bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Effects of global change on animal biodiversity in boreal forest landscape: an assemblage dissimilarity analysis

Ilhem Bouderbala[1,2,4,*], Guillemette Labadie[2], Jean-Michel Béland[3], Yan Boulanger[3], Christian Hébert[3], Patrick Desrosiers[1,4,5], Antoine Allard[1,4], Daniel Fortin[2,4]

January 31, 2022

[1] Département de physique, de génie physique et d'optique, Université Laval, Québec (Qc), Canada G1V 0A6

[2] Département de biologie, Université Laval, Québec (Qc), Canada G1V 0A6

[3] Centre de foresterie des Laurentides, Service canadien des forêts, Québec (Qc), Canada G1V 4C7

[4] Centre interdisciplinaire en modélisation mathématique de l'Université Laval, Québec (Qc), Canada G1V 0A6

[5] Centre de recherche CERVO, Québec (Qc), Canada G1J 2G3

Abstract

Despite an increasing number of studies highlighting the impacts of climate change on boreal species, the main factors that will drive changes in species assemblages remain ambiguous. We quantify two climate-induced pathways based on direct and indirect effects on species occupancy and assemblage dissimilarity under different harvest management scenarios. The direct climate effects illustrate immediate impact of climate variables while the indirect effects are reflected through the changes in land cover composition. To understand the main causes in assemblage dissimilarity, we analyze the regional and the latitudinal species assemblage dissimilarity by decomposing it into *balanced variation in species occupancy and occurrence* and *occupancy and occurrence gradient*. We develop empirical models to predict the distribution of more than 100 bird and beetle species in the Côte-Nord region of Québec over the next century. Our results show the two pathways that are based on immediate and lagged climate change effects are complementary and alter biodiversity, mainly caused by balanced variation in species occupancy and occurrence. At the regional scale, both effects have an impact on decreasing the number of winning species. Yet, responses are much larger in magnitude under mixed climate effects (a mixture of direct and indirect effects). Regional assemblage dissimilarity reached 0.77 and 0.69 under mixed effects versus 0.09 and 0.10 under indirect effects for beetles and birds, respectively, between RCP8.5 and baseline

*ilhem.bouderbala.1@ulaval.ca

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

climate scenarios when considering harvest. Therefore, inclusion of climatic variables considers aspects other than just those related to forest landscapes, such as life-cycle of animal species. Latitudinally, assemblage dissimilarity increased following the climate conditions pattern. Our analysis contributes to the understanding of how climate change alters biodiversity by reshaping community composition and highlights the importance of climate variables in biodiversity prediction.

Keywords: Biodiversity modelling, climate change, assemblage dissimilarity, assemblage dissimilarity decomposition, boreal forests, latitudinal gradient.

1 Introduction

Global climate warming affects the functionality of ecosystems by modifying forest composition and biomass, which in turn has repercussions for biodiversity and species assemblages (Kelly and Goulden, 2008; Hillebrand et al., 2010; Thuiller et al., 2011; Pachauri et al., 2014; Zhang and Liang, 2014). In fact, many studies have anticipated that anthropogenic radiative forcing will alter boreal biodiversity and ecosystems (Pachauri et al., 2014; Tremblay et al., 2018; Cadieux et al., 2020). For example, global scale predictions have shown that the potential high emissions of greenhouse gases would lead mainly to negative effects on biodiversity (Pachauri et al., 2014). Instead, other results have been published anticipating an increase in biodiversity during this century, which is referred to the *the northern biodiversity paradox* (Matthews et al., 2004; Morin and Thuiller, 2009; Berteaux et al., 2010). This paradox suggests that the ecological niches of some "southerly" species would increase in size due to expansion beyond the northern periphery of their ranges (Berteaux et al., 2010).

In Canada, temperature has increased by 1.7 °C since 1948, twice as fast as the global average (Bush and Lemmen, 2019). This increase in temperature could lead to the northward migration of thermophilous hardwood tree species to the detriment of boreal conifers, particularly mid-to-late-successional species (Duveneck et al., 2014; Boulanger et al., 2017; Boulanger and Puigdevall, 2021). Moreover, climate change is expected to directly influence wildfire activity (Boulanger and Puigdevall, 2021), which would favour pioneer and fire-adapted boreal tree species (Boulanger et al., 2017). Significant changes in species composition are expected within the transition zone between boreal and temperate biomes, where several tree species are currently reaching their thermal limits (Brice et al., 2020; Boulanger and Puigdevall, 2021). Global warming could also drive the occurrence of more extreme climatic events, including severe droughts (Kumar, 2013; Masson-Delmotte et al., 2018), which are expected to reduce the productivity of several boreal

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

tree species through increasing metabolic respiration (Girardin et al., 2016). Climate-induced changes in insect outbreak regimes, notably those in spruce budworm (SBW) (*Choristoneura fumiferana*), which lead to severe defoliation and death of firs (*Abies* **spp.**) and spruces (*Picea* **spp.**), could adversely affect successional pathways within boreal forest stands (Pureswaran et al., 2015; Labadie et al., 2021).

Climate change might act on biodiversity in different ways