in regenerating cuts (**Figure 2.1**). Forest disturbance levels (i.e., proportion of cuts and roads, and burned areas) increased with intensification of LUC and CC (**Figure 2.3b**). 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 2.3c-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 2.1**), which reduced landscape complexity (**Figure 2.3d**). 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 change 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 improve 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 bottom-up cascading effects on moose and wolf numerical responses (Serrouya *et al.* 2021).

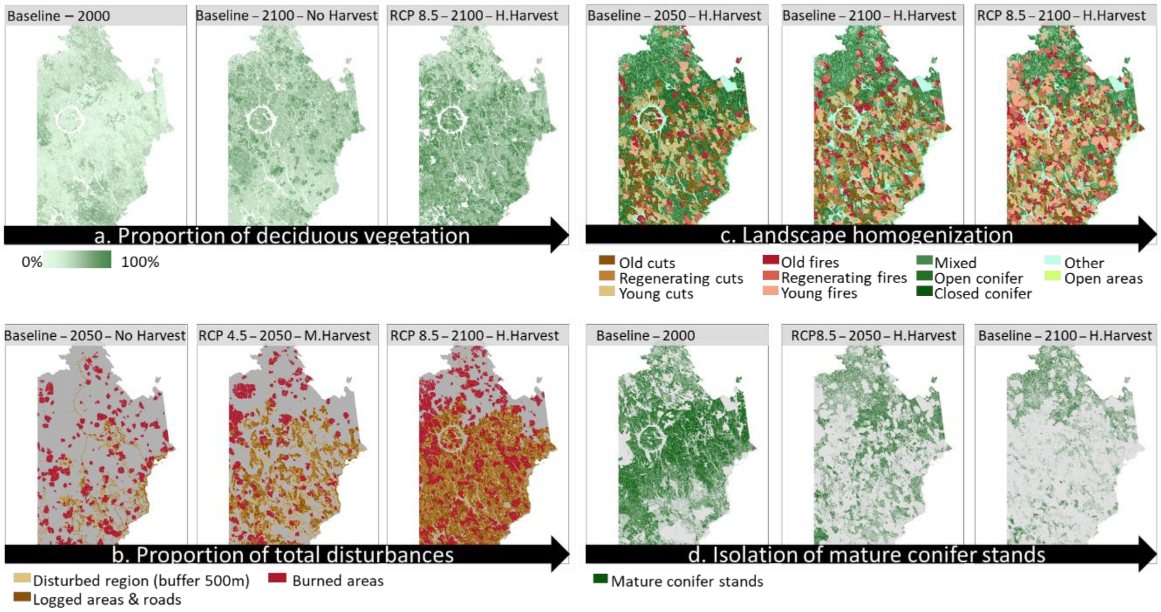

Figure 2.3. Changes in forest attributes induced by land-use (LUC) and climate (CC) changes. Maps showing a. the proportion of deciduous vegetation, b. the proportion of total disturbances, c. the homogenization of the landscape, and d. the isolation of mature conifer stands in the study area as a function of LUC (No harvest, High harvest [H.Harvest] and Medium harvest [M.Harvest]) and CC (Baseline, RCP4.5 and RCP8.5). For each forest attributes, we illustrated scenarios that maximized the gradient of variation.

We fixed caribou density in all simulations (a conservative assumption) to test the relative contribution of behavioral response and behavioral-numerical responses under changing landscape on caribou mortality rate. Thus, an increase in caribou mortality between scenarios necessarily implied an increase in 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 to an increase in wolf density (numerical response). 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 2.1a,b**, **Figure 2.4**). Indeed, caribou mortality increased along with the proportion of natural and anthropogenic disturbances as well as in deciduous vegetation (**Table 2.1a,b**, **Figure 2.4a,b**). Landscape homogenization by disturbance further exacerbated the negative effect of such disturbances on caribou mortality (**Table 2.1a,b**, **Figure 2.4c**). This is shown by the residual values of the landscape homogenization covariate showing a positive significant effect on the proportion of caribou killed (**Table 2.1a,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 2.1a,b**). Caribou mortality increased with the level of isolation of mature conifer stands (**Figure 2.4d**), 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 (**Figure 2.4-Figure 2.5**).

Table 2.1. Model results of forest attribute changes on the proportion of caribou killed. Coefficients (and standard errors) 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 500m 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 consequences of LUC and CC 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 Annexe E, **Table E 1**.

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) *	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

Significance levels: ****P < 0.001, ***P < 0.01, **P < 0.05, *P < 0.1.

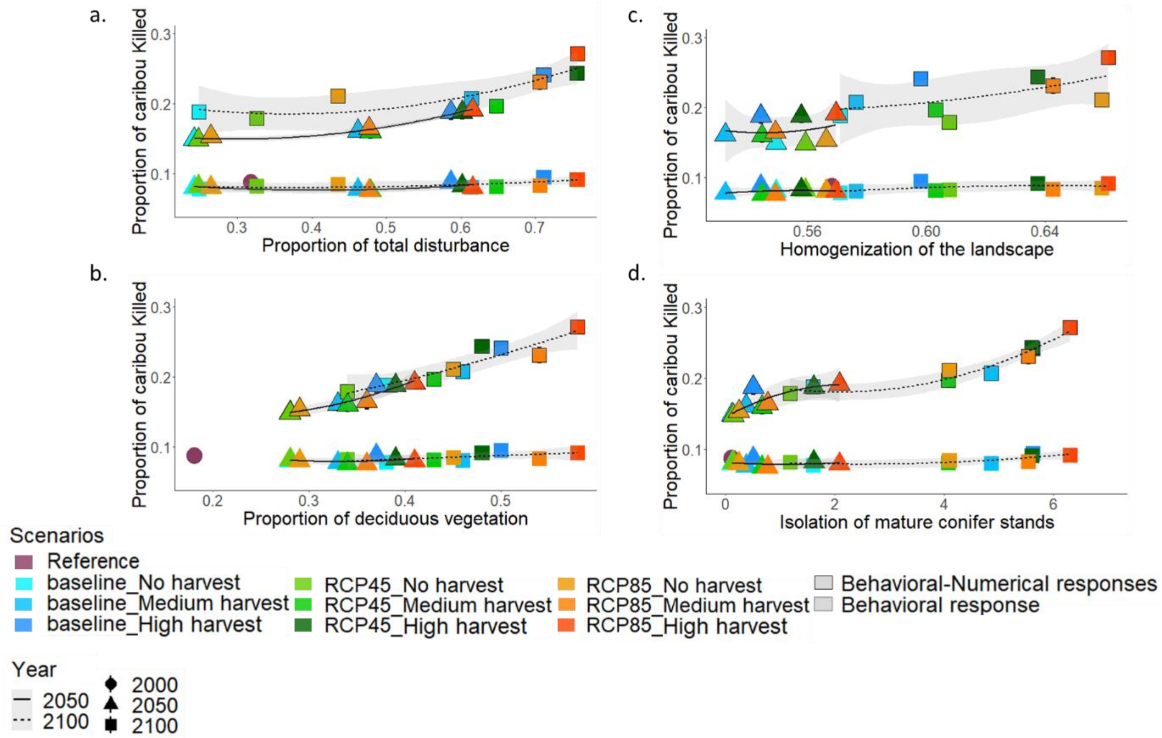

Figure 2.4. Relationships between the proportion of caribou killed and forest attributes. Proportion of caribou killed in 2000 (point in purple, determined as the reference), 2050 (triangle) and 2100 (square) in winter as a function of a. the proportion of total disturbances, b. the proportion of deciduous 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 3 different colors represented the 3 climate scenarios: baseline (blue), RCP4.5 (green) and RCP8.5 (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 represented the behavioral response, while shapes with black edge represented the behavioral-numerical responses of moose and wolf to emergent changes in forest landscape composition. Summer results can be found in Annexe E, **Figure E 1**.

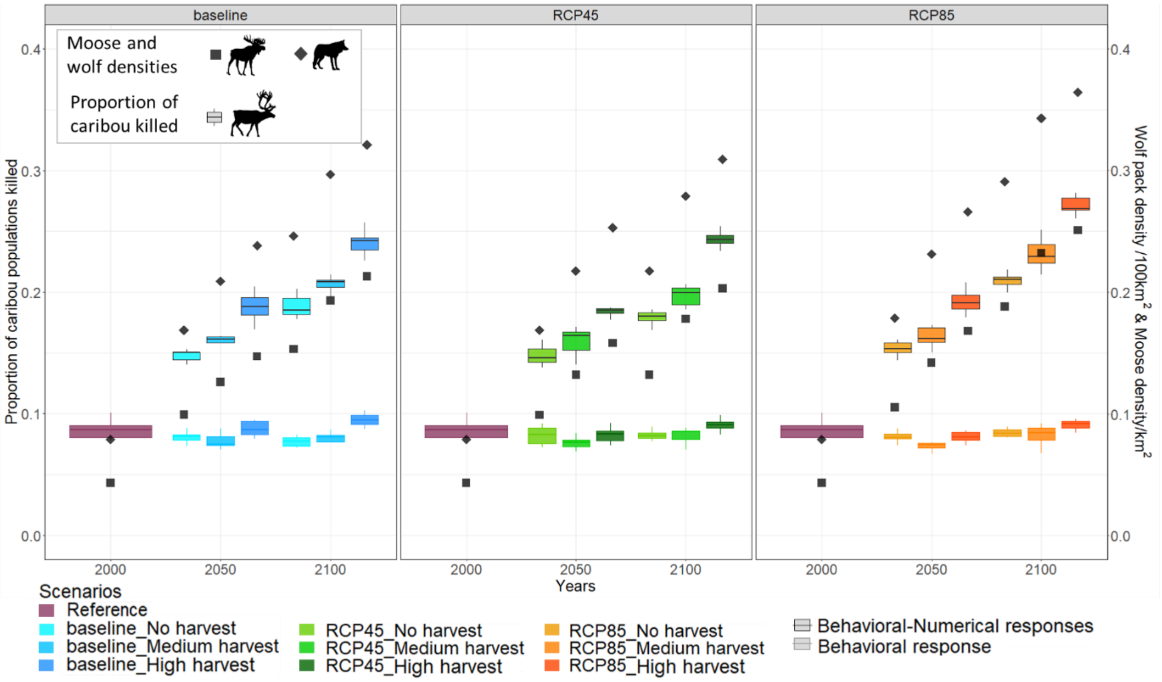

Figure 2.5. Changes in the proportion of caribou killed in function of land-use and climate change scenarios. Proportion of caribou killed by wolves in winter under three climate scenarios (Baseline in blue, RCP4.5 in green and RCP8.5 in orange) and three levels of land-use (No harvest in light, Medium 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 represented the behavioral response, while boxplots with black edge represented 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 the interquartile range. Summer results can be found in Annexe E, **Figure E 2**.

Our simulations showed that the numerical response of moose and then of wolf triggered by LUC and CC was the dominant process controlling caribou mortality. By 2100 under the most severe CC and LUC scenarios, the proportion of caribou killed was 3 times higher for simulations considering the behavioral-numerical responses compared to simulations including only the behavioral response (**Figure 2.4-Figure 2.5**). 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 2.1c**).

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 (Annexe B, **Figure B 8**). Wolf-moose encounter rate increased with moose density, such that each wolf spent more time handling moose and less attacking caribou. Although such 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 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*) (Roemer *et al.* 2002; DeCesare *et al.* 2010). 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 under first, changing landscape conditions, and then, changing climate. As a result, projected changes in deciduous vegetation, whether 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 including the behavioral and numerical responses. Results showed that LUC and CC had an additive effect in winter (Annexe B, **Table B 1**), but interactive in summer (Annexe E, **Table E 2**). Regardless, LUC consistently had a stronger impact than CC on caribou mortality (Annexe B, **Figure B 9**). Indeed, when averaging all climate scenarios, the high harvest scenario increased caribou mortality by 31% compared with simulations with no harvest in 2100 (**Figure 2.5**). 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 2.5**). 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 short-term impact, while CC will have a long-term impact. The negative effects of CC and LUC on caribou survival both increased over time (positive 'CC x year' and 'LUC x year' interaction terms). For example, in 2050, CC still had no detectable effect on predator-prey interactions ($P > 0.1$; Tukey honestly significant difference (HSD), Annexe B, **Table B 5**), 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 the optimistic CC (i.e., RCP4.5) and baseline conditions (*P* = 0.87; Tukey HSD). This was because the proportion of deciduous vegetation (from burned and non-impacted areas) was nearly the same under these two climatic 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 RCP8.5 scenario (Annexe B, **Figure B 9**), 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 RCP8.5, and then reached a maximum of 36% in 2100 (**Figure 2.5**). 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 climate change 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 affect 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's food, including disturbed areas where early-seral vegetation has emerged (Fortin *et al.* 2015; Labadie *et al.* 2021). While 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 (Wittmer *et al.* 2007; Labadie *et al.* 2021), resource availability (Thomsen *et al.* 2018; Ims *et al.* 2019; Serrouya *et al.* 2021), 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, 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 (Wittmer *et al.* 2013; Serrouya *et al.* 2019). For example, removal of predators and alternate prey increased survival of the endangered island fox in California (U.S.A.), 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 thus can 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, individual based models 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 semi-arid 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.

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Chapitre 3. The umbrella value of caribou for biodiversity conservation in boreal forest under global change

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3.1. Résumé

Comprendre l'impact des changements globaux sur l'effet parapluie des stratégies d'aménagement basées sur une unique espèce est d'une importance capitale pour la conservation des espèces. Nous avons évalué la résilience du caribou en tant qu'espèce parapluie pour la conservation de la biodiversité face aux changements globaux. Nous avons simulé la dynamique forestière et les déplacements d'espèces en interaction pour prévoir l'impact des stratégies d'aménagement sur la survie du caribou. Nous avons ensuite caractérisé les impacts simultanés sur la diversité des oiseaux et des coléoptères. Les stratégies d'aménagement, conçues pour la conservation de l'habitat du caribou, auraient un effet parapluie pour maintenir les assemblages d'espèces. Nous avons détecté un effet plus important de l'aménagent forestier par rapport aux changements climatiques sur la survie du caribou et la conservation de la biodiversité. Les actions de conservations conçues pour une unique espèce devraient avoir d'importants bénéfices pour la biodiversité malgré les changements globaux.

3.2. Abstract

How global change will impact the umbrella value of single-species management strategies remains an open question of critical conservation importance. We assessed the resilience 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. We then used predictive models of species occupancy to characterize concurrent impacts on bird and beetle diversity. We found that strategies that best mitigate human impact on boreal caribou were an effective umbrella for maintaining bird and beetle assemblages. We detected a stronger effect of land-use change compared to climate change on caribou survival and biodiversity conservation. The conservation status of some species makes it mandatory to develop strategies for their recovery. Our study shows that single-species conservation may have important umbrella benefits despite global change.

3.3. Introduction

Global climate and land-use changes are affecting biodiversity and food-webs by modifying environmental conditions (Wilmers & 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 focuses on a single species (i.e., an umbrella species, (Roberge & Angelstam 2004)) with the intent that sympatric species become concurrently protected. Conservation strategy of an effective umbrella species must therefore represent the conservation needs of sympatric species, and must provide protection from vertebrates to invertebrates (Rubinoff 2001). Some of the criteria for choosing such umbrella species are species with large home range, sensitivity to human-induced habitat changes, typical of its ecosystem, and its trophic role (Caro 2010). With climate-induced changes in the impact of natural and human disturbances, species assemblages could change to the point that an umbrella species and its conservation strategy may no longer be associated with the same species assemblages. Few studies, however, have assessed the consequences of global change on the effectiveness of conservation strategy designed around the needs of a given umbrella species for biodiversity conservation in a given biome (Lindenmayer & 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 population 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 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, with massive species losses and restructuring of 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*) are an umbrella species of North American boreal forests (Bichet *et al.* 2016; Drever *et al.* 2019) because of their large ranges and sensitivity to human-induced habitat changes, and because the management of their populations requires large areas of intact forests (Brown *et al.* 2003; Courtois *et al.* 2007; Hins *et al.* 2009; Fortin *et al.* 2013). Anthropogenic disturbance, such as logging and oil and gas extraction, are a major conservation challenge for all boreal biodiversity, including caribou (Trombulak & Frissell 2001; Environment Canada 2012). Co-occurrence of boreal caribou and their main predator, the gray wolf (*Canis lupus*), have increased dramatically due to anthropogenic disturbance (Environment Canada 2012). Disturbed areas provide high-quality food for deciduous-browsing moose (*Alces alces*) and deer (*Odocoileus* spp.). The subsequent increases in these prey populations trigger a numerical response in wolves, which intensifies predation rate for boreal caribou, causing apparent competition induced declines (Wittmer *et al.* 2005). In addition, climate-changed induced increases in wildfire will further contribute to increased deciduous forest cover, and thus competing prey for caribou (Boulanger & Pascual Puigdevall 2021). 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, other boreal 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.

Boreal caribou populations are threatened in Canada (Goverment 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, for example, the proposed management strategies, 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 2019c). As predation by wolves is considered the main driver of population decline (Rettie & 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 management strategy must be evaluated by considering the caribou–moose–wolf system entirely. As an umbrella species, the creation 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 landscape induced by CC and LUC, it is unclear, however, if the management strategy based on the current needs of boreal caribou would be effective at maintaining biodiversity. Moreover, it is also unclear to what extent the creation 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.

We compared the umbrella value of 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. We linked landscape simulation model (**Figure 3.1.1**) with individual-based models of caribou, moose and wolf agents (**Figure 3.1.2**) and empirical models of bird and beetle species distribution (**Figure 3.1.3**) 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 (**Figure 3.1.4**). 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, if boreal caribou is a good umbrella species, the management strategies associated with relatively low caribou mortality should also be linked to bird and beetle community similar to undisturbed landscapes. More specifically, we used animal (birds and beetles) assemblages 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.

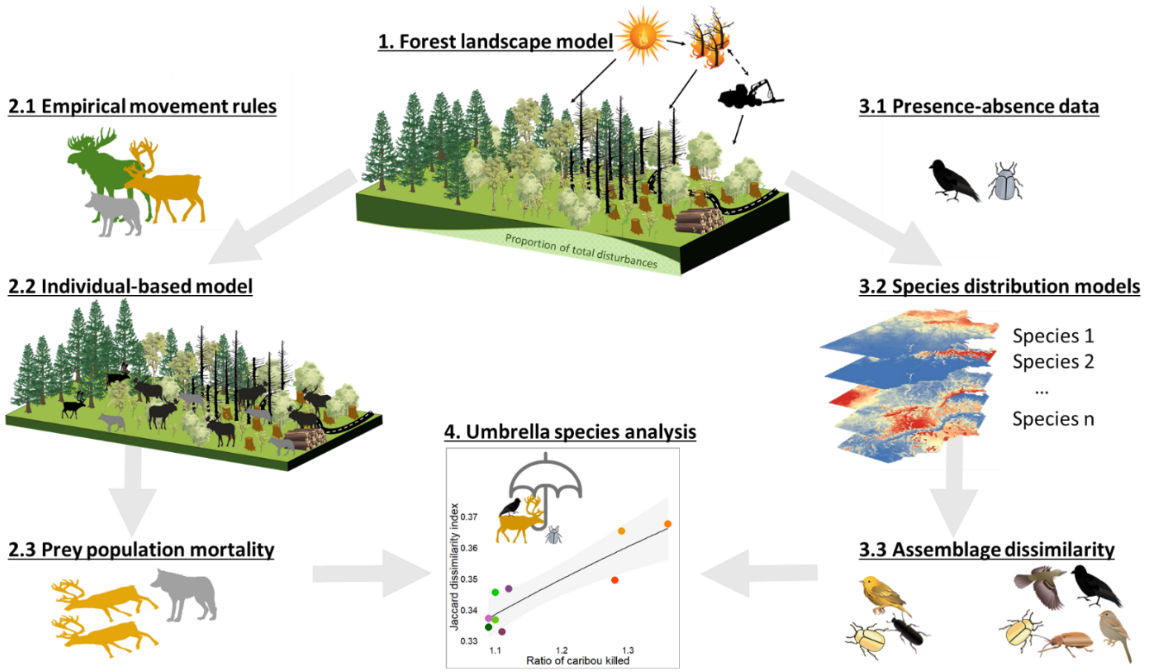

Figure 3.1. Conceptual representation of the simulation design implemented in this study. (1) A forest landscape model was used to simulate stand-scale (i.e., individual tree establishment, growth and mortality) and landscape-scale dynamics (seed dispersal, natural and anthropogenic disturbances), allowing 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).

3.3. Materials and methods

Study area

The study area (48°N-54°N, 63°W-73°W) covers 115 470 km² of Boreal forest and is located in the Côte-Nord region of Québec, Canada (**Figure 3.2**). 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). Our study area presents a latitudinal gradient of forest stand composition, with a dominance of old-growth coniferous forest and open forest with black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) in the north, and Black spruce with balsam fir, white birch (*Betula paperyfera*), white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*) in the south. Historically, forest harvesting mostly occurred in the southern part of the study area and gradually extended northward, while fires occurred mostly in the north.

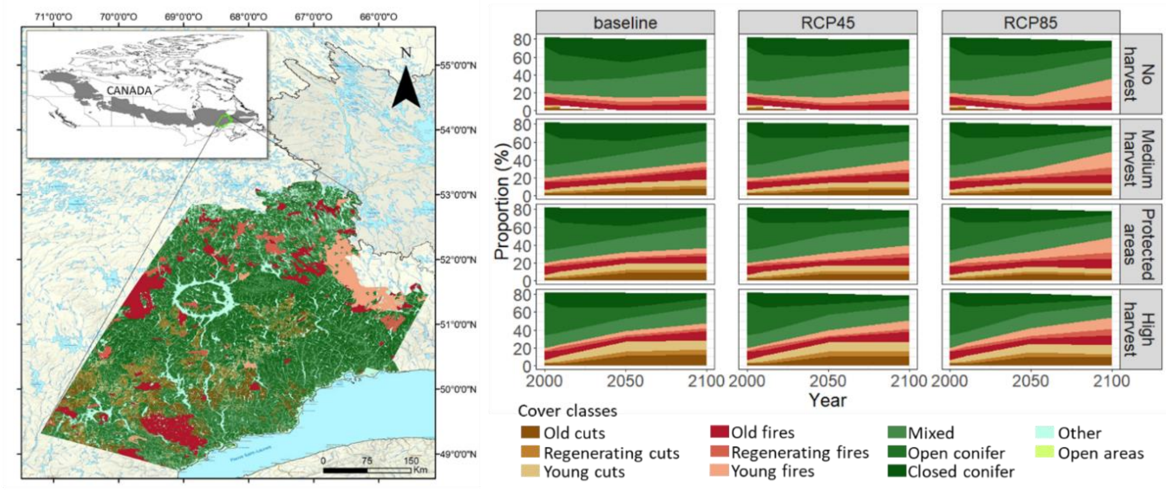

Figure 3.2. Temporal changes in land cover. Stacked trends in the proportion of cover classes for each of the four forest management scenarios under either baseline, RCP4.5 or RCP8.5 climate scenario. The remaining percent correspond to cover classes 'open' and 'other'.

Spatially explicit forest simulation model (Figure 3.1.1)

Climate scenarios

Future climate projections were based on two different radiative forcing scenarios, known as Representative Concentration Pathways (RCP, see Van Vuuren et al. (2011) for more information). We obtained future climate projections from the Canadian Earth System Model version 2 (CanESM2) ran under both RCP 4.5 and RCP 8.5. The ANUSPLIN method was used to downscale climate projection to a 10-km resolution (McKenney *et al.* 2013). Future mean annual temperatures are expected to increase between about 3°C (climate scenario RCP4.5) and 7.5°C (RCP8.5) in the study area by 2100 (compared with 2000), while average precipitation is projected to increase between 7% and 10% under RCP 8.5 and RCP 4.5 respectively (Boulanger *et al.* 2018). Monthly time series for each climate scenario (CC, baseline, RCP4.5, RCP8.5) were used to parameterize forest landscape simulations.

Forest landscapes 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 forest landscape model that dynamically simulates key forest ecosystem processes at both the stand- (e.g., tree establishment, growth, and competition) and landscape scales (Boulanger *et al.* 2018). It thus allows assessment of interacting ecological processes at broad spatial and temporal scales (Boulanger *et al.* 2018). This model has been thoroughly validated under various forest conditions (Boulanger *et al.* 2017; Taylor *et al.* 2017; Tremblay *et al.* 2018; Boulanger & Pascual Puigdevall 2021). A complete description of the model can be found in Tremblay et al. (2018). Forest landscapes were initialized for the conditions of year 2000 using the NFI attribute maps (Beaudoin *et al.* 2014) and provincial sample plots. Tree growth and regeneration as well as wildfires were climate-sensitive in simulations.

We simulated four forest management scenarios (i.e., land-use change scenarios, LUC, **Table 3.1**); 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 protected area scenario (Protected areas) consistent with the woodland and mountain caribou strategy 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 avoid caribou habitat and reduce rates of logging (Ministère des Forêts de la Faune et des Parcs 2019c). We integrated the protected areas and the adaptative logging rate within each targeted area to create temporary (50 or 150 years) or permanent conservation areas where no harvesting occurred (Annexe F, **Figure F 1**). In the remaining of the area, harvest rates were parameterized according to those proposed by the MFFP under this plan (varied between 3.3 and 10.6% per 10 years by forest management unit). Protected patch size varied between 0.06 km² to 2 037 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 to be harvested. 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 landscapes 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 steps. Except for scenarios involving the baseline climate, climate-sensitive parameters were allowed to change in 2010, 2040 and 2070, according to the climate corresponding to each forcing scenario (Boulanger & Pascual Puigdevall 2021). For the next steps of the analysis, we used landscapes resulting from LANDIS-II models for the years 2000 and 2100.

Table 3.1. 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 are 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	RCP4.5-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	RCP8.5-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

Habitat characteristics of simulated landscapes

To estimate forest composition and create 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) from the LANDIS-II biomass outputs. As LANDIS-II does not directly output crown closure, we used the random forest model built in Labadie et al. (2022) to predict crown closure covariate. The model was then applied on LANDIS-II outputs to predict crown closure all along the simulation, for each cell by using simulated species-specific biomass and stand age. Using species group and predicted crown closure, we created five land cover 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 updated every year by adding roads, recent (≤10 years), regenerating (11-20 years) and old (21-50 years) cuts/burned areas that LANDIS-II simulated.

Analysis of landscape structure and composition.

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) caribou management plan, disturbance levels were calculated as the percentage of nonoverlapping area of burns, roads, and cuts. Disturbed areas also included a 500-m buffer zone on each side of roads and around cuts. The proportion of total disturbances, burned areas and deciduous vegetation associated for each simulation was represented in Annexe F, **Table F 1**.

Landscape configuration metrics resulting from LANDIS-II simulations were calculated using 'landscapemetrics' package in R (Hesselbarth *et al.* 2019). We selected two metrics that reflect complementary aspects of landscape structure and may mediate responses to LUC and CC. At the patch level, we calculated the mean 'isolation index' (calculated as 1 – 'cohesion index'), characterised as the connectedness of patches belonging to a land cover class. If the value of the 'isolation index' was close to 0 implied that patches of the same class close to one another, whereas an increase in the value indicated that patches became isolated (Annexe F, **Table F 1**). The isolation index is used here as a proxy of the fragmentation and loss of the mature conifer stands. At the landscape level, we calculated the 'homogenization index' (calculated as 1 / 'conditional entropy', characterised as the complexity of a landscape pattern configuration). If the value of the 'homogenization index' is small, cells of one category are adjacent to cells of many other categories. Conversely, high 'homogenization index' values show that cells of one category are predominantly adjacent to only one other category of cells (Annexe F, **Table F 1**).

Movement rules derived from radio-collared caribou, moose and wolves (Figure 3.1.2.1)

To determine the effectiveness and 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). To identify species-specific movement rules in the IBM, we used empirical data collected for caribou, moose, and wolves over the study area.

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, the period of relatively high caribou mortality (Losier *et al.* 2015; Labadie *et al.* 2021). To test predictions based on whether individuals change their movement behaviour 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 8-h interval) using conditional logistic regression (see details in 2.4. Materials and Methods - *Movement rules derived from radio-tracking caribou, moose and wolves*) (Fortin *et al.* 2005). Details on GPS data and SSF models can be found in Annexe C: Data partitioning in Chapter 2 and 3. and Annexe D: Details of the calibration and validation of IBM in Chapter 2 and 3.

Habitat was characterized from 2004 to 2018 using the Canadian NFI forest cover maps (Beaudoin *et al.* 2014). To estimate forest composition, the relative proportions of species groups (conifer and deciduous species), treed land and tree crown closure maps from these NFI data were used. Five land cover classes were created as detailed in *Habitat characteristics for simulated landscapes* (above). Land cover maps were updated every year by adding roads, recent (≤10 years), regenerating (11-20 years) and old (21-50 years) cutblocks/burned areas based on information provided annually 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). Ages of forest stands (average age at the year of the survey) originating from natural disturbances or forest harvesting, and the distance to the nearest burned patch were also assessed within the pixel.

Individual-based model (IBM) (Figure 3.1.2.2)

A complete description of the model and how it was parameterized, calibrated, and validated can be found in the Annexe D: Details of the calibration and validation of IBM in Chapter 2 and 3. Below, we outline the major model components.

To determine the effectiveness of management strategies, 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 scenarios (see details in 2.4. Materials and Methods - *Individual-based model (IBM)*, and Annexe D: Details of the calibration and validation of IBM in Chapter 2 and 3). 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 forest landscape model for projections. The IBM simulated individual movements and interactions between prey and predators. Movements and predation events depended on species and landscape characteristics (see details in 2.4. Materials and Methods - *Individual-based model (IBM)*, and Annexe D: Details of the calibration and validation of IBM in Chapter 2 and 3). Empirical movement rules were determined using SSFs described in Annexe D: Details of the calibration and validation of IBM in Chapter 2 and 3 (Fortin *et al.* 2005) specific for each species. Prey could only die from predation, and they were then removed from the simulation. Simulations accounted for the typical numerical response of moose that follows forest harvesting (Potvin *et al.* 2005; Anderson *et al.* 2018), and the subsequent increase in wolf density (Messier 1994)(see details in 2.4. Materials and Methods - *Individual-based model (IBM)*, and Annexe F, **Table F 2**).

To model wolf, moose and caribou movements, and estimate wolf predation rate under the different scenarios, we ran the IBM for 1 year in years 2000 and 2100, with ten replicates. We thus ran a total of 130 simulations. We used one output of LANDIS-II simulation model per combination of CC and LUC scenario because we were more interested by the uncertainty of the IBM than of the forest landscape model. 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 outputs of individual-based models (Figure 3.1.2.3)

The cumulative impact of LUC and CC on the effectiveness of conservation strategy was thus assessed by comparing the simulated caribou mortalities predicted by the IBM in various CC and LUC scenarios.

To test how changes in forest structure and composition impacted the proportion of caribou killed (i.e., the 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 each covariates 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. For each generalized linear mixed model, we included a random intercept for scenarios.

Bird and beetle occurrence data (Figure 3.1.3.1)

We characterized boreal biodiversity based on predictive models of occupancy of birds and beetles previously developed from field observations (Bouderbala *et al.* 2022). For birds, models were based on presence-absence data from the Atlas of Breeding Birds (Regroupement QuébecOiseaux 2018). All birds were identified at the species level. For beetles, species abundance databases 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 presence-absence databases. For beetles, species-level identifications were used when possible; otherwise, the identification to the genus level was standardized (92% initial identifications were at the species level).

Species distribution models (Figure 3.1.3.2)

Bouderbala et al. (2022) previously developed species distribution models for 31 bird species and 77 beetle species (specific species are listed in Annexe G, **Table G 1**), which we used to evaluate umbrella value of management strategies designed around the needs of boreal caribou. Briefly, these models only included species that were recorded at ≥ 1% and ≥ 5% of all sites for birds and beetles, respectively, and that also had high goodness-of-fit (i.e., Area Under the Curve 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 generalized linear mixed models with a random intercept to account for differences among sampling years (see Bouderbala et al. (2022) for more details).

We used similarities in predicted probability of occurrence, combined with expert opinion to classify bird species according to their main habitat associations (mature forests or early-to-mid succession forests, Annexe G, **Table G 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 bird species were associated with mature forests, 20 with early-to-mid succession forests and 4 were considered generalist. Knowledge regarding beetle habitat associations was too scarce to allow similar classification and further habitat-related investigations. We then computed the occurrence probability maps of each species for each scenario (**Table 3.1**).

Analysis of outputs of species distribution models (Figure 3.1.3.3)

Impacts of LUC and CC on species assemblages were assessed by comparing species occupancy and species assemblage dissimilarity under each CC and LUC scenario in 2100. We predicted the 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*:

$$P_{s_{jk}} = \frac{\sum_{pixels} \log\left(p_{s_{jk}} + 1\right)}{N_{pixels}}$$

We evaluated the percent change in P_s between the reference scenario (No harvest under climate *j* scenario, Table 3.1) and each of the climate *j* and forest management scenario *k*, as:

$$\Delta P_{s_{jk-jref}} = \frac{P_{s_{jk}} - P_{s_{jref}}}{P_{s_{jref}}} \times 100$$

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 dissimilarity of species assemblages). Biodiversity change was calculated from the equation:

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

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

$$BC_{jk} = \frac{\sum_{species} \left|P_{s_{jk}} - P_{s_{jref}}\right|}{\sum_{species}(P_{s_{jk}} + P_{s_{jref}})}$$

where $P_{s_{jk}}$ and $P_{s_{jref}}$ 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.* 2020a).

To test how changes in forest structure and composition impacted the biodiversity change (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 biodiversity change is an index that compare two scenarios (scenario *jk* compared to the scenario of reference, **Table 3.1**), we calculated the percentage of change of each covariate of forest characteristics following:

$$Percentage\ of\ change\ (Covariate_{x_{jk}}) = \left(\frac{Covariate_{x_{jk}}}{Covariate_{x_{jref}}} - 1\right) \times 100$$

where $Covariate_{x_{jk}}$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 RCP8.5-Medium harvest and the value of the mean stand age of the landscape under the reference scenario (RCP8.5-No harvest, **Table 3.1**). This method was used to get a direct assessment of the effects of LUC while controlling for CC.

Umbrella effectiveness of a conservation strategy under global change (Figure 3.1.4)

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 management strategy effectiveness, 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 3.1**). 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.

3.3. Results

Projection of forest covers

LUC and CC changed the composition of boreal landscapes by initiating widespread secondary succession (**Figure 3.2**) and decreasing the proportion of old forests. The average stand age across the landscape was 97-, 71-, 66- and 53-year-old under Baseline-No harvest, Protected areas, Medium and High harvest scenarios respectively. Under each climate scenario, the proportion of post-harvest stands < 50-year-old were similar under the Medium harvest and Protected areas scenarios. Simulation outputs of Medium harvest and Protected areas scenarios were similar: at the end of 100 years, both scenarios ended up with comparable amounts of most forest age-class types and habitat available for species (**Figure 3.2**). CC also altered landscape composition mainly through important surge in area burned. 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, Populus tremuloides*) 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 (**Figure 3.2**). 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 RCP8.5 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).

Effectiveness of forest management on boreal caribou mortality

We determined the effectiveness of boreal caribou management strategies 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 creation of protected areas (Protected areas scenario) was equivalent as the proportion of caribou killed was nearly the same under both scenarios (Annexe H, **Figure H 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 would also impact 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) (Annexe H, **Figure H 2**). An overall increase in stand age is predicted to reduce the proportion of caribou killed by wolves (Pearson's correlation r = -0.83, $P < 0.01$) (Annexe H, **Figure H 2**).

Most important forest variables explaining bird and beetle presence

The probability of occurrence was significantly influenced by stand age, especially for bird species (Annexe G, **Table G 1**). This variable was selected for 14 (70%) bird species associated with early-to-mid succession forests, 4 (57%) bird species associated with mature forests, and 29 (38%) beetle species. Additionally, the proportion of cuts of at least one of the three age classes, was selected for 13 (65%) bird species associated with early-to-mid succession forests, 5 (71%) bird species associated with mature forests, and 28 (36%) beetle species (Annexe G, **Table G 1**). For those 5 bird species associated with mature forest, 80% were positively associated with the proportion of cuts older than 20-year-old or negatively associated with younger cuts (excepted for White-winged Crossbill, *Loxia leucoptera*), or both. On the 13 bird species associated with early-to-mid succession forests, 62% were positively associated with the proportion of cuts younger than 20-year-old.

Projected bird and beetle occupancy following climate change and forest management

Our situation indicates that, compared to the uncut landscape (No Harvest), approximately the same number of beetle species should decrease and increase their probability of occurrence in landscapes altered by the three forest management scenarios (i.e., Protected areas, Medium and High harvest scenarios), regardless of CC (**Figure 3.3**). 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 No harvest scenario, regardless CC (**Figure 3.3**). The great majority of increasing species were early successional species (94% associated with young forest and/or harvested forest ≤ 20-year-old; Annexe G, **Table G 1**). The highest decrease in the probability of occurrence was for bird species associated with mature forests, with the highest decrease under High harvest scenario, regardless of CC (**Figure 3.3**). Those species were associated with old forests and/or harvested forests older than 20-year-old (Annexe G, **Table G 1**). In addition, 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 a larger decrease in their probability of occurrence with CC, resulting in a larger negative percentage of changes in species index occupancy (**Figure 3.3**).

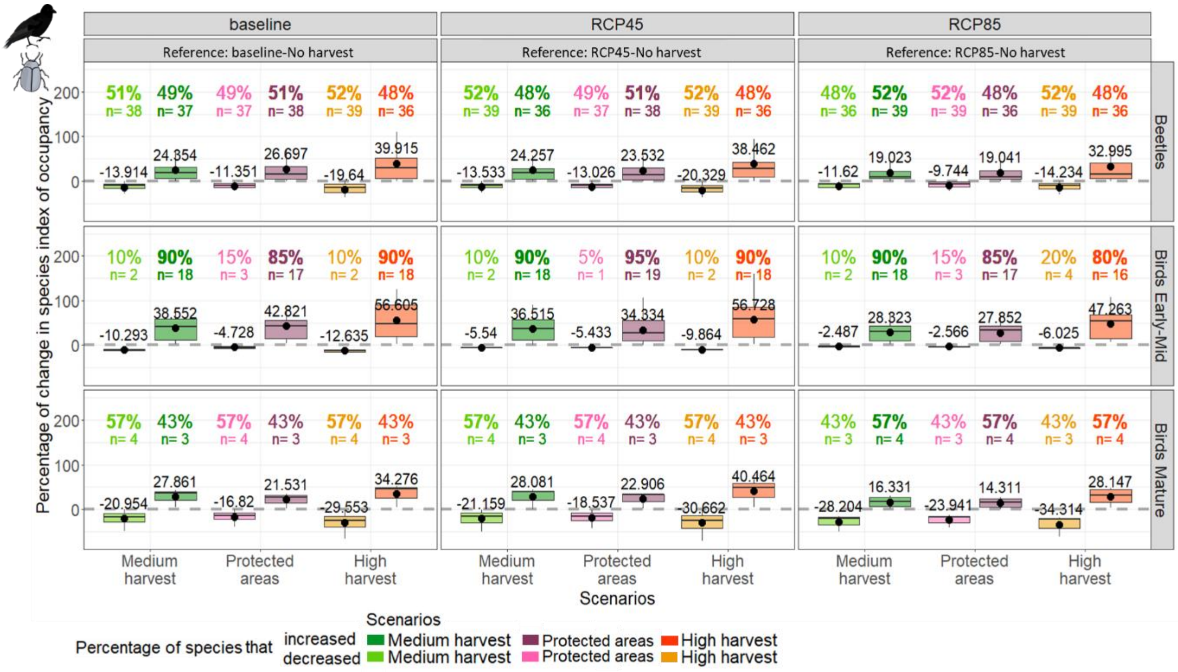

Figure 3.3. Percentage of change (boxplot) in species occupancy index between the harvested landscapes and the uncut landscape (No harvest) in 2100. Black points represent the mean percentage of change in species occupancy index and error bars represent 95% confidence intervals. Colored values represent 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 pair of declining and increasing species occurrence equal 100%. The grey dashed line represents a percentage of change in species index of occupancy equal to zero.

Variations in bird and beetle community 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 3.2**). Biodiversity change increased with increasing forest harvesting rates for all taxa (**Table 3.2**). 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% more species dissimilarity under RCP8.5 and RCP4.5 respectively than under no climate change (Annexe H, **Table H 1**). 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 (Annexe H, **Table H 1**).

More precisely, biodiversity change (JDI) increased with the proportion of cuts and roads (Pearson's correlation r = 0.88, $P < 0.01$) and deciduous vegetation (Pearson's correlation r = 0.95, $P < 0.01$) (**Figure 3.4**). Biodiversity change decreased, however, as landscapes become increasingly comprised of older forests (Pearson's correlation r = -0.90, $P < 0.01$) (**Figure 3.4**). 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, $P < 0.01$) (**Figure 3.4**). Our analysis did not detect a significant/strong link between the proportion of burned areas, the isolation of mature conifer stands and biodiversity change (Pearson's correlation r = 0.30, $P = 0.43$ and Pearson's correlation r = 0.62, $P = 0.07$, respectively) (**Figure 3.4**).

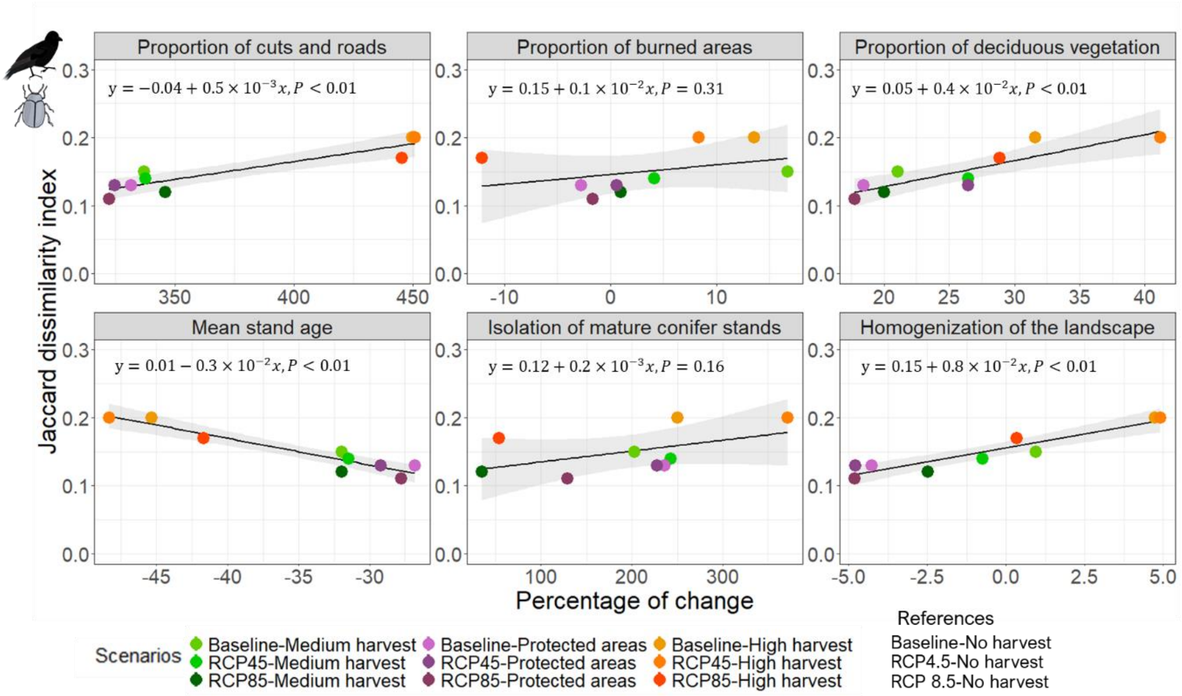

Figure 3.4. Change in biodiversity shown through the Jaccard dissimilarity indices (JDI) of animal species assemblages (all taxa combined) comparing landscape characteristics (Proportion of cuts and roads, Proportion of burned areas, Proportion of deciduous vegetation, Mean stand age, Isolation of mature 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.

Table 3.2. 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	RCP4.5-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	RCP8.5-No harvest
RCP85- Medium harvest	0.16	0.11	0.09	0.12	
RCP85-High harvest	0.21	0.16	0.12	0.17	

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 = 0.89, $P < 0.01$, **Figure 3.5**), which implies that bird and beetle community are less impacted (i.e., lower JDI) when conditions are more suitable for caribou survival (lower mortality). Compared to the current practice (High harvest scenario), biodiversity change and boreal caribou mortality decreased when a management strategy was implemented (**Table 3.2**, Annexe H, **Figure H 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 (Annexe H, **Figure H 3** and **Table H 1**). These results demonstrate that the effectiveness of management strategies also depends on the cumulative impacts of CC and LUC.

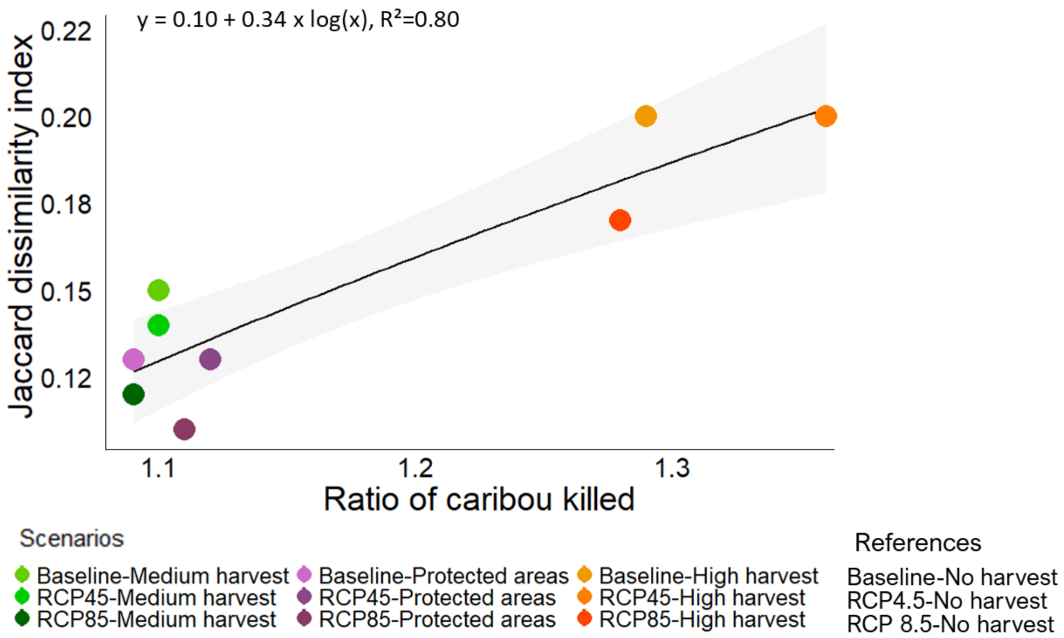

Figure 3.5. Change in biodiversity shown through the Jaccard dissimilarity indices (JDI) of animal species assemblages (all taxa combined) comparing the ratio of the proportion of caribou killed by wolf to the reference landscape in 2100. The reference scenarios used to calculate the biodiversity change and the ratio of caribou killed were the same. The grey ribbon indicates 95% CI.

3.3. Discussion

This work highlights future cumulative effects of climatic and land-use on forest characteristics, animal communities, and the umbrella value of boreal caribou management strategies to biodiversity conservation. Our results show a complex interplay among changes in vegetation structure and composition, boreal caribou mortality and biodiversity assemblages (**Figure 3.4**, Annexe H, **Figure H 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 a management strategy with lower impact on boreal caribou populations (Medium harvest and Protected areas scenarios) should also be more effective at preserving bird and beetle communities, but we further predict that their effectiveness 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 around the needs of boreal caribou can serve as an effective umbrella for conserving sufficient high-quality habitat of co-occurring species. We thus demonstrate that single-species management 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 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 per se. The second one, Protected areas, was simulated to evaluate the effect of the creation of specific conservation areas, aiming at minimizing the threat of anthropogenic disturbances while maximizing patches of high habitat quality for boreal caribou. The creation 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 in complex landscape with large mature stands (i.e., landscapes under conservation strategy scenarios). Previous studies have reported that landscape complexity have a positive effect on biodiversity (Janssen *et al.* 2009), and could be used to manipulate species interactions (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, cumulated with forest harvesting, are expected to be important drivers of landscape changes and subsequently of boreal community changes. 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 occurrence (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 (Annexe F, **Table F 2**), and consequently the predation risk for boreal caribou (Serrouya *et al.* 2021). Therefore, our simulations show a higher impact of forest composition on caribou mortality through apparent competition compared to the change in forest structure (Labadie *et al.* 2022). Management strategies that are expected to decrease the proportion of deciduous vegetation are thus predicted to be more effective with a higher 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 communities (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 community 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 to more deciduous vegetation represents not only a large change in forest composition but also a major net loss of old growth stands that many forested species depend on. 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 the western Canada (Schneider, Richard *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 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 in their probability of occurrence; while bird species associated with early-to-mid succession forests would have the highest increase in their probability of occurrence and would be more favored in this context of global change. 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 & Gauthier 2018). Strategies aiming at maintaining old-growth stands should thus have a higher umbrella value.

We show that management strategies decreased caribou mortality and biodiversity change compared to the current practice of forest harvesting, highlighting that the key factor to preserve boreal biodiversity is to reduce the level of forest harvesting at the regional scale. We show that a management that reduces the proportion of cuts, through the reduction of the level of forest harvesting per se or the creation of protected areas, should also avoid 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 the level of cuts, and consequently the decrease in their encounter rate with wolves, allows to reflect conditions at multiple levels (i.e., stand, landscape, and ecosystem) leading to the protection of a large number of other species.

In conclusion, while there are many uncertainties surrounding global change effects, 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 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 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 & Wildlife Service 1973; Government of Canada 2002). In this context, our study highlights that surrogate species, such as umbrella species, that benefit from governmental action plans may thus serve as a catalyst for research to inform approaches for biodiversity conservation.

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Conclusion générale

This thesis brings a better knowledge of the direct and indirect impacts of climate and land-use changes, through shifts in environmental characteristics, on species living in low productive environment, and how they ricochet within the food-web. More specifically, my work highlights the impacts of global change, through the increase in natural and anthropogenic disturbances, on trophic interactions and survival of boreal caribou. My project also provides new insight on the umbrella value of boreal caribou recovery strategy for the conservation of regional biodiversity in the context of global change. The increasing impact of human activities and natural disturbances on the planet means that many animal populations find themselves confronted with more fragmented and disturbed landscapes (Rands *et al.* 2010; Cardinale *et al.* 2012), as this is the case for the studied system. The consequences of climate change on boreal forest, with the increase in wildfires and insect outbreaks (Régnière et al. 2012, IPCC 2021), cumulated with anthropogenic disturbances create a huge challenge in making conservation plan. In this thesis, I focused on how behavioral ecology combined with spatial ecology can be used to define individual space-use and trophic interactions. One of the objectives was to provide concrete elements for a more effective management of wildlife and how to preserve biodiversity integrity in a context of global change. For example, I demonstrated how the increase in the availability of resources for moose through natural and anthropogenic disturbances, and the subsequent numerical responses of moose and wolves can trigger wolf-caribou-moose system. I also showed how some forest characteristics can be used to buffer the negative effects of climate and land-use changes. In this general conclusion, I begin with a discussion of the contributions of my work to ecology and wildlife management, followed by an exploration of the limitations of my study and future research prospects.

1. Contribution to ecology and wildlife management

1.1 Trophic propagation

Chapters 1 and 2 provide evidence that the increase in resource availability for moose propagates through food chains from herbivores to large carnivores. In the 1st chapter the increase in resource availability was partly induced by an insect outbreak and salvage logging, while in the 2nd chapter it was induced in the simulations by cumulative effects of natural (wildfires and insect outbreaks) and anthropogenic (forest harvesting) disturbances. In both chapters, I showed that variation in the rate of boreal caribou mortality was largely explained by the proportion of deciduous vegetation in the landscape, which affected local moose and wolf density, and consequently the predation risk. My results highlight the amplification of an indirect effect, the apparent competition, due to the increasing resource availability for moose. These results coincide with some other studies. For instance, in a low productive environment, such as in arctic, a change in trophic interactions following tundra greening was observed (Ims *et al.* 2019). Predator-mediated apparent competition has also been described in many other low productive systems, such as in semi-arid island (Roemer *et al.* 2002; Thomsen *et al.* 2018), or savanna ecosystems (Ng'weno *et al.* 2019), and would also be highly impacted by global changes, as my findings suggest.

In Chapter 1, I provide empirical evidence that an insect outbreak increases the availability of deciduous vegetation, generating a suite of spatial and demographic responses in moose, wolves, and boreal caribou indicative of disturbance-mediated apparent competition (Seip 1992; Serrouya *et al.* 2015). Pulses in the abundance of a species would destabilize a community when it induces a strong change in the abundance of other species or alters interaction frequencies (MacArthur 1955; Tylianakis & Morris 2017). In fact, by propagating through feeding links, even small changes can significantly impact ecological communities with increased risks for the stability of food webs (Montoya *et al.* 2009). Although insect outbreaks often disturb larger areas than wildfires and logging in boreal forests (Ressources naturelles Canada 2018), this impact on trophic interactions has been overlooked by researchers. My project was the first to evaluate the impact of an insect outbreak on survival of boreal caribou through direct and indirect food-web interactions. My results for this chapter have three major implications. First, while some studies showed changes in species distribution induced by insect outbreaks, I demonstrated cascading effects implying the entire food-web. Indeed, I showed that changes in the strength of interactions in one food web (SBW-conifer) can shape the properties of another (plant-caribou-moose-wolf). Second, my results bring new recommendations for boreal caribou management. Through the light of my results, I strongly recommend considering insect outbreaks as a natural disturbance which can negatively affect boreal caribou survival and to distinguish salvage logging from other cuts. The third major implication of my findings is particularly critical in the context of global change. Top-down and bottom-up control mechanisms that regulate ecological communities can potentially be altered by both anthropogenic disturbances and climate change (Barton *et al.* 2009; Muhly *et al.* 2013). By integrating the combined effects of insect outbreak simultaneously with other natural and anthropogenic disturbances, my study highlights how multiple disturbances can act cumulatively on a boreal system by altering the density, behavior and interactions of species at higher-trophic level. Differences in the impacts of clear-cuts and salvage logging reported in Chapter 1 also indicates that interactions between natural disturbances and anthropogenic disturbances can be expected (Lindenmayer & Noss 2006; Leverkus *et al.* 2018). In our case, spruce budworms could increase soil fertility by spreading their feces (Schowalter *et al.* 1986; Zimmer & Topp 2002), with the consequence that deciduous vegetation may growth faster and reach higher biomass in stands that have been more heavily impacted by the insect. This hypothesis could explain the higher moose density that we observed in salvage logged stands (Chapter 1).

We often fail to include human manipulations of food webs. As a node in the trophic network, however, humans clearly play important roles as a consumer, competitor, but also mutualist of other species. Accounting for the implications of humans on food web dynamics may not only help to clarify the ecological and socioecological costs/benefits of management strategies around focal species like boreal caribou, it may also help minimize unintended consequences of our decisions. The latter may include how salvage logging or herbicide applications and planting of disturbed forests to benefit one tree species over others can interrupt natural successional dynamics with unintended indirect effects on other species (Eveleigh *et al.* 2007).

1.2. Impact of global change on trophic interactions

The effects of climate change on species can be mediated by the environmental context (e.g., anthropogenic disturbances) and have community and ecosystem-level consequences (Laws 2017; Bartley *et al.* 2019). For example, in Chapter 1, I found that the impact of spruce budworm outbreak was exacerbated by salvage logging. Furthermore, my findings in Chapter 2 showed a cumulative effect of land-use and climate changes, through changes in forest composition and structure. However, land-use change had an earlier and stronger effect compared to climate change on trophic interactions and caribou survival. My project provides examples of cumulative effects (Riffell *et al.* 1996) between natural and anthropogenic disturbances on food web properties. As also highlighted by other studies (Mantyka-pringle *et al.* 2012; Northrup *et al.* 2019), it is a critical advancement to project both effects of climate and land-use changes, and I suggest that projections ignoring cumulative, even synergisms, between climate and land-use changes likely underestimate negative consequences on ecological communities.

I provide strong evidence that the numerical response of moose and wolves is the key determinant of mortality rates of caribou compared to the behavioral response of prey and predators and would strengthen over time in a changing climate and forest landscape. Conservation actions aimed at maintaining species affected by apparent competition should thus focus on the major driver that cause species decline at short-term: the numerical response of alternative prey and predators driven by land use changes. In some areas, control of alternative prey and predators have been implemented (Roemer & Donlan 2004; Wittmer *et al.* 2013), but this strategy can be effective only if it is combined with a longer-term solution, such as reductions in habitat alteration (Robichaud & Knopff 2015; Serrouya *et al.* 2019). Indeed, in all my chapters, I demonstrate that changes in landscape structure and composition induced by natural and anthropogenic disturbances have a large impact on species occurrence and trophic interactions. Changes in species assemblage can have tremendous impacts by altering community size, composition, and structure, especially if keystone species are affected or if there is an ecological drift of dominant species (Jackson & Blois 2015). Such changes in species assemblage can in turn trigger ecosystem services and resilience (Pecl *et al.* 2017). An important finding of my project is that human activities, through land-use change, have a stronger impact compared to natural disturbances. For example, in the Chapter 3, I highlighted that it would not be possible to maintain regional biodiversity if the level of forest management stays at its current rate. However, with a reduction of forest harvesting (by creating more protected areas, or by decreasing the level of logging), it should be possible to maintain biodiversity and greatly decrease the mortality rate of caribou. An alternative to business-as-usual management with a reduction of logging rate, extension of the logging rotation period and an increasing in the area set aside from forestry may be essential to protect biodiversity (Bichet *et al.* 2016). Furthermore, these forest management actions would preserve non-timber ecosystem services in the boreal forest (Triviño *et al.* 2017).

My results showed the importance of maintaining complex landscape with low proportion of total disturbances. By acting on the reduction of anthropogenic activities, we can also act on climate change impacts and on the climate itself (Hansen *et al.* 2001). For example, during storm events, areas subject to logging activities with the associated construction of roads can be more affected by land sliding and flooding (Swanson & Dyrness 1975). An increased risk of drought can also be induced by the deforestation of large areas, because of the possible reductions in transpiration, cloud formation and rainfall (Segal *et al.* 1988; Dickinson 1991). Moreover, habitat management to restore predator-prey dynamics has also the benefit of enhancing boreal carbon conservation (Yona *et al.* 2019). My project thus provides evidence that strategies enhancing habitat complexity and reducing the isolation of high-quality habitat can potentially buffer the cumulated negative effects of climate and land-use changes. This could be an effective conservation plan for such specialist species of low productive ecosystems. I also recommend considering behavioral response of species but also their potential numerical response associated to changes in landscape composition, to better considerate environmental change impacts.

Resource pulses are expected to increase due to the cumulated direct and indirect effects of climate and land-use changes. In my project, I only focus on one resource pulse, the deciduous vegetation, but global change triggers a large and various amount of additional recourse pulses. For example, insect outbreaks also represent a resource pulse for birds (Martin *et al.* 2006; Venier & Holmes 2010). Species living in low productive system would be highly impacted, as their trophic interactions, with asymmetrical change in vegetation composition under global change (Wang & Friedl 2019; Wang *et al.* 2020). Although lichen is not a limiting resource for caribou in boreal forest, the increase in fire occurrence would cause long-term reduction in lichen availability (Rupp *et al.* 2006). Furthermore, climate and land-use changes are predicted to increase resource availability for moose resulting in an increased moose density. This would fundamentally alter the structure of the food webs involving boreal caribou, making indirect interactions stronger through apparent competition. Species vulnerability to climate change has been mostly determined through direct impacts induced by abiotic changes and less on indirect impact induced by changes in species interactions (Pacifici *et al.* 2015; Thomsen *et al.* 2018), although the latter may result in stronger effects on species than the direct abiotic effects (Ockendon *et al.* 2014). While there are an increasing number of studies that try to assess the impact of global change on species and their biotic interactions (Barber *et al.* 2018; Dey *et al.* 2018; Thomsen *et al.* 2018), it is extremely challenging to consider all drivers and effects of global changes, especially if the effects are indirect.

My project contributes to highlight the usefulness of cumulated approaches to have a better understanding on the current and future impact of global change on species and their trophic interactions. In Chapter 1, I combined telemetry data, aerial survey, and field sampling to demonstrate the impact of an insect outbreak on trophic interactions. Few studies have examined the combined effect of projected changes in land-use and in climate on multi-species trophic interactions. I contribute filling this gap in the Chapter 2 by combining a spatially explicit simulation model of forest landscapes and a spatially explicit, individual-based model of multiple species enmeshed in a boreal food web. The fact that we can link climate and land-use conditions to deciduous vegetation growth and to higher level, such as herbivore and predator food web, is a very strong facet and force of the combined use of these models. The major strength of this approach resides in the possibility to include main food web members, direct and indirect effects of disturbances and the complexity of the system. Indeed, simpler models are not able to integrate or underestimate impacts of the complex ecosystems and all their interactions. This can be explained by my results, such as those from other studies (Ferger *et al.* 2017; Northrup *et al.* 2019), showing that multiple disturbances can produce larger effects compared to single. Moreover, forest landscape and individual-based models can be used to test scenarios over large spatiotemporal scales. I used a 100-year window, which is quite long compared to the current forest planning time horizon of 5 years in Quebec (Ministère des Forêts de la Faune et des Parcs 2022). I also showed that climate change is expected to further impact the landscape and consequently boreal caribou after a certain time lag. Regarding this result, the 100-year period seems adequate to allow me to consider the effects of a changing climate as its effects on landscape (e.g., forest growth, proportion of burned areas) are predicted to become more pronounced by the end of this century, due to the lag in vegetation response (Kellomäki *et al.* 2008; Stralberg *et al.* 2015; Kellomaki 2017). This combined approach is a good tool to acquire a mechanistic understanding of the spatial distribution of animal populations in heterogeneous and dynamic environments. The results of these models can help identifying larger ecosystem characteristics and their expected change due to natural and anthropogenic disturbances such as determining potential regime shifts, ecosystem resilience, disturbance threshold, etc. However, while forest landscape models provide a range of useful information on vegetation types and disturbances, they are time-consuming and expensive to implement. My project will allow to reuse the projections we made to answer other questions on the boreal ecosystem within the study area. In the third chapter, I assess the consequences of global change on the umbrella value of management strategies designed to meet the needs of a single species for biodiversity conservation in a given biome. In addition to the combined approach used in the Chapter 2, I used species distribution models, with less detailed information than with boreal caribou populations, for two other taxa, to predict species range shift induced by global change. This combined approach allowed me to compare the consequences of four management strategies on species distribution or trophic interactions in a context of global change. It is thus a useful tool for managers and decision-makers according to environmental impact evaluation.

1.3. Umbrella species and global change

Understanding how global change affects not only single species, but entire food webs, is critical for anticipating shifts in ecological communities and the ecosystem services they provide. However, projections of the cumulative impacts of climate and land-use changes on species become more and more difficult as many studies suggest considering trophic interactions (Filazzola *et al.* 2020), environmental changes (Sentis *et al.* 2017), multiple disturbances (Northrup *et al.* 2019), resource availability (Stoner *et al.* 2018), dispersal ability (Barbet-Massin *et al.* 2012), energy expenditure (Semeniuk *et al.* 2012), and more. The results I showed in Chapter 3 allow to have another perspective. I test a methodology to quantify the impact of various forest management cumulated with climate change, which can be used to define appropriate planning guidelines for biodiversity conservation, including boreal caribou. My analyses did not measure how well boreal caribou perform as umbrella species to other possible species, but rather they assessed the effectiveness and umbrella value of management strategies planned around the needs for a single species. More precisely, I evaluated the efficiency of management strategies on their ability to maintain species assemblages and species mortality rate typical of an uncut landscape subject only to natural disturbances. More than the species-specific richness or abundance, it is the assemblages of species and the maintenance of their biotic interactions that partly regulate the functioning of an ecosystem and its capacity for resilience (McCann 2000). I used multiple measures to characterize environmental changes, such as the proportion of disturbances, and deciduous vegetation, but also the isolation of mature conifer stands and an index of landscape heterogeneity. This approach was necessary to evaluate the impact of global change on the umbrella value of boreal caribou management strategy in protecting larger community (Thornton *et al.* 2016). The occupancy indices developed in this third chapter allow to predict the decline of species associated with mature forest and the dissimilarity in species assemblages according to various management and climate scenarios. My findings are consistent with recent studies showing that either no management or less-intensive harvesting regimes benefit biodiversity (Triviño *et al.* 2017) and ultimately boreal caribou (Bichet *et al.* 2016). Caribou conservation management can conserve sufficient high-quality habitat for other cooccurring species depending on old-growth forest. Because boreal forest is highly affected by disturbances, mixed stands are expected to always be present in the landscape, and benefit to species associated with deciduous vegetation. Boreal caribou conservation can thus provide substantial umbrella coverage for the sympatric community and benefits well beyond protection of a single species (Caro 2010; Thornton *et al.* 2016). To integrate ecosystem complexity adequately, I focused on a specific species and its food web, as well as on the environmental characteristics of the study area. Indeed, I determined how global change, through the increase in wildfires and forest harvesting, can affect landscape composition, stand-age and heterogeneity and the long-term dynamics of critical forest structure (e.g., isolation of mature conifer stands). Furthermore, I determined that global change and the consequent changes in environmental conditions threaten boreal caribou populations by altering trophic interactions, and concurrently influence entire assemblages of taxa, such as birds and beetles. My findings thus support that single-species and ecosystem-based approach can provide complementary biodiversity conservation strategies (Lindenmayer *et al.* 2007; Caro 2010; Thornton *et al.* 2016).

My project focuses on boreal caribou as an umbrella species, which allowed me to provide new information on its conservation. General guidelines for habitat management of boreal caribou require a level of landscape disturbance not exceeding 35%. Under the baseline climate scenario, I projected that landscape disturbance would range between about 58% (under the Protected areas scenario) and 71% (under High harvest scenario in 2100, which apply the current rate of forest harvesting in the province of Quebec). Of this total percentage of disturbances, only 17% and 19% respectively were attributed to wildfires. These results highlight the urgent need to project the consequences on forest management in the long term. Once a stand is logged or burned, it will be characterized as disturbed for at least 40 years (Environment Canada 2011) and is thus predicted to have a long-term effect on the ecosystem. Contrary to wildfires, or other natural disturbances, forest harvesting and especially salvage logging, can disrupt post-disturbance succession (Leverkus *et al.* 2020), removes many unique biological legacies (i.e., persisting living and dead forest structures), and reduces habitat quality of wildlife (Lindenmayer & Noss 2006; Norvez *et al.* 2013; Thorn *et al.* 2018). Salvage logging may have a higher negative impact than clear-cutting because salvage logging constitutes a sequence of disturbances, where natural disturbance and logging interact (Leverkus *et al.* 2018). I strongly recommend considering species behavior, population survival and trophic interactions when creating general guidelines for the conservation of a species. While it is important to determine a maximum threshold level of landscape disturbance, my study highlights the necessity to consider the entire system with predator and apparent competitor. Indeed, in Chapters 2 and 3, the simulation without harvesting (i.e., 25% of total disturbances within the landscape) predicted 19% of caribou mortality in 2100, under the baseline climate scenario. Even with a proportion of total disturbances under the recommended threshold of 35%, I project a significant decline of boreal caribou. When focusing solely on the population level, it is thus possible to neglect the mechanisms causing changes in population dynamics and potentially ignore critical threats leading to their decline. I highlighted that changes in environment characteristics, such as forest composition and structure, would impact the behaviors of individuals, and would also result in some species numerical response subsequent to the change in vegetation composition. Ultimately, global change creates a potentially daring conservation situation: boreal caribou populations are trapped within an historical range that is collapsing between intensive anthropogenic disturbances in the south and areas occupied by migratory caribou in the north with different behaviors anti-predatory strategies.

2. Future research prospects

2.1. Spatially explicit models

This study showed important effects of landscape composition and structure on predator-prey interactions within the caribou-moose-wolf system. The individual-based model I used was a simplification of the reality designed specifically to meet my objectives. Therefore, the model did not consider wolf territoriality and caribou site fidelity. It would be interesting to consider this behavior in the model on landscape use and trophic interactions. Furthermore, in the context of global change, species dispersal abilities and the possibility for species to disperse toward less extensive disturbed areas, would be important to consider. Due to the increase in disturbances, boreal caribou populations have already experienced range retractions from historical distributions and were pushed northward as forestry and other developments expand (COSEWIC 2002). In addition to the asymmetry in the resource availability between prey, apparent competition could be strengthened with an increase in other apparent competitors, such as other ungulates browsing deciduous vegetation. Indeed, change in trophic interactions is not limited to the response of a single generalist species; entire suites of species may respond and trigger changes in food web dynamics. For instance, in the caribou-moose-wolf system, global change has already induced a northward shift of coyote, a potential predator, and deer, a species that can carry the meningeal brain worm (*Paralephostrongulus tenuis*) that is lethal to caribou and moose. The arrival of either species can thus alter the current food web (Hody & Kays 2018; Kennedy-Slaney *et al.* 2018). This redistribution of new generalist species into systems previously devoid of their presence would trigger new trophic interactions (Bartley *et al.* 2019). It would thus be relevant to integrate the arrival of these new species in the individual-based model. It would also be possible to include in the IBM the manipulation of moose populations through hunting, to evaluate how it could alter the impact of climate and land-use changes on moose abundance, and ultimately on boreal caribou survival. This forced decrease in moose density aimed for the decrease in wolf density and, consequently, in the number of boreal caribou killed by wolves.

In the context of global change, climate change can also impact individual habitat selection through change in weather condition. For example, Tablado *et al.* (2014) demonstrated that changes in snow depth and ice condition led reindeer (*Rangifer tarandus*) to shift from their usually preferred high-elevation pastures to lowland forested areas, a riskier environment for calves. Within the study area, Courbin et al. (2009) found that boreal caribou and wolves selected areas with shallow snow, a behavior that can be altered by the future expected climate change. This change in habitat use was only linked to change in climatic conditions and was independent of disturbance-mediated apparent competition process. Weather conditions were not included in the individual-based model I used, but these recent studies highlighted the importance to consider climatic variations which affect predator-prey interactions. Moreover, a more direct effect on caribou survival can be induced by climate change that are not mediated by predation (DeMars *et al.* 2021). For instance, meteorological changes may influence energy expenditure and resource availability and consequently impact individual survival (DeMars *et al.* 2021). The effects of climate change could therefore be underestimated in our projections in the Chapters 2 and 3.

The spatially explicit models I used in Chapter 2 and 3 can offer a decision support system. The modeling approach developed in the thesis is a way to identify and validate, on a credible scientific basis, the effectiveness of management strategies and to propose targets for the conservation of boreal caribou, or eventually for other species. Maintaining the total disturbance below the 35% threshold constitutes a biological basis for the guidelines of the federal action plan and the guidelines of Quebec (Équipe de rétablissement du caribou forestier du Québec 2013; Environment and Climate Change Canada 2018). The models I developed allow to test likely outcomes of management strategies that consider both disturbance levels and climate change. While this contribution is already important, it also would be useful to simulate different forest managements along a more detailed gradient in the level of disturbances to identify an effective conservation target (e.g., harvest level, and landscape structure and composition). These models would help to evaluate the effectiveness of proposed management strategies at maintaining or decreasing the total disturbance rate below the 35% threshold.

2.2. Species assemblages and umbrella species

In the Chapter 3, I considered that birds and beetles can change their occurrence only as a function of habitat changes. It would thus be relevant to add the species dispersal abilities in species distribution models to better predict change in species occurrence at the regional scale (Barbet-Massin *et al.* 2012). We also showed the importance of considering trophic interactions. It would thus be interesting to forecast bird distribution as a function of resource availability and other species, such as predators, in addition to environment variable. For example, insects are a resource for many bird species that can influence their probability of occurrence, particularly during insect outbreaks. Moreover, with the predicted impacts of environmental change on species interactions, we can anticipate changes in species abundances, distributions, and assemblages. The novel associations of species that have not co-evolved would result in new interactions and therefore could have detrimental impacts on the fitness of some species (Gilman *et al.* 2010). Consequently, exploring the response of species co-occurrence can provide additional insights into species interactions and how those interactions will impact the role of an umbrella species under global changes.

In the Chapter 3, conservation outcomes could be improved using multiple species as umbrella with heterogeneous ecological needs and sensitivities to different potential threats. Moreover, the use of multiple species could generate wider appeal and a more diverse representation of habitats and landscape elements (Roberge & Angelstam 2004; Veríssimo *et al.* 2014; Osgood *et al.* 2020). The use of umbrella species-complex could be a way to improve the effectiveness of both current and future conservation measures. Another interest to use species-complex is that species considered less charismatic, such as beetles, could benefit from the high charisma of other species, such as boreal caribou, which attract more conservation attention and funds. As I initiated with multispecies modelling, it would be interesting to test conservation scenario with other species to improve the evaluation, quantification, and prediction of the impacts that global change produces in ecosystems' properties (Ortiz *et al.* 2017). Furthermore, the dismantle of forest roads under Protected areas scenario was not simulated, although initially planed by the Ministère des Forêts de la Faune et des Parcs of Quebec (Ministère des Forêts de la Faune et des Parcs 2019c). While the effect of roads is well known for wolf-caribou interactions (Whittington *et al.* 2011; Leclerc *et al.* 2012), it remains to be investigated to what extent the forest roads impact species assemblage, and eventually detect more differences with scenarios that "only" decrease the level of harvesting.

In conclusion, my research project contributes to a long-standing interest in ecology regarding the impact of global change on biodiversity that are driven by changes in landscapes and interspecific interactions. Very few studies have examined the combined effects of projected changes in land-use and climate on multi-species trophic interactions, and more specifically the indirect impacts driven by interspecific interactions such as behavioral or numeric responses. I highlight the important effects of an asymmetrical change in resource availability, which can propagate within the food web. Determining changes in trophic interactions can also help to apply conservation actions to protect biodiversity in a context of global change. I show that multiple disturbances (i.e., wildfires, insect outbreaks, and forest harvesting) can act together to change the structure and the composition of the landscape and concurrently trigger trophic interactions and biodiversity integrity. While it is very challenging to consider all the drivers of global change, I show that anthropogenic disturbances are expected to have the earliest and highest impact compared to climate change-induced impacts. This has globally relevant and urgent implications for biodiversity conservation – focus first on reducing negative impacts of anthropogenic activities as an effective longer-term climate change biodiversity conservation strategy. Finally, my findings bring important advances to the development of management strategies that can balance human activities, climate change and biodiversity conservation.

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Annexe A: Supplementary results in Chapter 1 on caribou habitat selection

Table A 1. Summary of the habitat selection models of caribou that died and of caribou that remained alive during the study. Mixed-effects logistic regression models of habitat selection of a. 95 caribou which remained alive throughout the study b. 23 caribou which died during the course of the study during the winter period in the Côte-Nord region, Québec (Canada), with their selection coefficients (β); standard error (SE) and P value. Reference category is open conifer forest. SBW_{cut} represents areas infested by spruce budworm (SBW) for at least 1 year and then cut.

	a. Caribou (n=95 alive individuals)			**b. Caribou (n=23 dead individuals)**		
Variables	**β**	**SE**	***P* value**	**β**	**SE**	***P* value**
Conifer dense	-0.149	0.011	< 0.001	-0.380	0.018	< 0.001
Mixed	0.052	0.011	< 0.001	0.161	0.021	< 0.001
Open	0.144	0.012	< 0.001	0.169	0.028	< 0.001
Other	-1.193	0.011	< 0.001	-1.470	0.020	< 0.001
Burned (<5 years old)	-2.867	0.093	< 0.001	-2.913	0.450	< 0.001
Burned (6-20 years old)	-1.429	0.055	< 0.001	-1.885	0.448	< 0.001
Burned (≥ 21 years old)	-0.348	0.019	< 0.001	-0.502	0.029	< 0.001
Cut (<5 years old)	-0.458	0.027	< 0.001	-2.577	0.0128	< 0.001
Cut (6-20 years old)	-1.236	0.036	< 0.001	-0.841	0.0059	< 0.001
Cut (≥ 21 years old)	-0.033	0.068	0.629	-0.625	0.066	< 0.001
Distance to road	0.620	0.005	< 0.001	0.484	0.009	< 0.001
SBW cumulative severity	-1.682	0.621	0.007	0.585	0.366	0.110
SBW_{cut}	-2.383	0.466	< 0.001	-2.046	0.838	0.015

Random effects	**Variance**	**95% CI**	**Variance**	**95% CI**
SBW cumulative severity	22.489	(13.969, 36.240)	1.733	(0.801, 3.748)
SBW_{cut}	6.117	(3.411, 10.969)	6.166	(2.090, 18.182)

Annexe B: Supplementary information in Chapter 2

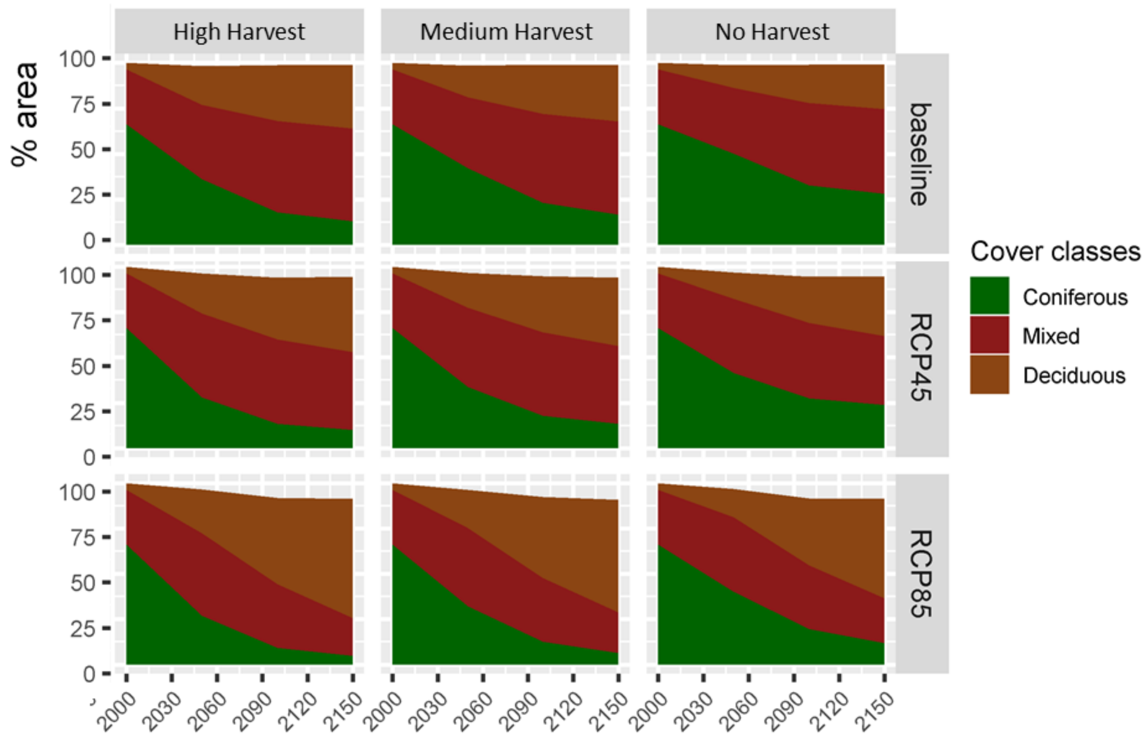

Figure B 1. Stacked trends in cover classes in the study area. The percentage of the area covered by the three cover classes were represented under either baseline, RCP 4.5 or RCP 8.5 climate scenario and under either High, Medium and No harvest land-use scenario.

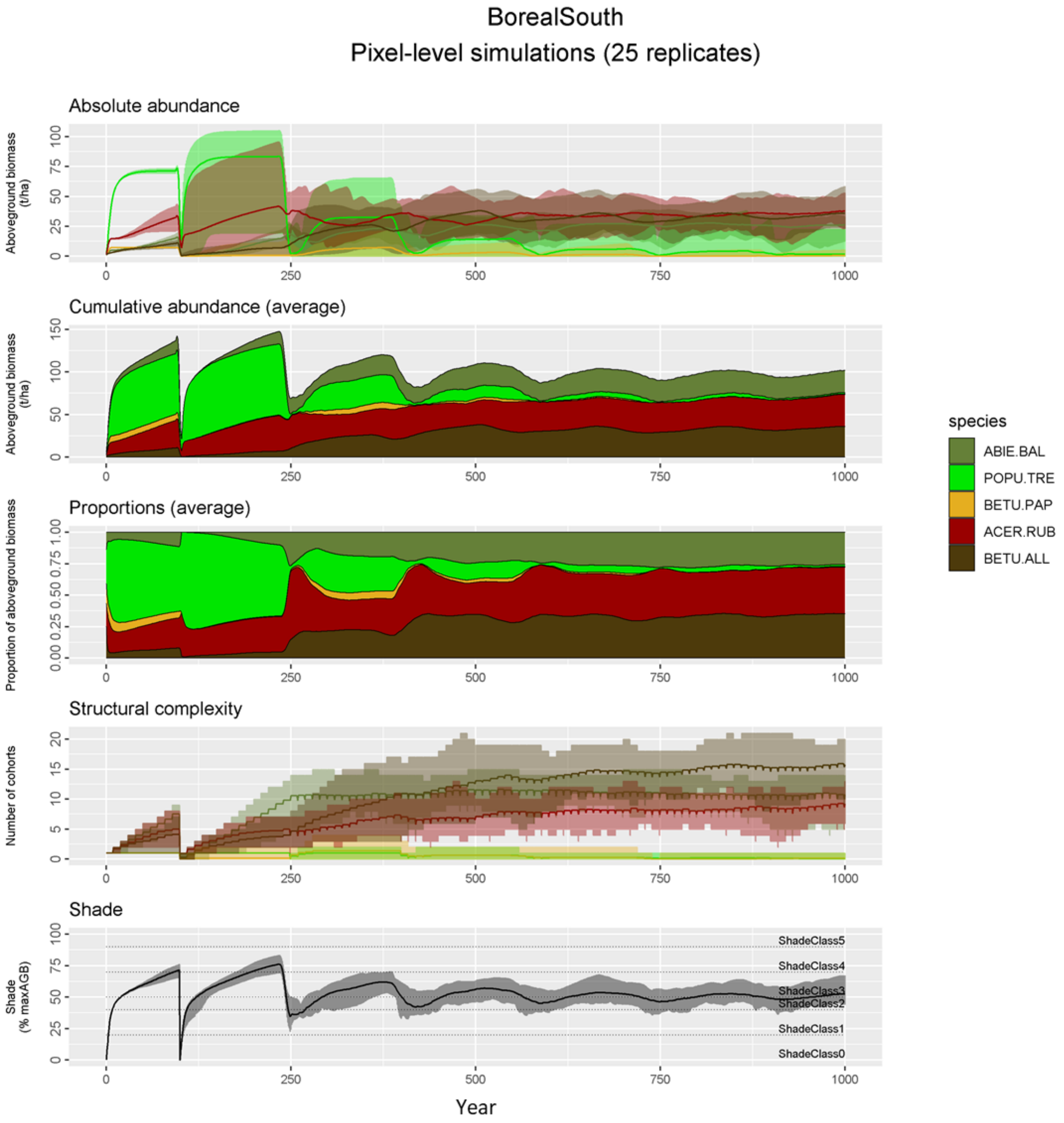

Figure B 2. Pixel-level simulations of one specific land type chosen among the 80 land types defined for that quadrat. It was subjectively chosen to represent the most common land cover types of the southern boreal forest in the Eastern Boreal Shield. The pixel-level simulation assesses the realism of emerging succession as simulated by LANDIS-II Biomass Succession, to minimise biases as best as we can. Pixel size was 6.25 ha. (250-m resolution). Forest harvesting occurred at t = 100 years. The simulations represent the absolute abundance, the cumulative abundance, and the proportion and structural complexity of balsam fir (Abies balsamea, ABIE.BAL), trembling aspen (Populus tremuloides, POPU.TRE), white birch (Betula papyrifera, BETU.PAP), red maple (Acer rubrum, ACER.RUB), and yellow birch (Betula alleghaniensis, BETU.ALL).

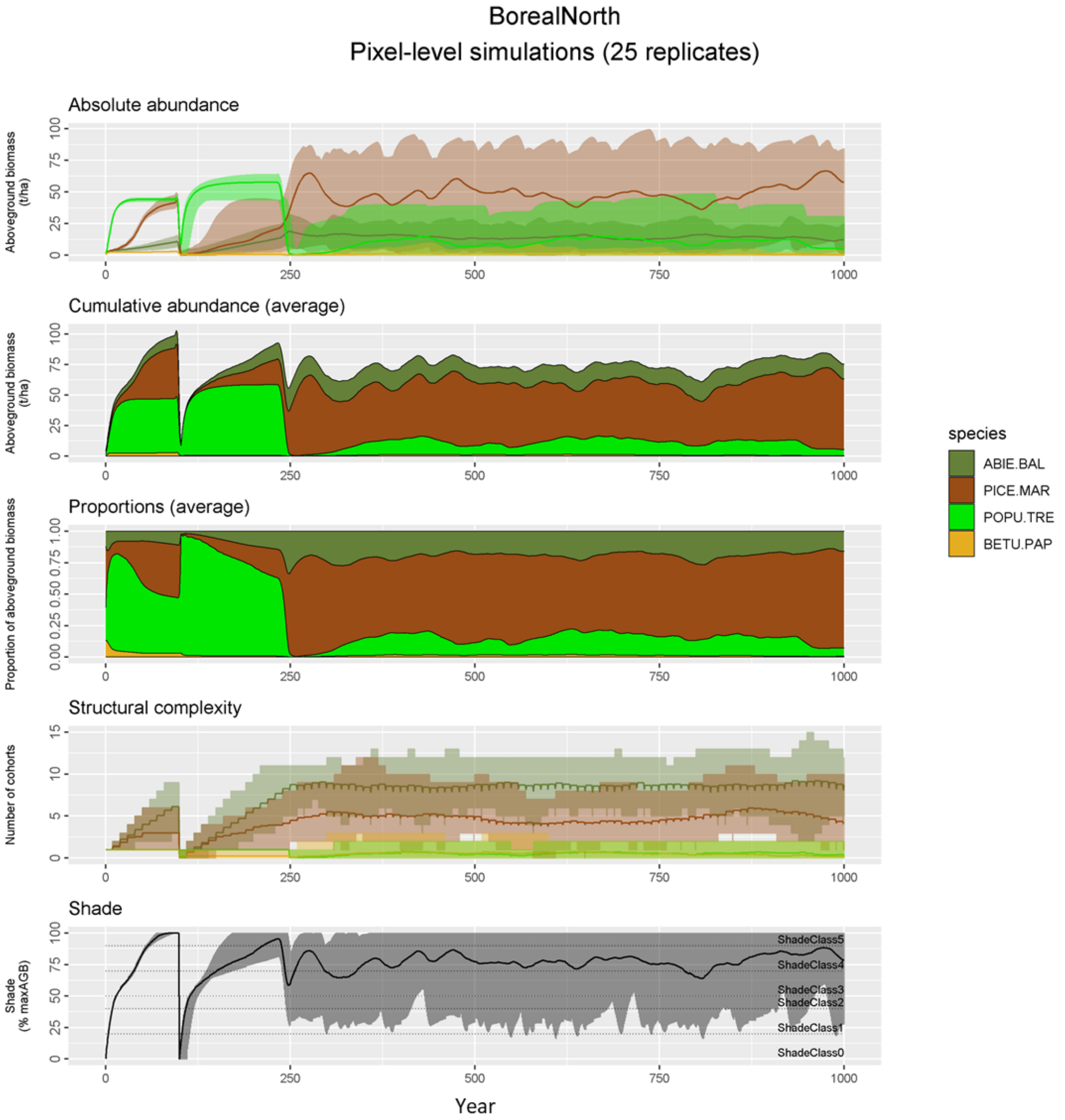

Figure B 3. Pixel-level simulations of one specific land type chosen among the 80 land types defined for that quadrat. It was subjectively chosen to represent the most common land cover types of the northern boreal forest in the Eastern Boreal Shield. The pixel-level simulation assesses the realism of emerging succession as simulated by LANDIS-II Biomass Succession, to minimise biases as best as we can. Pixel size was 6.25 ha. (250-m resolution). Forest harvesting occurred at t=100years. The simulations represent the absolute abundance, the cumulative abundance, and the proportion and structural complexity of balsam fir (*Abies balsamea*, ABIE.BAL), black spruce (*Picea mariana,* PICE.MAR), Trembling Aspen (*Populus tremuloides*, POPU.TRE), and White birch (*Betula papyrifera*, BETU.PAP).

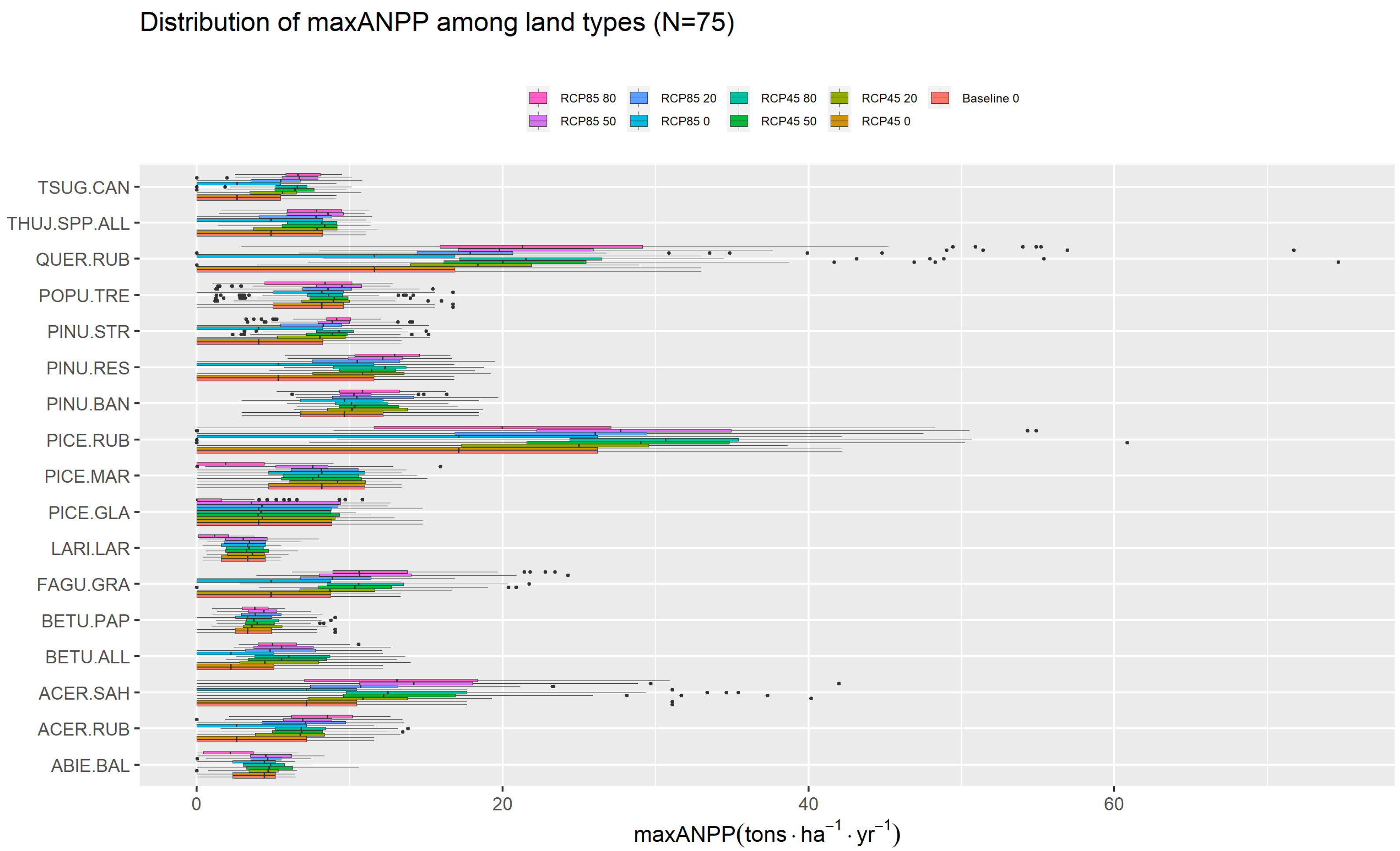

Figure B 4. Distribution of the parameter values derived from Picus outputs among land types for maximum annual net primary productivity (maxANPP). The succession dynamics simulated by LANDIS-II depended on those values, in interaction with maximum aboveground biomass (maxB), species establishment probabilities (probEST), landscape configuration, initial conditions, disturbances, and static species parameters such as longevity and seed dispersal distances.

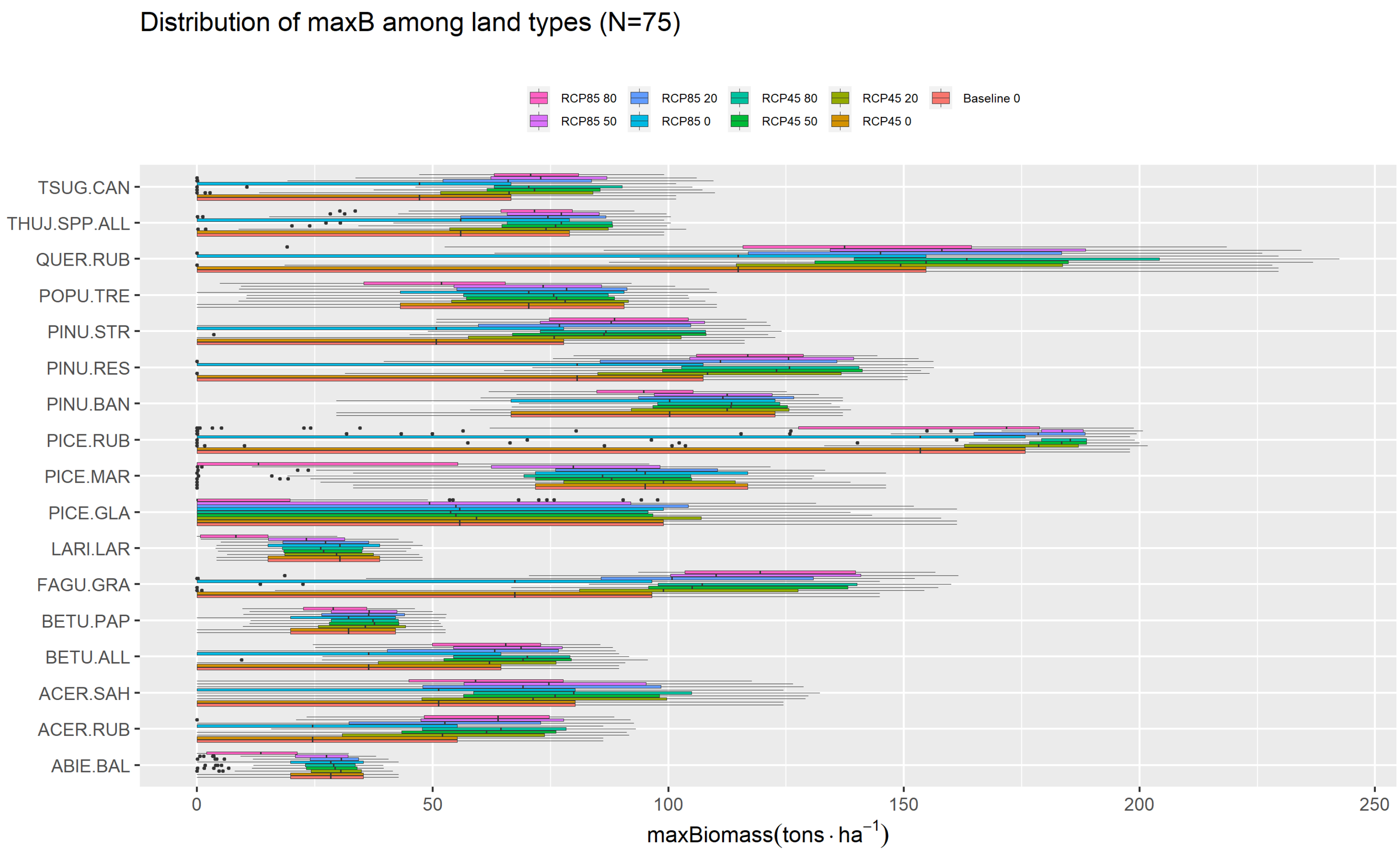

Figure B 5. Distribution of the parameter values derived from Picus outputs among land types for maximum aboveground biomass (maxB). The succession dynamics simulated by LANDIS-II depended on those values, in interaction with maximum annual net primary productivity (maxANPP), species establishment probabilities (probEST), landscape configuration, initial conditions, disturbances, and static species parameters such as longevity and seed dispersal distances.

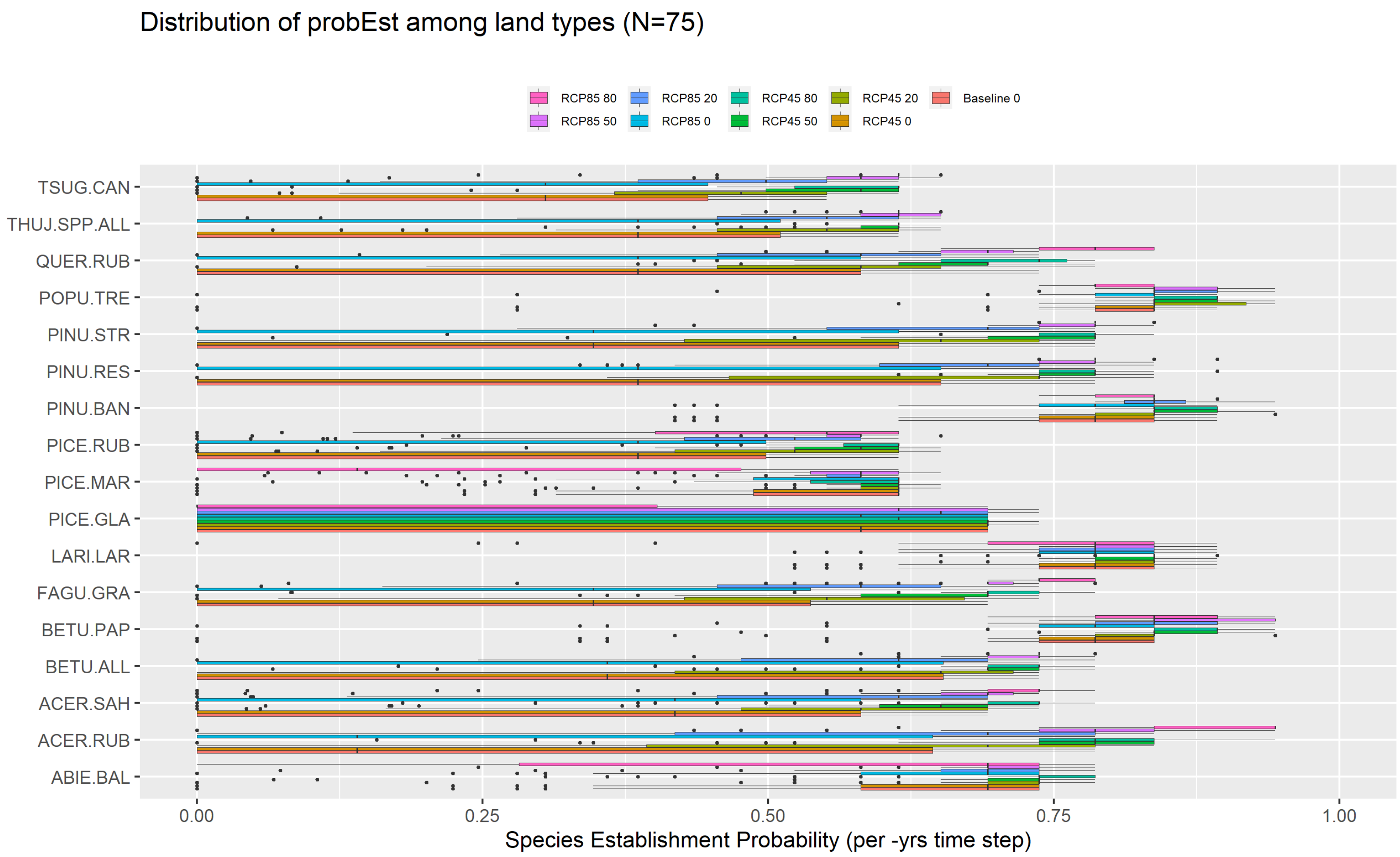

Figure B 6. Distribution of the parameter values derived from Picus outputs among land types for species establishment probabilities (probEST). The succession dynamics simulated by LANDIS-II depended on those values, in interaction with maximum annual net primary productivity (maxANPP), maximum aboveground biomass (maxB), landscape configuration, initial conditions, disturbances, and static species parameters such as longevity and seed dispersal distances.

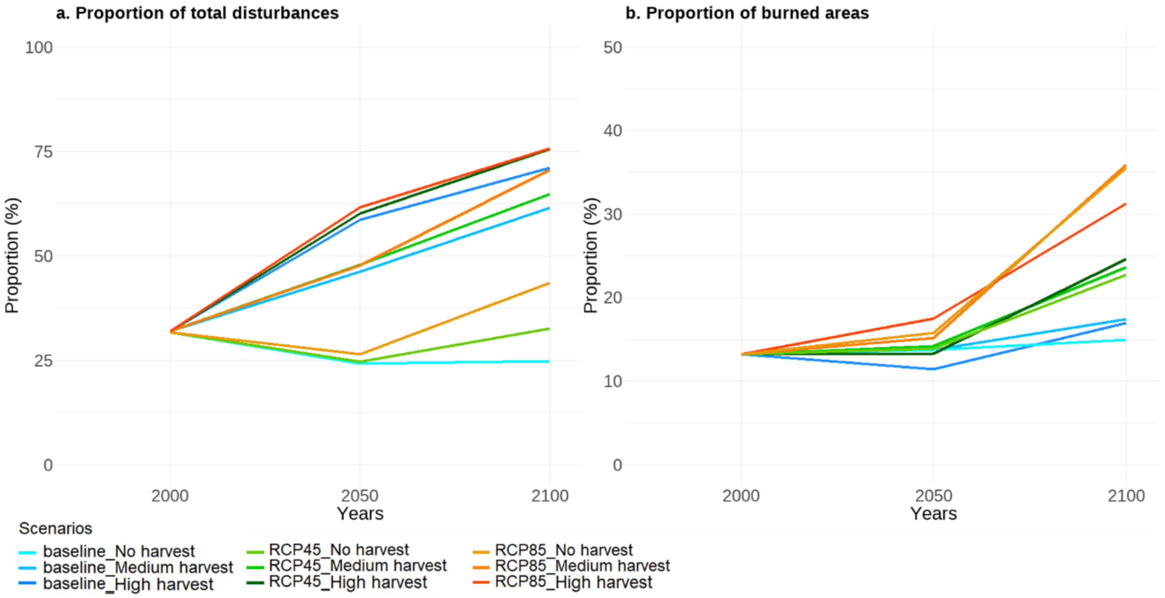

Figure B 7. a. Proportion of total disturbances areas calculated according to Environment Canada (2011) criteria (i.e., cuts and roads with a 500-m buffer and burned); b. Proportion of burned areas under each scenario.

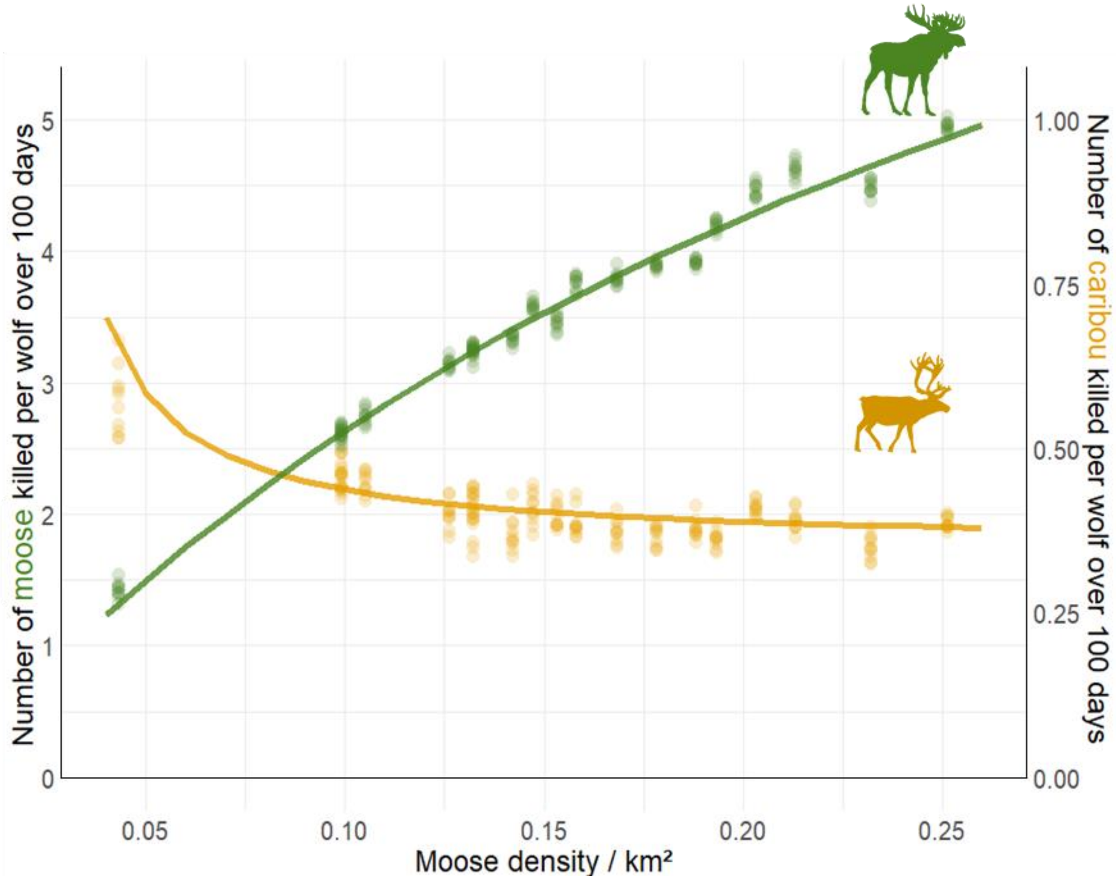

Figure B 8. Number of prey killed per wolf over 100 days, as a function of moose density. The number of moose killed by each wolf are represented in green in the left Y-axis, while the number of caribou are represented in yellow in the right Y-axis. Each point represented one replicate of a simulation.

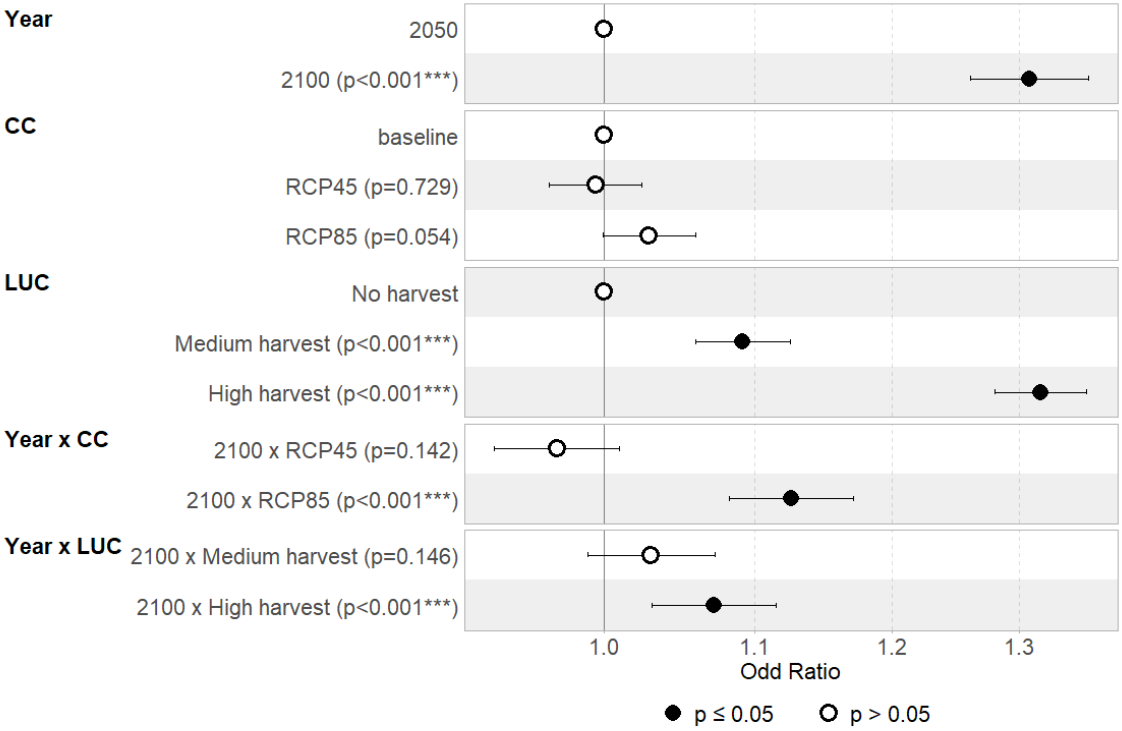

Figure B 9. Impacts of land-use (LUC) and climate (CC) changes on caribou survival in 2050 and 2100. The odd ratio is the exponentiate of beta coefficients of the selected logistic-binomial generalized linear model (see candidate models in Annexe B, **Table B 1**). The intercept for the fixed effects is the logit estimate for the year 2050, baseline and no harvest. An odd 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 outcome 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 Annexe B, **Table B 2**.

Table B 1. Candidate logistic-binomial models of the number of caribou killed by wolves in winter based on the different sets of fixed effect terms included. The baseline model (m1) only includes the additive effects of the three variables characterizing the study design, i.e., climate change (CC), land-use change (LUC) scenarios and the year of simulation (2050 and 2100). Models 2-4 (m2, m3 and m4) include interaction terms. The model in bold is the top-ranking models based on the AIC (Akaike's Information Criterion) and the log-likelihood (logLik) ratio test of nested models. Summer results can be found in Annexe E, **Table E 2**.

	Numerical response					
Variable	**df**	**AIC**	**logLik**	**Chisq**	**df**	***P*-value**
m1: Year + CC + LUC	6	1641.53	-814.76			
m2: m1+Year*CC + Year*LUC	**10**	**1574.59**	**-777.30**	**74.93**	**4**	**< 0.001**
m3: m2+CC*LUC	14	1576.98	-774.49	5.61	4	0.230
m4: m3 + Year *CC *LUC	18	1582.33	-773.17	2.65	4	0.618

Table B 2. Parameter estimates from the selected logistic-binomial GLM (i.e., m2 in Annexe B, **Table B 1**) considering only winter data. The intercept for the fixed effects is the logit estimate for the year 2050, baseline and no harvest. The other estimates are contrasts (i.e., differences on the logit scale) between the other levels of the categorical variables. Summer results can be found in Annexe E, **Table E 3**.

	Numerical response			
Variable	**β**	**SE**	**z-value**	***P*-value**
Intercept	-1.740	0.014	-122.016	< 0.001
Year 2100	0.269	0.019	14.115	< 0.001
RCP4.5	-0.005	0.015	-0.346	0.729
RCP8.5	0.028	0.015	1.930	0.053
Medium Harvest	0.088	0.015	5.726	< 0.001
High Harvest	0.276	0.015	18.520	< 0.001
2100 x RCP4.5	-0.030	0.020	-1.468	0.142
2100 x RCP8.5	0.119	0.020	5.954	< 0.001
2100 x Medium Harvest	0.030	0.021	1.455	0.146
2100 x High Harvest	0.070	0.020	3.489	< 0.001

Table B 3. Parameter estimates from post-hoc Tukey honestly significant difference between all pairwise comparisons for the model considering data collected during the winter.

Significance levels: ****$P < 0.001$, ***$P < 0.01$, **$P < 0.05$, *$P < 0.1$. Summer results can be found in Annexe E, **Table E 4**.

Variable	**Numerical response**			
	Mean difference	**95% CI**		***P*-value**
		Lower bound	**Upper bound**	
Year				
2100-2050	0.053	0.049	0.057	< 0.001 ****
CC				
RCP4.5-baseline	-0.001	-0.007	0.004	0.872
RCP8.5-baseline	0.017	0.011	0.022	< 0.001 ****
RCP8.5-RCP4.5	0.018	0.012	0.023	<0.001 ****
LUC				
Medium harvest-No harvest	0.017	0.012	0.023	< 0.001 ****
High harvest-No harvest	0.051	0.046	0.057	< 0.001 ****
High harvest-Medium harvest	0.034	0.024	0.039	< 0.001 ****
Year x CC				
2050:RCP45-2050:baseline	0.003	-0.006	0.013	0.901
2050:RCP85-2050:baseline	0.008	-0.001	0.018	0.133
2100:RCP45-2100:baseline	-0.006	-0.015	0.004	0.499
2100:RCP85-2100:baseline	0.026	0.016	0.035	< 0.001 ****
2050:RCP85-2050:RCP45	0.005	-0.005	0.014	0.702
2100:RCP85-2100:RCP45	0.031	0.022	0.041	< 0.001 ****
2100:baseline-2050:baseline	0.050	0.041	0.060	< 0.001 ****
2100:RCP45-2050:RCP45	0.041	0.032	0.051	< 0.001 ****
2100:RCP85-2050:RCP85	0.068	0.058	0.077	< 0.001 ****
2100:RCP45-2050:baseline	0.045	0.035	0.054	< 0.001 ****
2100:RCP85-2050:baseline	0.076	0.067	0.086	< 0.001 ****

2050:RCP45-2100:baseline	-0.047	-0.056	-0.038	< 0.001 ****
2050:RCP85-2100:baseline	-0.042	-0.052	-0.033	< 0.001 ****
2100:RCP85-2050:RCP45	0.073	0.063	0.082	< 0.001 ****
2050:RCP85-2100:RCP45	-0.037	-0.046	-0.027	< 0.001 ****
Year x LUC				
2050:Medium harvest-2050:No harvest	0.016	0.006	0.025	< 0.001 ****
2050: High harvest-2050:No harvest	0.043	0.033	0.052	< 0.001 ****
2100:Medium harvest-2100:No harvest	0.019	0.009	0.028	< 0.001 ****
2100: High harvest-2100:No harvest	0.059	0.050	0.069	< 0.001 ****
2050: High harvest-2050:Medium harvest	0.027	0.018	0.037	< 0.001 ****
2100: High harvest-2100:Medium harvest	0.040	0.031	0.050	< 0.001 ****
2100:NoHarvest-2050:NoHarvest	0.047	0.037	0.056	< 0.001 ****
2100:Medium harvest-2050:Medium harvest	0.050	0.040	0.059	< 0.001 ****
2100: High harvest-2050: High harvest	0.063	0.054	0.073	< 0.001 ****
2100:Medium harvest-2050:NoHarvest	0.066	0.056	0.075	< 0.001 ****
2100: High harvest-2050:NoHarvest	0.106	0.097	0.116	< 0.001 ****
2050:Medium harvest-2100:NoHarvest	-0.031	-0.040	-0.021	< 0.001 ****
2050: High harvest-2100:NoHarvest	-0.004	-0.0132	0.006	0.863
2100: High harvest-2050:Medium harvest	0.090	0.081	0.100	< 0.001 ****
2050: High harvest-2100:Medium harvest	-0.023	-0.032	-0.013	< 0.001 ****

Table B 4. Values of habitat characteristics of a. landscape homogeneity, b. percentage of deciduous vegetation and c. isolation of mature conifer stands (a value close to 0 indicate aggregated patches, while a higher value indicated the isolation of patches) as a function of the different scenarios.

a. Landscape homogeneity

	Baseline			RCP 4.5			RCP 8.5		
	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest
2000	0.57	0.57	0.57	0.57	0.57	0.57	0.57	0.57	0.57
2050	0.55	0.53	0.54	0.56	0.54	0.56	0.57	0.55	0.57
2100	0.57	0.58	0.60	0.61	0.60	0.64	0.66	0.64	0.66

b. Deciduous vegetation (%)

	Baseline			RCP 4.5			RCP 8.5		
	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest
2000	18	18	18	18	18	18	18	18	18
2050	28	33	37	28	34	39	29	36	41
2100	38	46	50	34	43	48	45	54	58

c. Isolation of mature conifer stands (%)

	Baseline			RCP 4.5			RCP 8.5		
	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest
2000	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
2050	0.1	0.4	0.5	0.2	0.7	1.6	0.3	0.8	2.1
2100	1.6	4.9	5.6	1.2	4.1	5.6	4.1	5.5	6.3

Table B 5. Values and sources used for starting densities and to parameterize individual-based model to simulate predator-prey dynamics.

Species/Agents	Parameter/Variable	Value	Reference
Moose, prey	Reference density	4.3 individuals / 100km²	(Courbin et al. 2014)
	Distance max / 8-hours	Winter: 2036m Summer: 3467m	Determined with empirical data
Caribou, prey	Reference density	1.9 individuals / 100km²	(Équipe de rétablissement du caribou forestier du Québec 2013)
	Distance max / 8-hours	Winter: 7528m Summer: 7010m	Determined with empirical data
Wolf, predator	Reference density	0.08 pack/ 100km²	(Jolicoeur and Hénault 2002)
	Distance max / 8-hours	Hunting mode: Winter: 22746m Summer: 24018m	Determined with empirical data
		Stationary mode: Winter and Summer: 200m	(Webb et al. 2006)
	Handling time (Hunting mode)	Caribou: 24h Moose: 72h	(Hayes et al. 2000)

Annexe C: Data partitioning in Chapter 2 and 3.

We started the analysis with GPS-data from 68 female caribou, 15 moose, and 16 wolves. We discarded individuals with too few observations to keep only those with at least 100 observations (as Losier et al. (2015)). Data from 53 caribou, 15 moose, and 10 wolves were then used for movement analysis. Step-selection functions were estimated using generalized estimating equations (GEE), an approach that corrects for the bias of variance estimates due to autocorrelation between observations. GEE requires partitioning the data into independent clusters. Following Prima et al. (2017), we needed at least 20 clusters to remove bias. For caribou, each individual was used as a cluster in the analysis, which represented 50 in summer and 53 in winter. By contrast, we used destructive sampling for the other two species to obtain at least 20 clusters because fewer individuals were available. Autocorrelation analyses showed that steps were independent for wolf and moose beyond lag 1 during winter and lag 2 in summer. While considering these lags (see Fortin et al. (2015)), we created 23 and 26 clusters for wolves and 30 and 22 clusters moose for in winter, and summer, respectively. All statistical analyses were performed using the R4.1.2 software (R Core Team 2021).

Annexe D: Details of the calibration and validation of IBM in Chapter 2 and 3

To calibrate the IBM, simulations were run for the years 2005, 2007, 2009, 2011, 2013, 2015 and 2018, 3 times for each year and each season (42 simulations).

SSF scores

To calibrate and validate the model, we first compared the relative probability 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 by this equation:

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

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 step lengths (SL) and turning angles (TA) of random steps were drawn within a radius of the 99th percentile maximum step length 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 patch 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 ticks since the last time this animal was on the polygon. Each visited patch were recorded for 4 days. The weights were -2, -0.7 and -3 for caribou, moose, and wolves respectively. In other words, the more virtual agent stays within a polygon, the more the weight is negative, and the more the coefficient to choose the same polygon decrease.

Parameters for hunting a prey

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 and 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.

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 than the landscape where empirical data was collected, the different land cover types should be selected or avoided similarly by agent 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, 3 times for each year and each season (3 replicates x 7 years x 2 seasons = 42 simulations). We then compared the relative probability of selection of land cover types and step length distributions between empirical data and the output of the simulations conducted under the same landscape conditions. We did minor adjustments on IBM inputs to reproduce adequately the behaviors of the actual radio-collared animals (Annexe D, **Table D 1**). 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 S4 table 1. We observed that virtual agents selected or avoided land cover types similarly to radio-collared boreal caribou, moose, and wolves in the different seasons (Annexe D, **Figure D 1 – Figure D 3**, respectively).

We also compared the distribution of step lengths between agent individuals and radio-collared individuals (Annexe D, **Figure D 4 – Figure D 5**). We observed that virtual agents and radio-collared individuals had a similar step length distribution.

Moose and wolf numerical response

We found that moose occurred at a density of 0.60 individual/10 km² (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 ($R^2 = 0.24$, $P < 0.001$, n = 48). We used this relationship to determine the future density of moose in function of the forecasted proportion of deciduous within the study area (Annexe D, **Table D 2**). Then, with the equation created by Messier et al. (1984) we determined the associated density of wolves (Annexe D, **Table D 2**).

Table D 1. Parameter estimates (β) and standard errors (SE) of step-selection function for radio-collared boreal caribou (n =68), moose (n = 15), and wolves (n = 16), during two biological seasons. The $\overline{r}_s$ of *k*-Fold cross validation is also given for each of the model.

VARIABLE	**SUMMER**					
	Caribou	Adjusted coefficient	Moose	Adjusted coefficient	Wolf	Adjusted coefficient
Ln(step length)	-0.337±0.008*		-0.240 ± 0.027*		-0.807 ± 0.040*	
Step length	0.730 ± 0.011*		1.152 ± 0.054*		0.009 ± 0.009	
Turning angle	0.003 ± 0.010		-0.017 ± 0.030		-0.023 ± 0.044	
LAND-COVER TYPE^A						
Closed-canopy mature conifer	-0.022 ± 0.021		0.144 ± 0.073*		-0.535 ± 0.133*	
Mixed/deciduous	-0.096 ± 0.024*		0.137 ± 0.070		-0.167 ± 0.124	
Open	-0.304 ± 0.210		0.482 ± 0.429		-0.113 ± 0.479	
Other	-0.785 ± 0.033*		-0.619 ± 0.102*		-0.111 ± 0.114	
Burned 0-10	-0.246 ± 0.194		0.898 ± 0.222*		0.432 ± 0.154*	
Burned 10-20	-0.554 ± 0.242*		0.875 ± 0.283*		0.553 ± 0.169*	
Burned 20-50	0.278 ± 0.066*		0.511 ± 0.176*		0.599 ± 0.195*	
Cuts 0-10	-0.880 ± 0. 120*		0.294 ± 0.108*		-0.259 ± 0.109*	
Cuts10-20	-0.742 ± 0.206*				0.267 ± 0.249	
Cuts 20-50	1.152 ± 0.339*	-1.152			0.208 ± 0.252	-1.708
DISTANCE TO ROAD^B (m)						
250	-1.605 ± 0.107*		-0.293 ± 0.519		0.979 ± 0.127*	
251–500	-1.241 ± 0.088*		-0.898 ± 0.587*		0.432 ± 0.146*	
501–1000	-0.321 ± 0.053*		-0.069 ± 0.282		0.505 ± 0.142*	
1001–1500	-0.192 ± 0.046		-0.094 ± 0.233		0.143 ± 0.172	
***K*-FOLD ($\overline{r}_s$)**	0.92		0.91		0.92	

VARIABLE	**WINTER**					
	Caribou	Adjusted coefficient	Moose	Adjusted coefficient	Wolf	Adjusted coefficient
Ln(step length)	-0.695 ± 0.005*		-0.922 ± 0.017*		-1.059 ± 0.019*	
Step length	0.500 ± 0.006*		1.825 ± 0.064*		-0.006 ± 0.005	
Turning angle	0.002 ± 0.006		-0.037 ± 0.017*		-0.011 ± 0.022	
LAND-COVER TYPE^{A}						
Closed-canopy mature conifer	-0.038 ± 0.012		0.084 ± 0.043		-0.169 ± 0.062	
Mixed/deciduous	-0.082 ± 0.013*		0.171 ± 0.040*		-0.149 ± 0.061	
Open	-0.203 ± 0.086		-0.829 ± 0.666		0.365 ± 0.242	
Other	-0.678 ± 0.017*		-0.570 ± 0.081*		0.098 ± 0.056	
Burned 0-10	-0.628 ± 0.084*		0.021 ± 0.182		0.326 ± 0.076*	
Burned 10-20	-0.577 ± 0.175*		-0.888 ± 0.531		0.770 ± 0.088*	
Burned 20-50	-0.047 ± 0.051		-0.491 ± 0.179		0.401 ± 0.095*	
Cuts 0-10	-0.340 ± 0.057*		0.064 ± 0.076		0.032 ± 0.059	
Cuts10-20	-0.364 ± 0.074*				-0.294 ± 0.157	
Cuts 20-50	-0.713± 0.079*				0.094 ± 0.156	
DISTANCE TO ROAD^{B} **(m)**						
250	-0.694 ± 0.044*		-1.224 ± 0.597*		0.528 ± 0.067*	
251–500	-0.483 ± 0.040*		-0.279 ± 0.364		0.365 ± 0.122*	
501–1000	-0.267 ± 0.030*		-0.246 ± 0.240		0.398 ± 0.070*	
1001–1500	-0.135 ± 0.026		-0.160± 0.172		0.354 ± 0.077*	
***K*-FOLD ($\bar{r}_s$)**	0.89		0.83		0.98	

[a] Reference land-cover is open conifer forest

[b] Reference distance to road is >1500 m

* Coefficient with $P < 0.05$

Table D 2. Values of a. the percentage of deciduous land cover and b. the associated number of moose and c. wolf packs as a function of the different simulation scenarios. Wolf packs are constituted with 4 wolves. Moose density and the number of wolf packs were used to model the behavioral-numerical responses.

a. Percentage of deciduous vegetation

	Baseline			RCP 4.5			RCP 8.5		
	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest
2000	18%	18%	18%	18%	18%	18%	18%	18%	18%
2050	28%	33%	37%	28%	34%	39%	29%	36%	41%
2100	38%	46%	50%	34%	43%	48%	45%	54%	58%

b. Moose density (Ind./100km²)

	Baseline			RCP 4.5			RCP 8.5		
	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest
2000	4.33	4.33	4.33	4.33	4.33	4.33	4.33	4.33	4.33
2050	9.94	12.63	14.74	9.94	13.16	15.77	10.48	14.21	16.80
2100	15.26	19.31	21.28	13.16	17.81	20.30	18.82	23.21	25.11

c. Wolf pack density (Pack/100km²)

	Baseline			RCP 4.5			RCP 8.5		
	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest	No harvest	Medium harvest	High harvest
2000	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
2050	0.17	0.21	0.24	0.17	0.22	0.25	0.18	0.23	0.27
2100	0.24	0.30	0.32	0.22	0.28	0.31	0.29	0.34	0.36

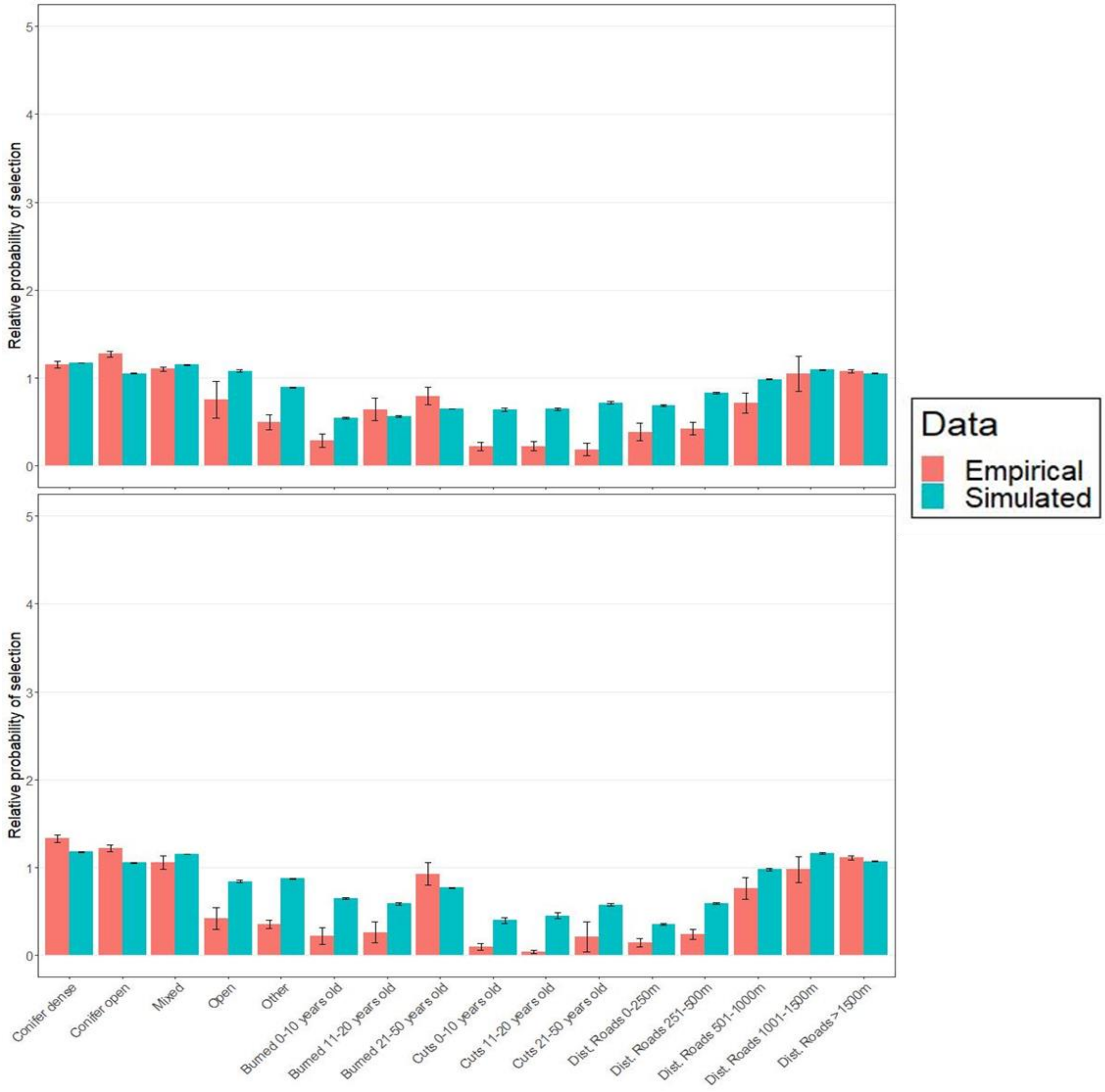

Figure D 1. Relative probability of selection (± standard error) of different land cover types by radio-collared boreal caribou and caribou agents during <u>winter</u> (top) and <u>summer</u> (bottom)in the Côte Nord region, Québec, Canada.

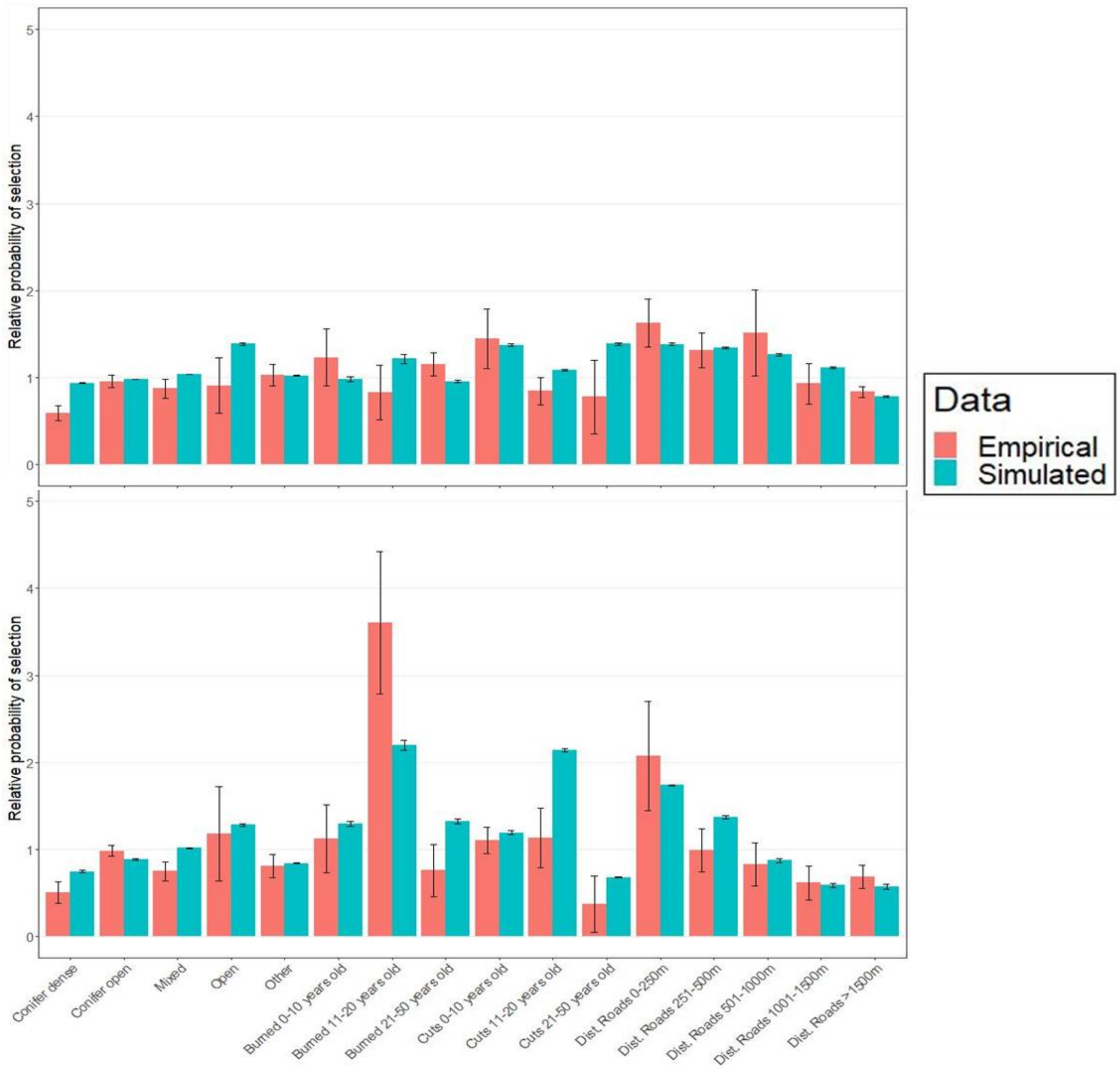

Figure D 2. Relative probability of selection (± standard error) of different land cover types by radio-collared wolves and wolf agents during (top) winter and (bottom) summer in the Côte Nord region, Québec, Canada.

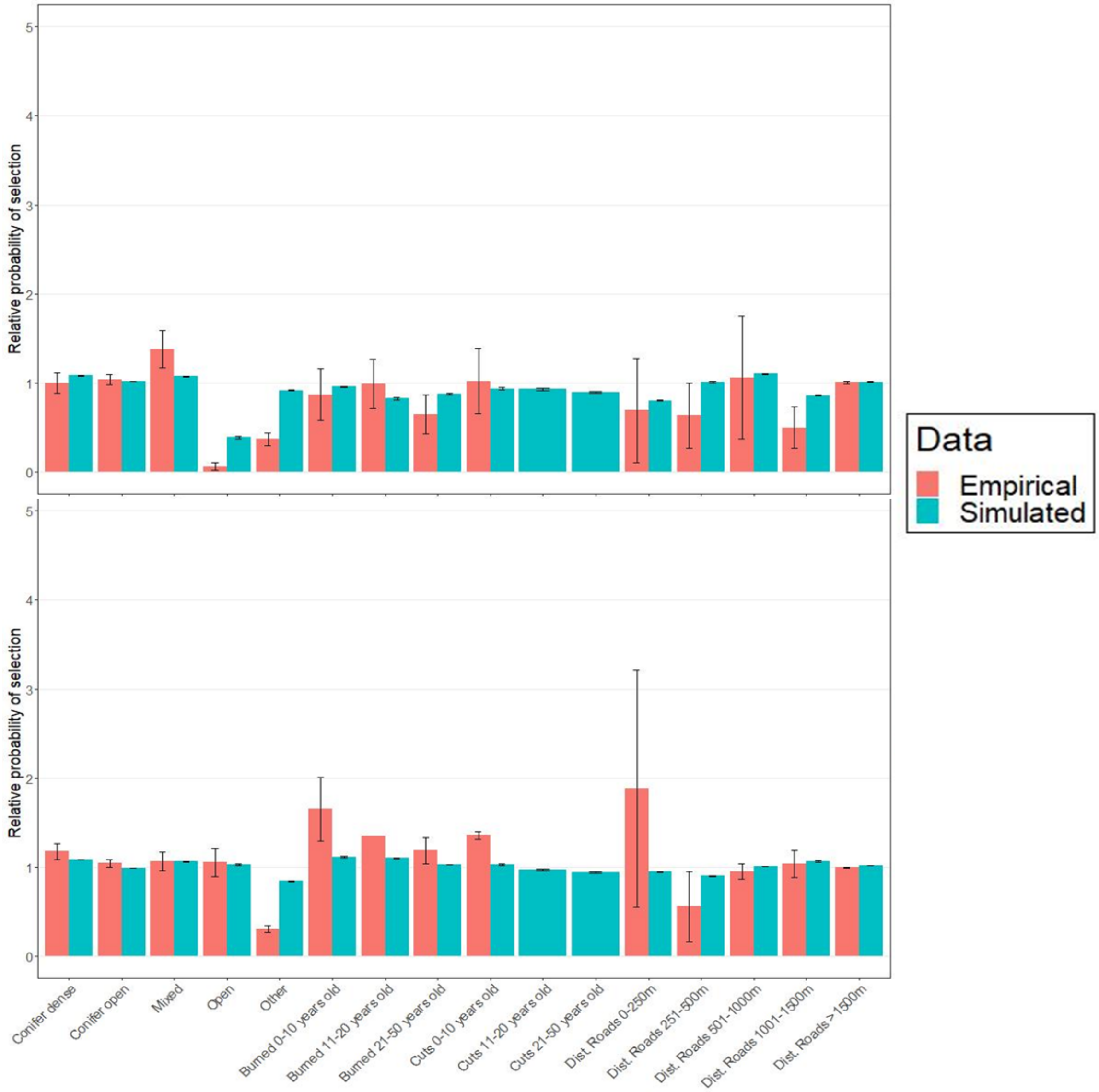

Figure D 3. Relative probability of selection (± standard error) of different land cover types by radio-collared moose and moose agents during (top) winter and (bottom) summer in the Côte Nord region, Québec, Canada.

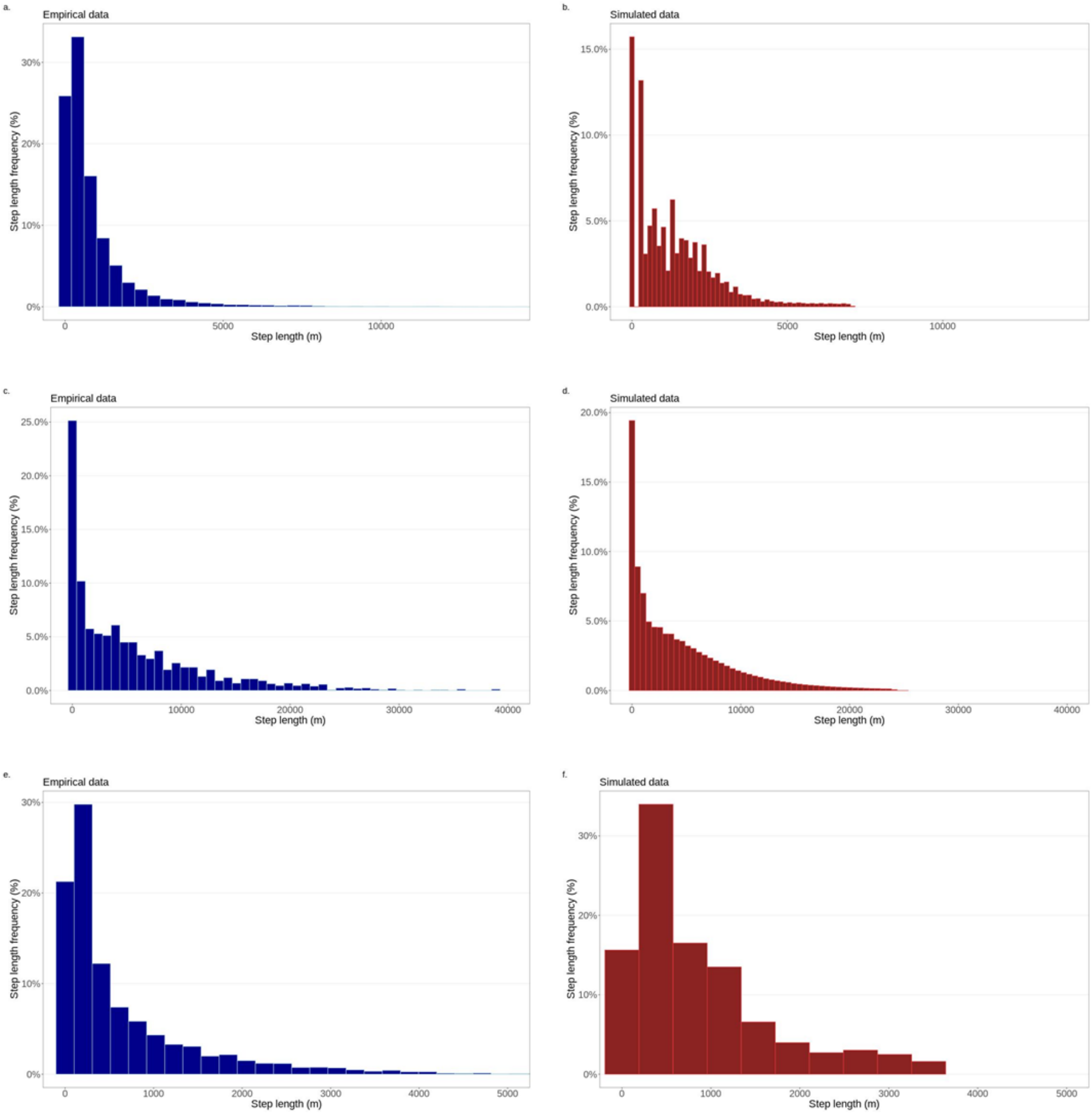

Figure D 4. Step length frequency (%) of radio collared (blue) and simulated (red) caribou, wolves, and moose (top to bottom) as a function of step length during <u>summer</u>.

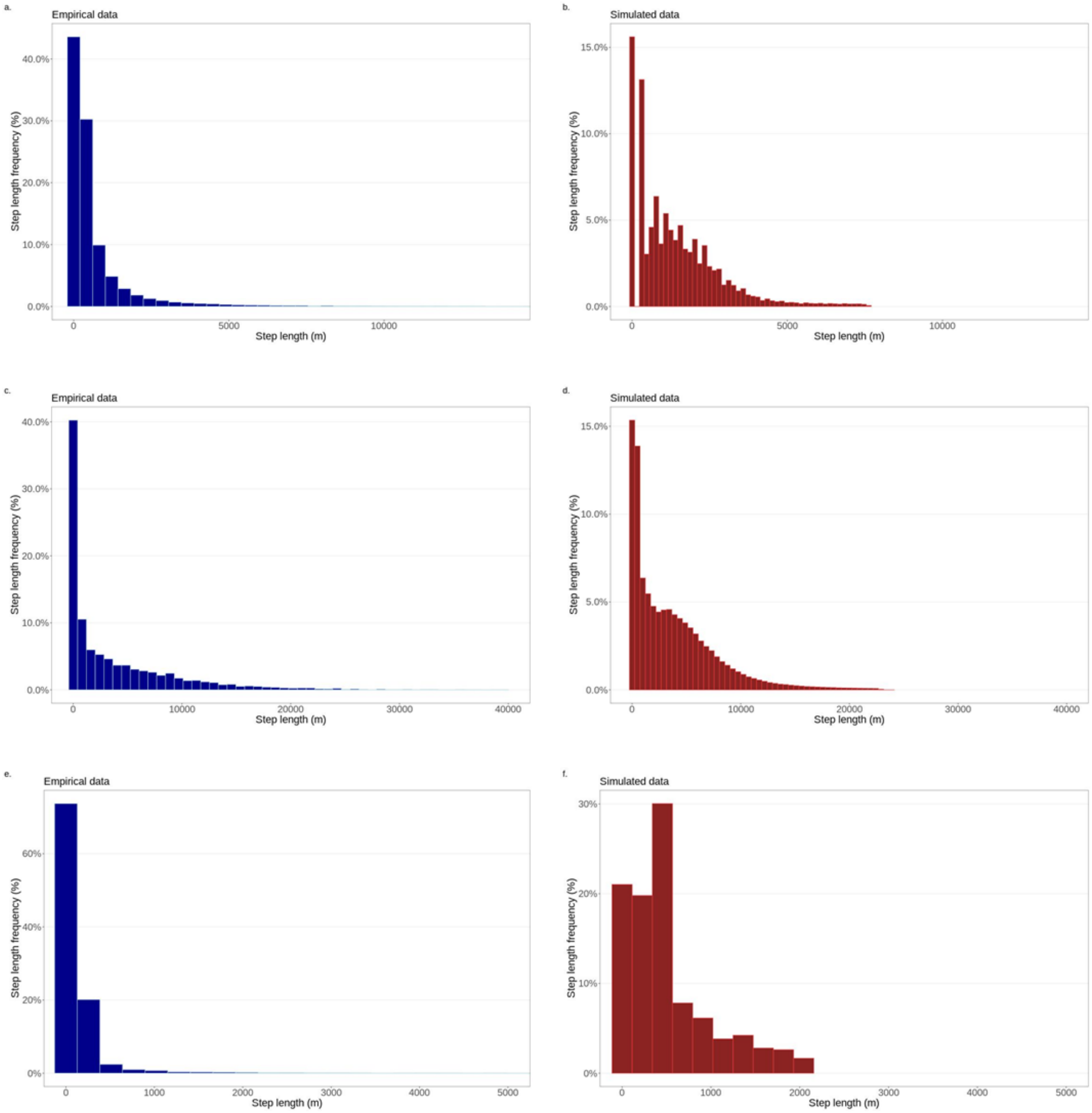

Figure D 5. Step length frequency (%) of radio collared (blue) and simulated (red) caribou, wolves, and moose (top to bottom) as a function of step length during winter.

Annexe E: Summer results in Chapter 2

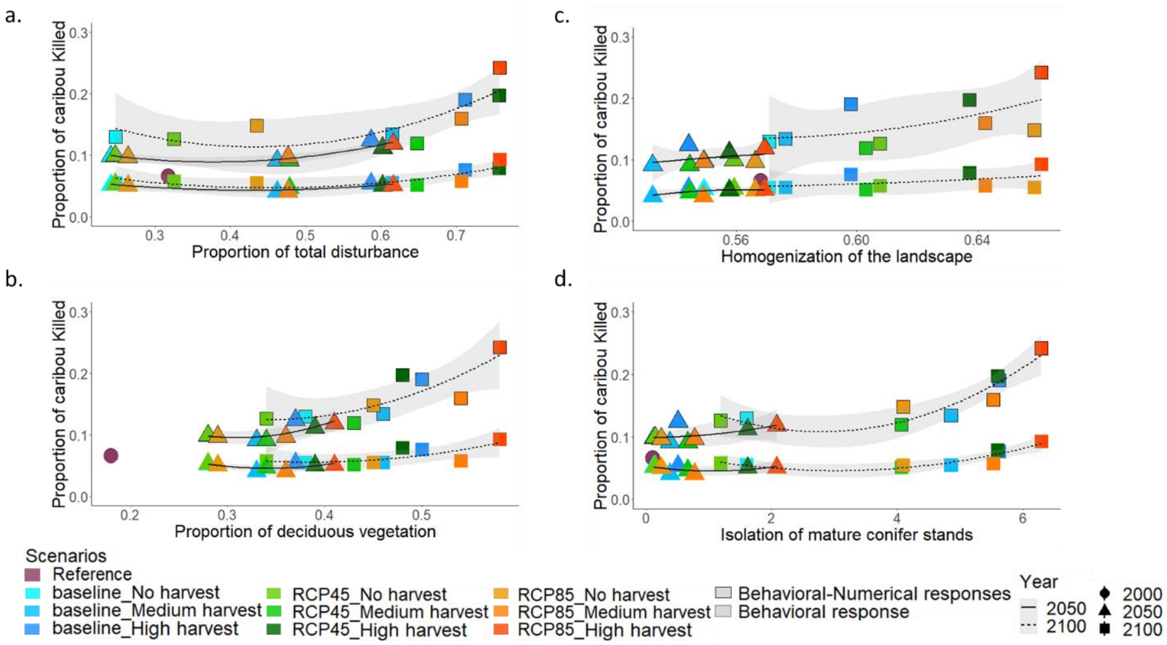

Figure E 1. Relationships between the proportion of caribou killed and forest attributes in <u>summer</u>. Proportion of caribou killed in 2000 (point in purple, determined as the reference), 2050 (triangle) and 2100 (square) as a function of a. the proportion of total disturbances, b. the proportion 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 3 different colors represented the 3 climate scenarios: baseline (blue), RCP4.5 (green) and RCP8.5 (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 represented the behavioral response, while shapes with black edge represented the behavioral-numerical responses of moose and wolf to emergent changes in forest landscape composition.

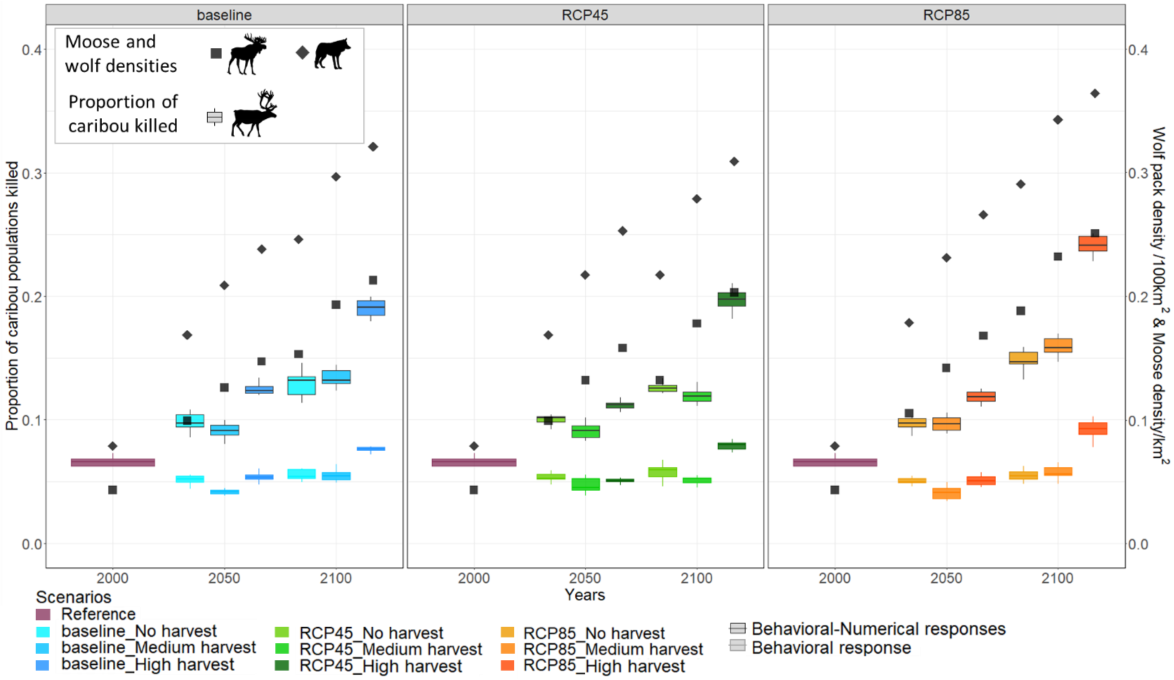

Figure E 2. Temporal changes in the proportion of caribou killed in function of land-use change and climate change scenarios in summer. Proportion of caribou killed by wolves under three climate scenarios (Baseline in blue, RCP4.5 in green and RCP8.5 in orange) and three levels of land-use (No harvest 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 represented the behavioral response, while boxplots with black edge represented 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 the interquartile range.

Table E 1. Model results regarding the proportion of caribou killed in summer as a function of changes in forest attribute. Coefficients (and standard errors) of generalized linear mixed models relate the proportion of caribou killed by wolves 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 prey killed by wolf, we assumed a logit link and binomially distributed errors.

Variable	**a. Behavioral response**	**b. Behavioral-Numerical responses**	**c. |Effect ratio|**
Proportion of cuts and roads	0.354 (0.088) ****	0.831 (0.048) ****	2.347
Proportion of burned areas	1.047 (0.240) ****	2.634 (0.210) ****	2.516
Residuals for proportion of deciduous	-0.002 (0.005)	0.043 (0.005) ****	21.500
Residuals for isolation of mature conifer stands	0.105 (0.023) ****	0.037 (0.020) *	0.352
Residuals for landscape homogenization	12.346 (1.732) ****	11.125 (1.517) **	0.901

Significance levels: ****P < 0.001, ***P < 0.01, **P < 0.05, *P < 0.1.

Table E 2. Candidate logistic-binomial models of the number of caribou killed by wolves in summer based on the different sets of fixed effect terms included. The baseline model (m1) only includes the additive effects of the three variables characterizing the study design, i.e., climate change (CC) and land-use change (LUC) scenarios, and the year of simulation (2050 and 2100). Models 2-4 (m2, m3 and m4) include interaction terms. The model in bold is the most parsimonious (i.e., best) models based on the AIC (Akaike's Information Criterion) and the log-likelihood (logLik) ratio tests of nested models.

	Numerical response					
Variable	**df**	**AIC**	**logLik**	**Chisq**	**df**	***P*-value**
m1: Year + CC + LUC	6	1874.69	-931.35			
m2: m1+Year*CC + Year*LUC	10	1533.37	-756.68	349.32	4	<0.001
m3: m2+CC*LUC	14	1521.90	-746-95	19.47	4	<0.001
m4: m3 + Year *CC *LUC	**18**	**1498.31**	**-731.16**	**31.56**	**4**	**<0.001**

Table E 3. Parameter estimates from the selected logistic-binomial GLM (i.e., m4 in Annexe E, **Table E 2**) considering data collected during the summer. The intercept for the fixed effects is the logit estimate for the year 2050, baseline and no harvest. The other estimates are contrasts (i.e., differences on the logit scale) between the other levels of the categorical variables.

	Numerical response			
Variable	**β**	**SE**	**z-value**	***P*-value**
Intercept	-2.218	0.023	-97.724	< 0.001
Year 2100	0.314	0.030	10.374	< 0.001
RCP4.5	0.009	0.032	0.287	0.774
RCP8.5	-0.013	0.032	-0.408	0.683
Medium Harvest	-0.082	0.033	-2.501	0.012
High Harvest	0.264	0.031	8.650	< 0.001
2100 x RCP4.5	-0.043	0.043	-0.995	0.320
2100 x RCP8.5	0.166	0.042	3.925	< 0.001
2100 x Medium Harvest	0.118	0.043	2.727	0.006
2100 x High Harvest	0.191	0.040	4.730	< 0.001
RCP4.5 x Medium Harvest	-0.008	0.046	-0.176	0.860
RCP8.5 x Medium Harvest	0.076	0.046	1.664	0.096
RCP4.5 x High Harvest	-0.127	0.044	-2.922	0.003
RCP8.5 x High Harvest	-0.041	0.044	-0.946	0.344
2100 x RCP4.5 x Medium Harvest	-0.089	0.061	-1.458	0.145
2100 x RCP8.5 x Medium Harvest	-0.027	0.060	-0.448	0.654
2100 x RCP4.5 x High Harvest	0.03	0.057	3.526	< 0.001
2100 x RCP8.5 x High Harvest	0.192	0.057	3.393	< 0.001

Table E 4. Parameter estimates from post-hoc Tukey honestly significant difference between all pairwise comparisons for the model considering data collected during the summer. Significance levels: ****P < 0.001, ***P < 0.01, **P < 0.05, *P < 0.1.

Variable	Numerical response			
	Mean difference	95% CI Lower bound	95% CI Upper bound	*P*-value
Year				
2100-2050	0.057	0.055	0.059	< 0.001 ****
CC				
RCP4.5-baseline	-0.004	-0.007	-0.001	0.006 ***
RCP8.5-baseline	0.015	0.013	0.018	< 0.001 ****
RCP8.5-RCP4.5	0.019	0.017	0.022	< 0.001 ****
LUC				
Medium harvest-No harvest	-0.001	-0.004	0.002	0.651
High harvest-No harvest	0.048	0.045	0.050	< 0.001 ****
High harvest-Medium harvest	0.049	0.046	0.052	< 0.001 ****
Year x CC				
2050:RCP45-2050:baseline	-0.004	-0.009	0.001	0.253
2050:RCP85-2050:baseline	-0.001	-0.005	0.004	0.999
2100:RCP45-2100:baseline	-0.004	-0.009	0.001	0.225
2100:RCP85-2100:baseline	0.032	0.027	0.037	< 0.001 ****
2050:RCP85-2050:RCP45	0.003	-0.002	0.008	0.418
2100:RCP85-2100:RCP45	0.036	0.030	0.040	< 0.001 ****
2100:baseline-2050:baseline	0.047	0.042	0.052	< 0.001 ****
2100:RCP45-2050:RCP45	0.047	0.042	0.052	< 0.001 ****
2100:RCP85-2050:RCP85	0.079	0.074	0.084	< 0.001 ****
2100:RCP45-2050:baseline	0.043	0.038	0.048	< 0.001 ****
2100:RCP85-2050:baseline	0.078	0.073	0.083	< 0.001 ****
2050:RCP45-2100:baseline	-0.051	-0.056	-0.046	< 0.001 ****

2050:RCP85-2100:baseline	-0.047	-0.052	-0.042	< 0.001 ****
2100:RCP85-2050:RCP45	0.082	0.077	0.087	< 0.001 ****
2050:RCP85-2100:RCP45	-0.043	-0.048	-0.038	< 0.001 ****
Year x LUC				
2050:Medium harvest-2050:No harvest	-0.005	-0.010	-0.001	0.048**
2050: High harvest-2050:No harvest	0.020	0.015	0.025	< 0.001 ****
2100:Medium harvest-2100:No harvest	0.003	-0.002	0.008	0.569
2100: High harvest-2100:No harvest	0.075	0.070	0.080	< 0.001 ****
2050: High harvest-2050:Medium harvest	0.025	0.020	0.030	< 0.001 ****
2100: High harvest-2100:Medium harvest	0.072	0.067	0.077	< 0.001 ****
2100:NoHarvest-2050:NoHarvest	0.036	0.031	0.041	< 0.001 ****
2100:Medium harvest-2050:Medium harvest	0.044	0.039	0.049	< 0.001 ****
2100: High harvest-2050: High harvest	0.091	0.086	0.096	< 0.001 ****
2100:Medium harvest-2050:NoHarvest	0.039	0.034	0.044	< 0.001 ****
2100: High harvest-2050:NoHarvest	0.112	0.106	0.117	< 0.001 ****
2050:Medium harvest-2100:NoHarvest	-0.042	-0.047	-0.037	< 0.001 ****
2050: High harvest-2100:NoHarvest	-0.016	-0.021	-0.011	< 0.001 ****
2100: High harvest-2050:Medium harvest	0.116	0.112	0.122	< 0.001 ****
2050: High harvest-2100:Medium harvest	-0.019	-0.024	-0.014	< 0.001 ****
Year x LUC x CC				
2100:baseline:NoHarvest-2050:baseline:NoHarvest	0.031	0.020	0.042	< 0.001 ****
2050:RCP45:NoHarvest-2050:baseline:NoHarvest	0.000	-0.009	0.011	0.999
2100:RCP45:NoHarvest-2050:baseline:NoHarvest	0.027	0.017	0.038	< 0.001 ****
2050:RCP85:NoHarvest-2050:baseline:NoHarvest	-0.001	-0.011	0.009	0.999

2100:RCP85:NoHarvest-2050:baseline:NoHarvest	0.049	0.039	0.060	< 0.001 ****
2050:baseline:Medium harvest-2050:baseline:NoHarvest	-0.006	-0.017	0.003	0.671
2100:baseline:Medium harvest-2050:baseline:NoHarvest	0.035	0.024	0.046	< 0.001 ****
2050:RCP45:Medium harvest-2050:baseline:NoHarvest	-0.006	-0.017	0.003	0.692
2100:RCP45:Medium harvest-2050:baseline:NoHarvest	0.021	0.010	0.031	< 0.001 ****
2050:RCP85:Medium harvest-2050:baseline:NoHarvest	-0.001	-0.012	0.009	0.999
2100:RCP85:Medium harvest-2050:baseline:NoHarvest	0.061	0.050	0.071	< 0.001 ****
2050:baseline:High harvest-2050:baseline:NoHarvest	0.026	0.015	0.036	< 0.001 ****
2100:baseline:High harvest-2050:baseline:NoHarvest	0.092	0.081	0.102	< 0.001 ****
2050:RCP45:High harvest-2050:baseline:NoHarvest	0.013	0.002	0.024	0.001***
2100:RCP45:High harvest-2050:baseline:NoHarvest	0.098	0.087	0.109	< 0.001 ****
2050:RCP85:High harvest-2050:baseline:NoHarvest	0.020	0.009	0.030	0.000****
2100:RCP85:High harvest-2050:baseline:NoHarvest	0.143	0.132	0.154	< 0.001 ****
2050:RCP45:NoHarvest-2100:baseline:NoHarvest	-0.030	-0.041	-0.020	< 0.001 ****
2100:RCP45:NoHarvest-2100:baseline:NoHarvest	-0.003	-0.014	0.006	0.998
2050:RCP85:NoHarvest-2100:baseline:NoHarvest	-0.032	-0.043	-0.022	< 0.001 ****
2100:RCP85:NoHarvest-2100:baseline:NoHarvest	0.018	0.007	0.029	0.000****
2050:baseline:Medium harvest-2100:baseline:NoHarvest	-0.038	-0.049	-0.027	< 0.001 ****
2100:baseline:Medium harvest-2100:baseline:NoHarvest	0.004	-0.006	0.014	0.996
2050:RCP45:Medium harvest-2100:baseline:NoHarvest	-0.038	-0.049	-0.027	< 0.001 ****
2100:RCP45:Medium harvest-2100:baseline:NoHarvest	-0.010	-0.021	0.000	0.070*
2050:RCP85:Medium harvest-2100:baseline:NoHarvest	-0.033	-0.043	-0.022	< 0.001 ****
2100:RCP85:Medium harvest-2100:baseline:NoHarvest	0.029	0.018	0.040	< 0.001 ****
2050:baseline:High harvest-2100:baseline:NoHarvest	-0.005	-0.016	0.005	0.929
2100:baseline:High harvest-2100:baseline:NoHarvest	0.060	0.049	0.071	< 0.001 ****
2050:RCP45:High harvest-	-0.017	-0.028	-0.007	0.000****

2100:baseline:NoHarvest				
2100:RCP45:High harvest-2100:baseline:NoHarvest	0.067	0.056	0.077	< 0.001 ****
2050:RCP85:High harvest-2100:baseline:NoHarvest	-0.011	-0.022	-0.000	0.026***
2100:RCP85:High harvest-2100:baseline:NoHarvest	0.111	0.101	0.122	< 0.001 ****
2100:RCP45:NoHarvest-2050:RCP45:NoHarvest	0.027	0.016	0.037	< 0.001 ****
2050:RCP85:NoHarvest-2050:RCP45:NoHarvest	-0.001	-0.012	0.008	0.999
2100:RCP85:NoHarvest-2050:RCP45:NoHarvest	0.049	0.038	0.059	< 0.001 ****
2050:baseline:Medium harvest-2050:RCP45:NoHarvest	-0.007	-0.018	0.002	0.471
2100:baseline:Medium harvest-2050:RCP45:NoHarvest	0.034	0.024	0.045	< 0.001 ****
2050:RCP45:Medium harvest-2050:RCP45:NoHarvest	-0.007	-0.018	0.002	0.492
2100:RCP45:Medium harvest-2050:RCP45:NoHarvest	0.020	0.009	0.031	< 0.001 ****
2050:RCP85:Medium harvest-2050:RCP45:NoHarvest	-0.002	-0.013	0.008	0.999
2100:RCP85:Medium harvest-2050:RCP45:NoHarvest	0.060	0.049	0.070	< 0.001 ****
2050:baseline:High harvest-2050:RCP45:NoHarvest	0.025	0.014	0.035	< 0.001 ****
2100:baseline:High harvest-2050:RCP45:NoHarvest	0.091	0.080	0.102	< 0.001 ****
2050:RCP45:High harvest-2050:RCP45:NoHarvest	0.012	0.002	0.023	0.004***
2100:RCP45:High harvest-2050:RCP45:NoHarvest	0.097	0.087	0.108	< 0.001 ****
2050:RCP85:High harvest-2050:RCP45:NoHarvest	0.019	0.008	0.030	0.000****
2100:RCP85:High harvest-2050:RCP45:NoHarvest	0.142	0.131	0.153	< 0.001 ****
2050:RCP85:NoHarvest-2100:RCP45:NoHarvest	-0.028	-0.039	-0.018	< 0.001 ****
2100:RCP85:NoHarvest-2100:RCP45:NoHarvest	0.022	0.011	0.032	< 0.001 ****
2050:baseline:Medium harvest-2100:RCP45:NoHarvest	-0.034	-0.045	-0.024	< 0.001 ****
2100:baseline:Medium harvest-2100:RCP45:NoHarvest	0.007	-0.002	0.018	0.457
2050:RCP45:Medium harvest-2100:RCP45:NoHarvest	-0.034	-0.045	-0.024	< 0.001 ****
2100:RCP45:Medium harvest-2100:RCP45:NoHarvest	-0.006	-0.017	0.004	0.754
2050:RCP85:Medium harvest-2100:RCP45:NoHarvest	-0.029	-0.040	-0.018	< 0.001 ****

2100:RCP85:Medium harvest-2100:RCP45:NoHarvest	0.033	0.022	0.043	< 0.001 ****
2050:baseline:High harvest-2100:RCP45:NoHarvest	-0.001	-0.012	0.008	0.999
2100:baseline:High harvest-2100:RCP45:NoHarvest	0.064	0.053	0.075	< 0.001 ****
2050:RCP45:High harvest-2100:RCP45:NoHarvest	-0.014	-0.024	-0.003	0.000****
2100:RCP45:High harvest-2100:RCP45:NoHarvest	0.070	0.060	0.081	< 0.001 ****
2050:RCP85:High harvest-2100:RCP45:NoHarvest	-0.007	-0.018	0.003	0.523
2100:RCP85:High harvest-2100:RCP45:NoHarvest	0.115	0.104	0.126	< 0.001 ****
2100:RCP85:NoHarvest-2050:RCP85:NoHarvest	0.051	0.040	0.061	< 0.001 ****
2050:baseline:Medium harvest-2050:RCP85:NoHarvest	-0.005	-0.016	0.004	0.895
2100:baseline:Medium harvest-2050:RCP85:NoHarvest	0.036	0.026	0.047	< 0.001 ****
2050:RCP45:Medium harvest-2050:RCP85:NoHarvest	-0.005	-0.016	0.004	0.906
2100:RCP45:Medium harvest-2050:RCP85:NoHarvest	0.022	0.011	0.033	< 0.001 ****
2050:RCP85:Medium harvest-2050:RCP85:NoHarvest	-0.000	-0.011	0.010	0.999
2100:RCP85:Medium harvest-2050:RCP85:NoHarvest	0.062	0.051	0.072	< 0.001 ****
2050:baseline:High harvest-2050:RCP85:NoHarvest	0.027	0.016	0.037	< 0.001 ****
2100:baseline:High harvest-2050:RCP85:NoHarvest	0.093	0.082	0.104	< 0.001 ****
2050:RCP45:High harvest-2050:RCP85:NoHarvest	0.014	0.004	0.025	0.000****
2100:RCP45:High harvest-2050:RCP85:NoHarvest	0.099	0.089	0.110	< 0.001 ****
2050:RCP85:High harvest-2050:RCP85:NoHarvest	0.021	0.010	0.032	< 0.001 ****
2100:RCP85:High harvest-2050:RCP85:NoHarvest	0.144	0.133	0.155	< 0.001 ****
2050:baseline:Medium harvest-2100:RCP85:NoHarvest	-0.056	-0.067	-0.046	< 0.001 ****
2100:baseline:Medium harvest-2100:RCP85:NoHarvest	-0.014	-0.024	-0.003	0.000****
2050:RCP45:Medium harvest-2100:RCP85:NoHarvest	-0.056	-0.067	-0.046	< 0.001 ****
2100:RCP45:Medium harvest-2100:RCP85:NoHarvest	-0.028	-0.039	-0.017	< 0.001 ****
2050:RCP85:Medium harvest-2100:RCP85:NoHarvest	-0.051	-0.062	-0.040	< 0.001 ****
2100:RCP85:Medium harvest-	0.011	0.000	0.021	0.032***

2100:RCP85:NoHarvest				
2050:baseline:High harvest-2100:RCP85:NoHarvest	-0.023	-0.034	-0.013	< 0.001 ****
2100:baseline:High harvest-2100:RCP85:NoHarvest	0.042	0.031	0.053	< 0.001 ****
2050:RCP45:High harvest-2100:RCP85:NoHarvest	-0.036	-0.046	-0.025	< 0.001 ****
2100:RCP45:High harvest-2100:RCP85:NoHarvest	0.048	0.038	0.059	< 0.001 ****
2050:RCP85:High harvest-2100:RCP85:NoHarvest	-0.029	-0.040	-0.018	< 0.001 ****
2100:RCP85:High harvest-2100:RCP85:NoHarvest	0.093	0.082	0.104	< 0.001 ****
2100:baseline:Medium harvest-2050:baseline:Medium harvest	0.042	0.031	0.053	< 0.001 ****
2050:RCP45:Medium harvest-2050:baseline:Medium harvest	0.000	-0.010	0.010	0.999
2100:RCP45:Medium harvest-2050:baseline:Medium harvest	0.028	0.017	0.038	< 0.001 ****
2050:RCP85:Medium harvest-2050:baseline:Medium harvest	0.005	-0.005	0.016	0.945
2100:RCP85:Medium harvest-2050:baseline:Medium harvest	0.068	0.057	0.078	< 0.001 ****
2050:baseline:High harvest-2050:baseline:Medium harvest	0.033	0.022	0.043	< 0.001 ****
2100:baseline:High harvest-2050:baseline:Medium harvest	0.099	0.088	0.109	< 0.001 ****
2050:RCP45:High harvest-2050:baseline:Medium harvest	0.020	0.009	0.031	< 0.001 ****
2100:RCP45:High harvest-2050:baseline:Medium harvest	0.105	0.094	0.116	< 0.001 ****
2050:RCP85:High harvest-2050:baseline:Medium harvest	0.027	0.016	0.037	< 0.001 ****
2100:RCP85:High harvest-2050:baseline:Medium harvest	0.150	0.139	0.161	< 0.001 ****
2050:RCP45:Medium harvest-2100:baseline:Medium harvest	-0.042	-0.053	-0.031	< 0.001 ****
2100:RCP45:Medium harvest-2100:baseline:Medium harvest	-0.014	-0.025	-0.003	0.000****
2050:RCP85:Medium harvest-2100:baseline:Medium harvest	-0.037	-0.048	-0.026	< 0.001 ****
2100:RCP85:Medium harvest-2100:baseline:Medium harvest	0.025	0.014	0.036	< 0.001 ****
2050:baseline:High harvest-2100:baseline:Medium harvest	-0.009	-0.020	0.001	0.130
2100:baseline:High harvest-2100:baseline:Medium harvest	0.056	0.045	0.067	< 0.001 ****
2050:RCP45:High harvest-2100:baseline:Medium harvest	-0.021	-0.032	-0.011	< 0.001 ****
2100:RCP45:High harvest-2100:baseline:Medium harvest	0.063	0.052	0.073	< 0.001 ****

2050:RCP85:High harvest-2100:baseline:Medium harvest	-0.015	-0.026	-0.004	0.000****
2100:RCP85:High harvest-2100:baseline:Medium harvest	0.107	0.097	0.118	< 0.001 ****
2100:RCP45:Medium harvest-2050:RCP45:Medium harvest	0.028	0.017	0.038	< 0.001 ****
2050:RCP85:Medium harvest-2050:RCP45:Medium harvest	0.005	-0.005	0.016	0.952
2100:RCP85:Medium harvest-2050:RCP45:Medium harvest	0.067	0.057	0.078	< 0.001 ****
2050:baseline:High harvest-2050:RCP45:Medium harvest	0.032	0.022	0.043	< 0.001 ****
2100:baseline:High harvest-2050:RCP45:Medium harvest	0.099	0.088	0.109	< 0.001 ****
2050:RCP45:High harvest-2050:RCP45:Medium harvest	0.020	0.009	0.031	< 0.001 ****
2100:RCP45:High harvest-2050:RCP45:Medium harvest	0.105	0.094	0.116	< 0.001 ****
2050:RCP85:High harvest-2050:RCP45:Medium harvest	0.027	0.016	0.037	< 0.001 ****
2100:RCP85:High harvest-2050:RCP45:Medium harvest	0.150	0.139	0.161	< 0.001 ****
2050:RCP85:Medium harvest-2100:RCP45:Medium harvest	-0.022	-0.033	-0.012	< 0.001 ****
2100:RCP85:Medium harvest-2100:RCP45:Medium harvest	0.039	0.029	0.050	< 0.001 ****
2050:baseline:High harvest-2100:RCP45:Medium harvest	0.004	-0.005	0.015	0.980
2100:baseline:High harvest-2100:RCP45:Medium harvest	0.070	0.060	0.081	< 0.001 ****
2050:RCP45:High harvest-2100:RCP45:Medium harvest	-0.007	-0.018	0.003	0.548
2100:RCP45:High harvest-2100:RCP45:Medium harvest	0.077	0.066	0.088	< 0.001 ****
2050:RCP85:High harvest-2100:RCP45:Medium harvest	-0.000	-0.011	0.009	0.999
2100:RCP85:High harvest-2100:RCP45:Medium harvest	0.122	0.111	0.133	< 0.001 ****
2100:RCP85:Medium harvest-2050:RCP85:Medium harvest	0.062	0.051	0.073	< 0.001 ****
2050:baseline:High harvest-2050:RCP85:Medium harvest	0.027	0.016	0.038	< 0.001 ****
2100:baseline:High harvest-2050:RCP85:Medium harvest	0.093	0.083	0.104	< 0.001 ****
2050:RCP45:High harvest-2050:RCP85:Medium harvest	0.015	0.004	0.026	0.000****
2100:RCP45:High harvest-2050:RCP85:Medium harvest	0.100	0.089	0.111	< 0.001 ****
2050:RCP85:High harvest-2050:RCP85:Medium harvest	0.021	0.011	0.032	< 0.001 ****

2100:RCP85:High harvest-2050:RCP85:Medium harvest	0.145	0.134	0.155	< 0.001 ****
2050:baseline:High harvest-2100:RCP85:Medium harvest	-0.034	-0.045	-0.024	< 0.001 ****
2100:baseline:High harvest-2100:RCP85:Medium harvest	0.031	0.020	0.041	< 0.001 ****
2050:RCP45:High harvest-2100:RCP85:Medium harvest	-0.047	-0.058	-0.036	< 0.001 ****
2100:RCP45:High harvest-2100:RCP85:Medium harvest	0.037	0.026	0.048	< 0.001 ****
2050:RCP85:High harvest-2100:RCP85:Medium harvest	-0.040	-0.051	-0.030	< 0.001 ****
2100:RCP85:High harvest-2100:RCP85:Medium harvest	0.082	0.071	0.093	< 0.001 ****
2100:baseline:High harvest-2050:baseline:High harvest	0.066	0.055	0.076	< 0.001 ****
2050:RCP45:High harvest-2050:baseline:High harvest	-0.012	-0.023	-0.001	0.008***
2100:RCP45:High harvest-2050:baseline:High harvest	0.072	0.061	0.083	< 0.001 ****
2050:RCP85:High harvest-2050:baseline:High harvest	-0.005	-0.016	0.004	0.902
2100:RCP85:High harvest-2050:baseline:High harvest	0.117	0.106	0.128	< 0.001 ****
2050:RCP45:High harvest-2100:baseline:High harvest	-0.078	-0.089	-0.067	< 0.001 ****
2100:RCP45:High harvest-2100:baseline:High harvest	0.006	-0.004	0.017	0.779
2050:RCP85:High harvest-2100:baseline:High harvest	-0.071	-0.082	-0.061	< 0.001 ****
2100:RCP85:High harvest-2100:baseline:High harvest	0.051	0.040	0.062	< 0.001 ****
2100:RCP45:High harvest-2050:RCP45:High harvest	0.084	0.074	0.095	< 0.001 ****
2050:RCP85:High harvest-2050:RCP45:High harvest	0.006	-0.004	0.017	0.776
2100:RCP85:High harvest-2050:RCP45:High harvest	0.129	0.119	0.140	< 0.001 ****
2050:RCP85:High harvest-2100:RCP45:High harvest	-0.078	-0.089	-0.067	< 0.001 ****
2100:RCP85:High harvest-2100:RCP45:High harvest	0.044	0.034	0.055	< 0.001 ****
2100:RCP85:High harvest-2050:RCP85:High harvest	0.123	0.112	0.133	< 0.001 ****

Annexe F: Supplementary materials in Chapter 3.

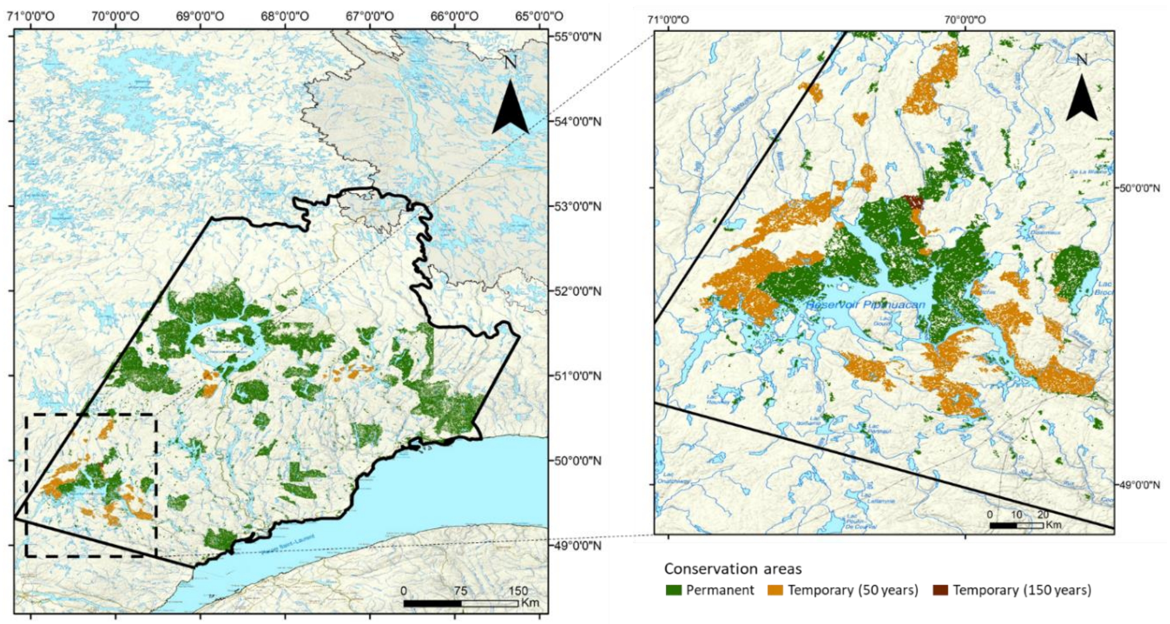

Figure F 1. Conservation areas of the Protected areas scenario showing the temporary (50 or 150 years) or permanent conservation areas where no harvesting take place during the time period considered.

Table F 1. Values of a. the percentage of total disturbances, b. burned areas, c. deciduous vegetation, d. landscape homogeneity, e. isolation of mature conifer stands, and f. stand age as a function of the different scenarios. Following Environment Canada's (2011) caribou recovery planning approach, the levels of disturbance were calculated as the percentage of the landscape of the nonoverlapping surface of burns, roads, and cuts. Disturbed areas also included a 500-m buffer zone on each side of roads and around cuts. If the value of the 'isolation index' was close to 0, patches of the same class were aggregated, whereas an increase in the value indicated that patches became isolated. If the value of the 'homogenization index' is small, cells of one category are adjacent to cells of many other categories. Conversely, high 'homogenization index' values show that cells of one category are predominantly adjacent to only one other category of cells.

a. Percentage of total disturbances

	Baseline				RCP 4.5				RCP 8.5			
	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest
2000	32%	32%	32%	32%	32%	32%	32%	32%	32%	32%	32%	32%
2100	25%	58%	61%	71%	33%	63%	65%	76%	43%	68%	71%	76%

b. Percentage of burned areas

	Baseline				RCP 4.5				RCP 8.5			
	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest
2000	13%	13%	13%	13%	13%	13%	13%	13%	13%	13%	13%	13%
2100	15%	15%	17%	17%	23%	23%	24%	25%	36%	35%	36%	31%

c. Percentage of deciduous vegetation

	Baseline				RCP 4.5				RCP 8.5			
	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest
2000	18%	18%	18%	18%	18%	18%	18%	18%	18%	18%	18%	18%
2100	38%	45%	46%	50%	34%	43%	43%	48%	45%	53%	54%	58%

d. Landscape homogeneity

	Baseline				RCP 4.5				RCP 8.5			
	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest
2000	0.57	0.57	0.57	0.57	0.57	0.57	0.57	0.57	0.57	0.57	0.57	0.57
2100	0.57	0.55	0.58	0.60	0.61	0.58	0.60	0.64	0.66	0.63	0.64	0.66

e. Isolation of mature conifer stands (%)

	Baseline				RCP 4.5				RCP 8.5			
	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest
2000	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
2100	1.6	5.4	4.9	5.6	1.2	3.9	4.1	5.6	4.1	9.4	5.5	6.3

f. Mean stand age

	Baseline				RCP 4.5				RCP 8.5			
	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest
2000	64	64	64	64	64	64	64	64	64	64	64	64
2100	97	71	66	53	89	63	61	46	72	52	49	42

Table F 2. Values of a. the percentage of deciduous land cover and b. the associated number of moose and c. wolf packs as a function of the different simulation scenarios. Wolf packs are constituted with 4 wolves.

a. Percentage of deciduous vegetation

	Baseline				RCP 4.5				RCP 8.5			
	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest
2000	18%	18%	18%	18%	18%	18%	18%	18%	18%	18%	18%	18%
2100	38%	45%	46%	50%	34%	43%	43%	48%	45%	53%	54%	58%

b. Moose density (Ind./100km²)

	Baseline				RCP 4.5				RCP 8.5			
	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest
2000	4.33	4.33	4.33	4.33	4.33	4.33	4.33	4.33	4.33	4.33	4.33	4.33
2100	15.26	18.82	19.31	21.28	13.16	17.81	17.81	20.30	18.82	22.70	23.21	25.11

c. Wolf pack density (Pack/100km²)

	Baseline				RCP 4.5				RCP 8.5			
	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest	No harvest	Protected areas	Medium harvest	High harvest
2000	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
2100	0.24	0.29	0.30	0.32	0.22	0.28	0.28	0.31	0.29	0.34	0.34	0.36

Annexe G: Predictive models used in Chapter 3.

Table G 1. Predictive models of occupancy determined in Bouderbala et al. (2022) for 31 bird species and 77 beetle species.

	Code	***Species*** ***French name*** ***English name*** ***Scientific name***	***Main habitat associations***	***Model***
Birds	WCSP	Bruant à couronne blanche White-crowned sparrow *(Zonotrichia leucophrys)*	Early-Mid succession forests	$w(x) = -11.90 - 1.88 \times Age - 1.79 \times Age^2 - 12.13 \times dist._{Burned010} - 9.08 \times dist._{Burned010}^2 - 2.79 \times dist._{Burned2050} - 0.26 \times Prop_{Burned2050}$
	GRYE	Chevalier criard Greater yellowlegs (*Tringa melanoleuca*)	Early-Mid succession forests	$w(x) = -6.01 - 0.69 \times dist._{Burned010} - 1.03 \times dist._{Burned2050} + 0.55 \times dist._{Burned2050}^2 + 0.3 \times Prop_{Burned010}$
	OVEN	Paruline couronnée Ovenbird *(Seiurus aurocapilla)*	Early-Mid succession forests	$w(x) = -4.71 - 1.71 \times Age^2 + 0.52 \times dist._{Burned2050} - 2.07 \times Prop_{Cuts1020} - 0.72 \times Prop_{Open\ conifer} + 0.56 \times Prop_{mixed}$
	BLWA	Paruline à gorge orange Blackburnian warbler (*Setophaga fusca*)	Early-Mid succession forests	$w(x) = -4.15 + 0.33 \times Prop_{Cuts1020} - 0.25 \times Prop_{Cuts2050} - 0.33 \times Prop_{mixed} - 1.45 \times Prop_{open}$
	REVI	Viréo à œil rouge Red-eyed vireo (*Vireo olivaceus*)	Early-Mid succession forests	$w(x) = -1.77 - 0.20 \times Age - 0.65 \times Age^2 + 0.30 \times dist._{Burned010} - 0.13 \times dist._{Burned010}^2 + 0.28 \times dist._{Burned1020} + 0.11 \times dist._{Burned1020}^2 - 0.77 \times Prop_{Open\ conifer} + 0.42 \times Prop_{mixed}$
	WTSP	Bruant à gorge blanche White-throated sparrow (*Zonotrichia albicollis*)	Early-Mid succession forests	$w(x) = 2.86 - 0.65 \times Age + 0.52 \times Prop_{Cuts010} + 1.54 \times Prop_{Cuts1020} - 0.12 \times Prop_{mixed} - 0.31 \times Prop_{open}$
	BBWA	Paruline à poitrine baie Bay-breasted Warbler(*Setophaga castanea*)	Mature forests	$w(x) = -2.11 + 0.18 \times Age - 0.34 \times Age^2 + 0.13 \times Prop_{Closed\ conifer} - 0.29 \times Prop_{Cuts010} + 0.42 \times Prop_{Cuts2050} + 0.41 \times Prop_{Mixed}$

Birds	CMWA	Paruline tigrée Cape May warbler(*Setophaga tigrina)*	Mature forests	$w(x) = -1.90 + 0.28 \times Age - 0.32 \times Age^2$ $+ 0.43 \times dist._{Burned1020} - 0.13 \times dist._{Burned1020}^2$ $- 0.20 \times Prop_{Cuts1020} + 0.39 \times Prop_{Cuts2050}$ $+ 0.29 \times Prop_{Mixed}$
	CSWA	Paruline à flancs marron Chestnut-sided warbler (*Setophaga pensylvanica)*	Early-Mid succession forests	$w(x) = -5.45 - 0.78 \times dist._{Burned1020} - 0.56 \times Prop_{Open\ conifer}$ $+ 0.45 \times Prop_{Mixed}$
	WIWA	Paruline à calotte noire Wilson's warbler (*Cardellina pusilla)*	Early-Mid succession forests	$w(x) = -2.73 - 0.29 \times Age - 0.18 \times dist._{Burned1020}$ $+ 0.27 \times Prop_{Cuts010} + 0.30 \times Prop_{Cuts1020}$ $- 0.21 \times Prop_{Mixed}$
	RUBL	Quiscale rouilleux Rusty blackbird (*Euphagus carolinus)*	Early-Mid succession forests	$w(x) = -4.72 - 0.94 \times Age - 0.61 \times Age^2$ $- 1.36 \times dist._{Burned2050} - 0.25 \times Prop_{Burned2050}$
	BCCH	Mésange à tête noire Black-capped chickadee (*Poecile atricapillus)*	Early-Mid succession forests	$w(x) = -3.57 - 0.85 \times Age^2 + 0.20 \times dist._{Burned010}^2$ $- 0.73 \times Prop_{Open\ conifer}$
	BRCR	Grimpereau brun Brown creeper (*Certhia americana*)	Mature forests	$w(x) = -3.93 + 0.58 \times Age + 0.26 \times Age^2 - 0.38 \times dist._{Burned010}$ $- 0.39 \times dist._{Burned010}^2 + 0.71 \times dist._{Burned2050}$ $- 0.29 \times dist._{Burned2050}^2$
	FOSP	Bruant fauve Fox sparrow (*Passerella iliaca*)	Early-Mid succession forests	$w(x) = -1.84 + 0.42 \times Prop_{Cuts1020} + 0.11 \times Prop_{Mixed}$ $- 0.19 \times Prop_{Open} + 0.51 \times Prop_{Burned2050}$
	AMRE	Paruline flamboyante American redstart (*Setophaga ruticilla*)	Early-Mid succession forests	$w(x) = -2.29 - 0.32 \times Age - 0.40 \times Age^2 + 0.41 \times dist._{Burned010}$ $- 0.12 \times dist._{Burned010}^2 + 0.15 \times Prop_{Cuts2050}$ $- 0.30 \times Prop_{Open\ conifer} + 0.31 \times Prop_{Mixed}$
	SWTH	Grive à dos olive Swainson's thrush (*Catharus ustulatus*)	Mature forests	$w(x) = 1.09 + 0.33 \times dist._{Burned010} - 0.22 \times dist._{Burned010}^2$ $+ 0.52 \times dist._{Burned2050} - 0.13 \times dist._{Burned2050}^2$ $+ 0.19 \times Prop_{Closed\ conifer} + 0.52 \times Prop_{Cuts2050}$
	EVGR	Gros-bec errant Evening grosbeak (*Coccothraustes vespertinus)*	Mature forests	$w(x) = -4.29 - 0.40 \times Prop_{Cuts1020} + 0.25 \times Prop_{Cus2050}$ $+ 0.57 \times Prop_{Mixed}$
	PAWA	Paruline à couronne rousse Palm warbler (*Setophaga palmarum*)	Early-Mid succession forests	$w(x) = -4.71 - 0.72 \times Age - 1.12 \times Prop_{Cuts2050}$ $+ 0.27 \times Prop_{Burned1020}$

Birds	WWCR	Bec-croisé bifascié Two-barred crossbill (*Loxia leucoptera)*	Mature forests	$w(x) = -2.66 - 0.39 \times dist._{Burned010}^{2} + 0.18 \times Prop_{Cuts010} + 0.27 \times Prop_{Open\ conifer}$
	ALFL	Moucherolle des aulnes Alder flycatcher (*Empidonax alnorum*)	Early-Mid succession forests	$w(x) = -0.63 - 0.22 \times Age + 0.29 \times dist._{Burned010} - 0.12 \times dist._{Burned010}^{2} + 0.34 \times Prop_{Cuts010} + 0.33 \times Prop_{Cuts1020}$
	CAGO	Bernache du Canada Canada goose (*Branta canadensis*)	Early-Mid succession forests	$w(x) = -4.64 + 0.24 \times Prop_{Cuts010} - 0.43 \times Prop_{Mixed} + 0.31 \times Prop_{Open}$
	GCKI	Roitelet à couronne dorée Golden-crowned kinglet (*Regulus satrapa*)	Mature forests	$w(x) = -2.03 + 0.28 \times Age - 0.48 \times Prop_{Burned010} - 0.47 \times Prop_{Burned2050}$
	LISP	Bruant de Lincoln Lincoln's sparrow (*Melospiza lincolnii*)	Early-Mid succession forests	$w(x) = -1.66 - 0.31 \times Age + 0.27 \times Prop_{Cuts010} + 0.30 \times Prop_{Cuts1020} - 0.21 \times Prop_{Mixed} + 0.25 \times Prop_{Open}$
	TEWA	Paruline obscure Tennessee warbler (*Leiothlypis peregrina)*	Early-Mid succession forests	$w(x) = 0.65 + 0.14 \times Age - 0.21 \times Age^{2} + 0.19 \times dist._{Burned2050} + 0.36 \times Prop_{Cuts2050} + 0.14 \times Prop_{Mixed} - 0.21 \times Prop_{Burned2050}$
	DEJU	Junco ardoisé Dark-eyed junco (*Junco hyemalis)*	Early-Mid succession forests	$w(x) = -0.48 + 0.25 \times Age - 0.26 \times dist._{Burned010} - 0.26 \times Prop_{Mixed} - 0.44 \times Prop_{Open}$
	MAWA	Paruline à tête cendrée Magnolia warbler (*Setophaga magnolia*)	Early-Mid succession forests	$w(x) = 0.78 + 0.34 \times dist._{Burned010} - 0.16 \times dist._{Burned010}^{2} + 0.31 \times dist._{Burned2050} - 0.19 \times dist._{Burned2050}^{2} + 0.22 \times Prop_{Cuts1020} + 0.28 \times Prop_{Cuts2050} - 0.09 \times Prop_{Burned2050}$
	YEWA	Paruline jaune American yellow warbler (*Setophaga petechia)*	Early-Mid succession forests	$w(x) = -4.46 - 0.71 \times Age - 0.90 \times Prop_{Cuts010} - 0.75 \times Prop_{Cuts1020}$
	AMCR	Corneille d'Amérique American Crow (*Corvus brachyrhynchos*)	Generalist	$w(x) = -3.04 + 0.62 \times Age - 0.89 \times Age^{2} + 0.21 \times dist._{Burned010}^{2} - 0.91 \times Prop_{Closed\ conifer} - 0.44 \times Prop_{Open\ conifer} + 0.31 \times Prop_{Open}$
	AMGO	Chardonneret jaune American Goldfinch (*Spinus tristis*)	Generalist	$w(x) = -5.31 + 0.40 \times Age - 1.03 \times Age^{2} - 3.71 \times Prop_{Closed\ conifer} - 1.40 \times Prop_{Cuts1020} + 0.39 \times Prop_{Open\ conifer} + 0.13 \times Prop_{Open}$

Birds	CHSP	Bruant passerin Chipping Sparrow (*Spizella passerine*)	Generalist	$w(x) = -3.83 + 0.90 \times Age - 1.29 \times Age^2 - 0.42 \times dist._{Burned010} + 0.48 \times dist.^2_{Burned010} - 0.16 \times dist.^2_{Burned1020} - 0.82 \times Prop_{Open\ conifer} + 0.23 \times Prop_{Open}$
	SASP	Bruant des prés Savannah Sparrow (*Passerculus sandwichensis)*	Generalist	$w(x) = -4.72 + 0.99 \times Prop_{Cuts010} - 1.84 \times Prop_{Closed\ conifer} + 0.50 \times Prop_{Open}$

	Code	*Family*	*Genus*	*Species*	*Model*
Beetles	LATHCORALAPP	*Latridiidae*	*Corticaria*	*lapponica*	$w(x) = -12.94 + 0.61 \times dist._{Burned1020}$
	STAPBORSLAMF	*Staphylinidae*	*Boreostiba*	*frigida*	$w(x) = -12.93 + 1.94 \times Age$
	LATHCORASERR	*Latridiidae*	*Corticaria*	*serricollis*	$w(x) = -11.40 + 0.17 \times Prop_{Burned1020}$
	STAPLIOGTERM	*Staphylinidae*	*Liogluta*	*terminalis*	$w(x) = -23.01 + 1.91 \times Age + 2.66 \times dist.^2_{Burned1020}$
	CRYPCRYPCROU	*Cryptophagidae*	*Cryptophagus*	*croceus*	$w(x) = -11.12 + 0.87 \times Age - 1.53 \times Prop_{Closed\ conifer} + 0.53 \times Prop_{Cuts2050}$
	LATHCORASERT	*Latridiidae*	*Corticaria*	*serrata*	$w(x) = -10.93 - 1.07 \times dist.^2_{Burned010} + 0.28 \times dist.^2_{Burned2050}$
	STAPPROTPARQ	*Staphylinidae*	*Proteinus*	*parvulus*	$w(x) = -11.43 + 0.75 \times Prop_{Open\ conifer}$
	SCYDSTENTURT	*Staphylinidae*	*Stenichnus*	*turbatus*	$w(x) = -6.73 - 0.34 \times Prop_{Closed\ conifer}$
	STAPDINABORE	*Staphylinidae*	*Dinaraea*	*borealis*	$w(x) = -6.30 + 0.85 \times Age + 0.44 \times Prop_{mixed}$
	LEIOAGATEXIS	*Leiodidae*	*Agathidium*	*exiguum*	$w(x) = -5.49 + 0.35 \times Prop_{Burned1020}$
	STAPSTEH	*Staphylinidae*	*Stenichnus*	*NA*	$w(x) = -2.95 + 0.48 \times dist._{Burned1020} + 0.45 \times Prop_{Open}$
	SCOLPITKSPAR	*Curculionidae*	*Pityokteines*	*sparsus*	$w(x) = -3.22 - 0.28 \times Prop_{Closed\ conifer}$
	NITIEPURPLAZ	*Nitidulidae*	*Epuraea*	*planulata*	$w(x) = 8.07 + 2.10 \times Age + 2.76 \times Prop_{Closed\ conifer} + 3.86 \times Prop_{Cuts010} - 0.45 \times Prop_{Cuts2050}$
	SCYDSTENPEFS	*Staphylinidae*	*Stenichnus*	*perforatus*	$w(x) = -5.35 - 0.70 \times dist._{Burned1020}$

Beetles	RHIZRHIZDIMI	*Monotomidae*	*Rhizophagus*	*dimidiatus*	$w(x) = 4.01 + 1.49 \times Age + 1.64 \times Prop_{Closed\ conifer} + 1.01 \times Prop_{Cuts010} - 0.44 \times Prop_{Cuts1020}$
	SILVSILVBIDE	*Silvanidae*	*Silvanus*	*bidentatus*	$w(x) = -2.30 + 0.39 \times dist._{Burned1020}$
	LATHCORA	*Latridiidae*	*Corticaria*	*NA*	$w(x) = 3.27 - 0.60 \times dist._{Burned010} - 0.46 \times dist._{Burned2050}$
	CRYPATOM	*Cryptophagidae*	*Atomaria*	*NA*	$w(x) = 0.88 + 0.33 \times Prop_{Closed\ conifer} + 0.81 \times Prop_{Cuts010} - 0.50 \times Prop_{Cuts2050}$
	LEIOAGATFAWC	*Leiodidae*	*Agathidium*	*fawcettae*	$w(x) = -2.93 - 1.40 \times dist._{Burned010}^2$
	PTILPTIO	*Ptiliidae*	*Ptiliola*	*NA*	$w(x) = 0.36 - 0.54 \times Age^2 + 0.41 \times Prop_{Closed\ conifer} + 0.70 \times Prop_{Cuts010}$
	CLERZENOSANG	*Thanerocleridae*	*Zenodosus*	*sanguineus*	$w(x) = -3.76 - 0.50 \times dist._{Burned010} + 1.31 \times dist._{Burned2050} + 0.79 \times Prop_{Closed\ conifer} + 0.88 \times Prop_{Mixed}$
	STAPOMALRIVE	*Staphylinidae*	*Omalium*	*rivulare*	$w(x) = -3.87 - 0.89 \times dist._{Burned010}$
	NITIEPURBORD	*Nitidulidae*	*Epuraea*	*rufomarginata*	$w(x) = -2.57 - 0.40 \times dist._{Burned010} - 0.40 \times dist._{Burned1020} - 0.49 \times Prop_{Burned2050}$
	LYMEELATLUGU	*Lymexylidae*	*Hylecoetus*	*lugubris*	$w(x) = -2.82 + 0.42 \times Prop_{Closed\ conifer}$
	STAPPHLOLAPP	*Staphylinidae*	*Phloeostiba*	*lapponica*	$w(x) = 1.93 + 0.62 \times Prop_{Cuts010}$
	CURCRHYOMACS	*Curculionidae*	*Rhyncolus*	*macrops*	$w(x) = -2.53 - 0.84 \times dist._{Burned2050}^2$
	STAPACRO	*Staphylinidae*	*Acrotona*	*NA*	$w(x) = -4.10 - 0.43 \times dist._{Burned2050}$
	ELATNEOHTUME	*Elateridae*	*Neohypdonus*	*tumescens*	$w(x) = -3.93 - 0.93 \times Age - 1.06 \times dist._{Burned010} + 0.34 \times Prop_{Burned1020}$
	STAPSYNTGRAH	*Staphylinidae*	*Syntomium*	*grahami*	$w(x) = -3.19 + 0.80 \times Prop_{Cuts010}$
	LEIOAGATREPN	*Leiodidae*	*Agathidium*	*repentinum*	$w(x) = -4.52 + 1.06 \times Prop_{Cuts010}$

Beetles	STAPGABIMICQ	*Staphylinidae*	*Gabrius*	*microphthalmus*	$w(x) = -4.03 + 0.73 \times Age + 1.26 \times Age^2 - 0.98 \times dist._{Burned010}^{2} - 0.89 \times dist._{Burned1020}^{2}$
	MORDMORDBORE	*Mordellidae*	*Mordellaria*	*borealis*	$w(x) = -1.52 - 0.71 \times dist._{Burned010} - 1.11 \times dist._{Burned010}^{2} + 0.38 \times Prop_{Cuts010} + 0.50 \times Prop_{Cuts2050}$
	NITIEPURPARN	*Nitidulidae*	*Epuraea*	*parsonsi*	$w(x) = -2.68 + 0.45 \times dist._{Burned1020} - 0.77 \times dist._{Burned2050} - 0.44 \times Prop_{Closed\ conifer}$
	STAPACIDQUAR	*Staphylinidae*	*Acidota*	*quadrata*	$w(x) = -2.32 + 0.61 \times Age + 0.82 \times Age^2$
	CIIDCISZSTRU	*Ciidae*	*Cis*	*striolatus*	$w(x) = -3.32 - 0.92 \times dist._{Burned2050} + 0.99 \times Prop_{Cuts010}$
	STAPATHE	*Staphylinidae*	*Atheta*	*NA*	$w(x) = 2.15 + 0.27 \times Prop_{Closed\ conifer}$
	STAPQUEDPLAG	*Staphylinidae*	*Quedius*	*plagiatus*	$w(x) = 0.67 + 0.72 \times Age + 0.51 \times dist._{Burned1020} + 0.31 \times Prop_{Closed\ conifer} - 0.26 \times Prop_{Cuts2050} - 0.35 \times Prop_{Open}$
	STAPLIOGALAO	*Staphylinidae*	*Liogluta*	*aloconotoides*	$w(x) = -1.11 + 0.32 \times Age$
	ENDOPHYMPULE	*Endomychidae*	*Phymaphora*	*pulchella*	$w(x) = -3.22 + 0.86 \times dist._{Burned2050}$
	SCOLDRYOAUTO	*Curculionidae*	*Dryocoetes*	*autographus*	$w(x) = 0.91 + 0.53 \times Age + 0.91 \times Prop_{Cuts010}$
	SCOLDRYOBETU	*Curculionidae*	*Dryocoetes*	*betulae*	$w(x) = -1.91 + 0.31 \times Age + 0.15 \times dist._{Burned2050}^{2}$
	CUCUPEDIFUSC	*Cucujidae*	*Pediacus*	*fuscus*	$w(x) = -2.99 + 1.02 \times Age^2 - 0.64 \times dist._{Burned010} - 0.66 \times dist._{Burned1020}^{2} + 0.22 \times Prop_{Burned010} + 0.38 \times Prop_{Burned1020}$
	STAPGYRP	*Staphylinidae*	*Gyrophaena*	*NA*	$w(x) = -3.24 - 0.50 \times Age + 0.60 \times Prop_{Cuts010}$

Beetles	LEIOAGAT	*Leiodidae*	*Agathidium*	*NA*	$w(x) = -1.73 + +1.05 \times dist._{Burned1020} - 0.75 \times dist._{Burned1020}^2 + 0.44 \times Prop_{Burned2050}$
	NITIEPURLINA	*Nitidulidae*	*Epuraea*	*linearis*	$w(x) = -3.55 - 0.56 \times Age$
	NITIEPURTRUT	*Nitidulidae*	*Epuraea*	*truncatella*	$w(x) = 1.17 + 0.42 \times Prop_{Closed\ conifer} + 0.75 \times Prop_{Cuts010} - 0.70 \times Prop_{Cuts2050}$
	STAPOLOPROTL	*Staphylinidae*	*Olophrum*	*rotundicolle*	$w(x) = -0.96 + 0.41 \times Age + 0.33 \times Prop_{Cuts010}$
	PSELEUPL	*Staphylinidae*	*Euplectus*	*NA*	$w(x) = -1.68 + 0.31 \times dist._{Burned2050} - 0.51 \times Prop_{Open}$
	SCOLTRYDLINM	*Curculionidae*	*Trypodendron*	*lineatum*	$w(x) = -0.06 + 0.45 \times Age + 0.37 \times Prop_{Closed\ conifer} - 0.50 \times Prop_{Open}$
	SCYDBRACPUBP	*Staphylinidae*	*Brachycepsis*	*pubipennis*	$w(x) = -2.31 + 0.29 \times dist._{Burned1020}$
	STAPISCHSPLI	*Staphylinidae*	*Ischnosoma*	*splendidum*	$w(x) = -1.69 + 0.34 \times Prop_{Closed\ conifer} + 0.99 \times Prop_{Cuts010}$
	CERAGNATPRAT	*Cerambycidae*	*Gnathacmaeops*	*pratensis*	$w(x) = -3.59 - 0.82 \times Age - 0.75 \times dist._{Burned010} + 0.24 \times Prop_{Burned010}$
	SCYDPARACOYA	*Staphylinidae*	*Parascydmus*	*corpusculus*	$w(x) = -0.03 - 0.81 \times dist._{Burned010} + 1.05 \times Prop_{Cuts010}$
	CARAPLANDECC	*Carabidae*	*Platynus*	*decentis*	$w(x) = -3.01 + 0.72 \times Prop_{Cuts010}$
	SCIRCYPHVARB	*Scirtidae*	*Cyphon*	*variabilis*	$w(x) = -3.21 + 0.90 \times Prop_{Cuts010}$
	STAPTACIELON	*Staphylinidae*	*Tachinus*	*elongatus*	$w(x) = -2.44 - 0.43 \times dist._{Burned010}$
	STAPLEPSBREL	*Staphylinidae*	*Leptusa*	*brevicollis*	$w(x) = -1.86 - 0.46 \times Age - 0.89 \times Prop_{Cuts010}$
	CLERTHANUNDS	*Cleridae*	*Thanasimus*	*undatulus*	$w(x) = -0.67 - 0.97 \times dist._{Burned1020}^2 + 0.63 \times Prop_{Cuts010} - 0.52 \times Prop_{Cuts2050}$

Beetles	ELATCTENTRZO	*Elateridae*	*Pseudanostirus*	*triundulatus*	$w(x) = 1.54 - 0.46 \times dist._{Burned010} - 0.53 \times dist._{Burned1020}^{2} + 0.35 \times Prop_{Cuts010} - 0.24 \times Prop_{Cuts2050} + 0.43 \times Prop_{Burned1020}$
	CERAACMSPROT	*Cerambycidae*	*Acmaeops*	*proteus*	$w(x) = -1.80 - 0.67 \times dist._{Burned010} - 0.45 \times Prop_{Closed\ conifer}$
	STAPPLACPSUE	*Staphylinidae*	*Placusa*	*pseudosuecica*	$w(x) = -2.83 - 0.51 \times Prop_{Closed\ conifer} + 0.31 \times Prop_{Cuts1020} + 0.36 \times Prop_{Mixed}$
	TROGTHYMMARQ	*Trogossitidae*	*Thymalus*	*marginicollis*	$w(x) = -3.14 - 0.56 \times Age^{2} + 0.42 \times dist._{Burned1020}^{2} + 0.86 \times dist._{Burned2050} + 0.66 \times Prop_{Closed\ conifer}$
	CARAPTERADST	*Carabidae*	*Pterostichus*	*adstrictus*	$w(x) = -0.30 - 0.43 \times Age + 0.25 \times Prop_{Closed\ conifer}$
	ELATCTENWATS	*Elateridae*	*Pseudanostirus*	*watsoni*	$w(x) = -3.45 + 0.71 \times Age + 1.11 \times Age^{2} + 0.58 \times dist._{Burned1020} + 0.43 \times Prop_{Burned2050}$
	LEIOLEIO	*Leiodidae*	*Leiodes*	*NA*	$w(x) = -2.04 + 0.75 \times Age^{2} - 0.47 \times dist._{Burned010} - 0.32 \times Prop_{Open\ conifer} + 0.73 \times Prop_{Burned1020}$
	SCOLPITP	*Curculionidae*	*Pityophthorus*	*NA*	$w(x) = -1.85 - 0.82 \times dist._{Burned1020} + 0.87 \times Prop_{Cuts010}$
	CORYCLYPFUSG	*Corylophidae*	*Clypastraea*	*fusca*	$w(x) = -2.14 + 0.45 \times Age^{2} - 0.68 \times dist._{Burned010} + 0.57 \times Prop_{Cuts010}$
	CRYPCRYPDIFF	*Cryptophagidae*	*Cryptophagus*	*difficilis*	$w(x) = -1.01 - 0.70 \times Age - 0.99 \times Prop_{Cuts010} + 0.26 \times Prop_{Cuts2050} + 0.31 \times Prop_{Burned2050}$

Beetles	ELATSERIINCQ	*Elateridae*	*Sericus*	*incongruus*	$w(x) = -2.82 + 1.01 \times Age^2 - 0.99 \times Prop_{Closed\ conifer} - 0.88 \times Prop_{Cuts2050} + 0.75 \times Prop_{Burned1020}$
	MELAXYLILAEA	*Melandryidae*	*Xylita*	*laevigata*	$w(x) = -1.66 + 0.76 \times Prop_{Cuts010} - 0.78 \times Prop_{Cuts2050} + 0.62 \times Prop_{Burned1020}$
	NITIGLISVITT	*Nitidulidae*	*Glischrochilus*	*vittatus*	$w(x) = -3.18 - 0.55 \times dist._{Burned010} - 0.83 \times dist._{Burned2050} + 0.82 \times Prop_{Cuts010}$
	STAPQUEDRUST	*Staphylinidae*	*Quedius*	*rusticus*	$w(x) = -0.97 - 0.67 \times Age^2 + 0.44 \times Prop_{Closed\ conifer} + 0.37 \times Prop_{Mixed}$
	STAPPROT	*Staphylinidae*	*Proteinus*	*NA*	$w(x) = -0.04 + 0.28 \times Prop_{Closed\ conifer} - 0.31 \times Prop_{open\ conifer}$
	SCOLPOLYRUFP	*Curculionidae*	*Polygraphus*	*rufipennis*	$w(x) = 0.77 + 0.54 \times Age - 0.28 \times dist._{Burned010} + 0.34 \times Prop_{Closed\ conifer} + 0.71 \times Prop_{Cuts010}$
	LATHENICTENO	*Latridiidae*	*Enicmus*	*tenuicornis*	$w(x) = -0.66 + 0.22 \times Prop_{Closed\ conifer} + 0.34 \times Prop_{Open\ conifer}$
	NITIGLISSANS	*Nitidulidae*	*Glischrochilus*	*sanguinolentus*	$w(x) = 0.34 + 0.54 \times Age + 0.34 \times dist._{Burned1020} - 0.40 \times Prop_{Cuts2050}$
	PSELPSELBELX	*Staphylinidae*	*Pselaphus*	*bellax*	$w(x) = -2.64 - 1.08 \times dist._{Burned010} - 0.48 \times Prop_{Closed\ conifer} + 0.74 \times Prop_{Cuts1020} - 0.57 \times Prop_{Burned2050}$

Annexe H: Supplementary results in Chapter 3.

Table H 1. Jaccard dissimilarity index (JDI) contrasting prediction of species assemblages between the reference scenario and harvested landscapes in 2100, given climate change.

Scenarios	Birds (Mature)	Birds (Dec/Mixte)	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	0.20	0.13	0.13	0.15	Baseline-No harvest
RCP45- Medium harvest	0.22	0.14	0.14	0.16	
RCP45-High harvest	0.28	0.19	0.18	0.21	
RCP85-Protected areas	0.28	0.14	0.17	0.18	Baseline-No harvest
RCP85- Medium harvest	0.29	0.15	0.18	0.19	
RCP85-High harvest	0.30	0.19	0.20	0.22	

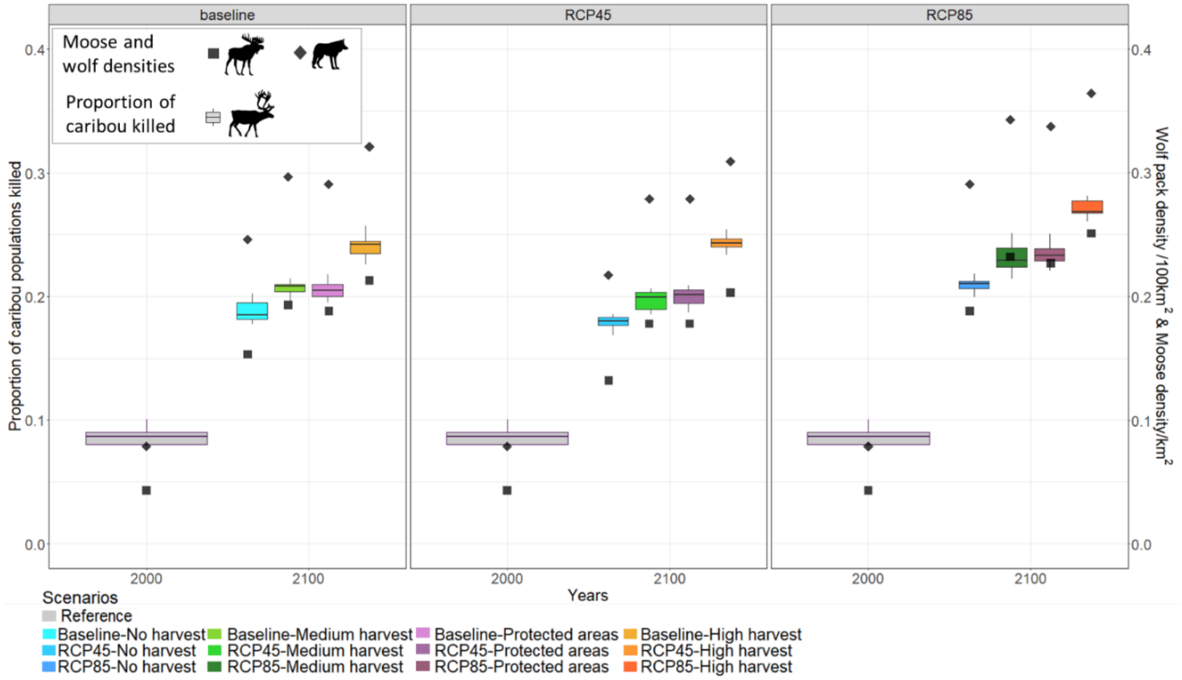

Figure H 1. Changes in the proportion of caribou killed as a function of land use change and climate change scenarios. Proportion of caribou killed by wolves in winter under three climate scenarios (Baseline in light, RCP4.5 in medium and RCP8.5 in dark color) and four forest managements (no harvest in blue, Medium harvest in green, Protected areas in purple, and High harvest in orange) in 2100. Results for the year in 2000 are represented in grey. Numerical responses of moose and wolf to emergent changes in forest landscape composition are shown with squares and diamonds representing moose and wolf density, respectively. Error bars represent 95% confidence intervals.

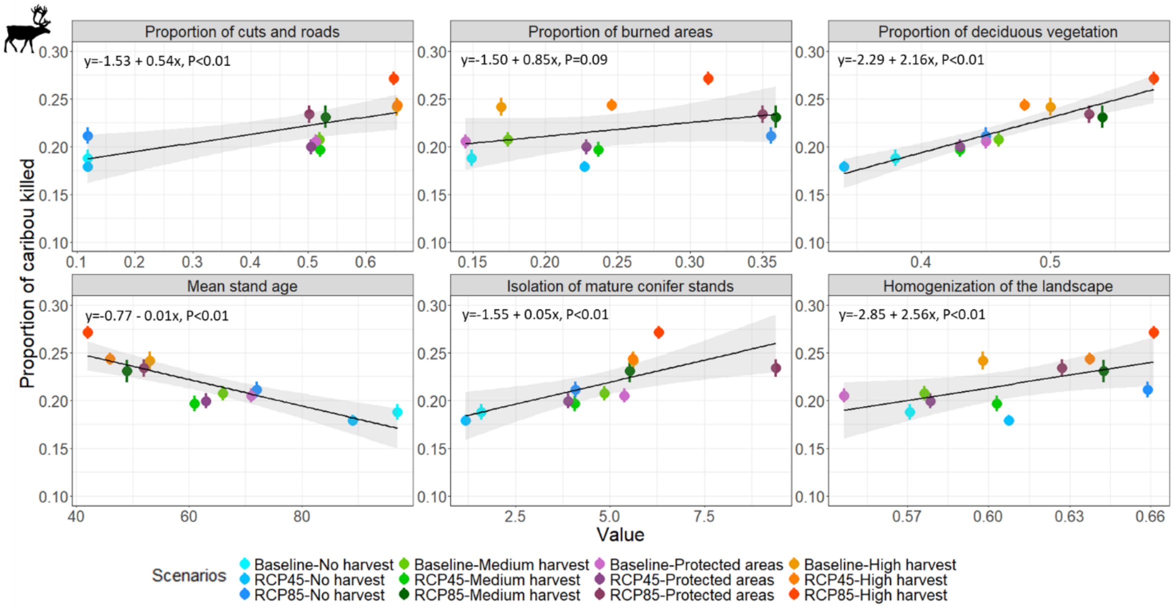

Figure H 2. Change in the proportion of caribou killed as a function of landscape characteristics in 2100: Proportion of cuts and roads, Proportion of burned areas, Proportion of deciduous vegetation, Mean stand age, Isolation of mature conifer stands and homogenization of the landscape**.** Equations come from generalized linear mixed models with a binomial distribution to relate the proportion of caribou mortalities to each covariate of forest characteristics.

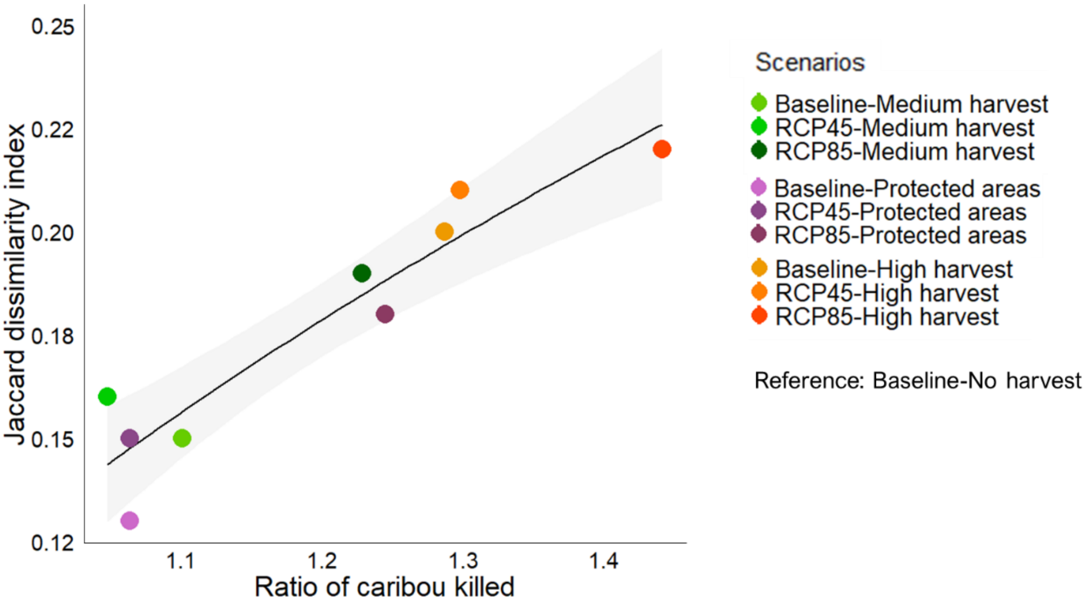

Figure H 3. Change in the Jaccard dissimilarity indices (JDI) of animal species assemblages (all taxa combined) comparing the ratio of the proportion of caribou killed by wolf to the reference landscape in 2100. The reference scenario used to calculate the JDI and the ratio of caribou killed was the same.

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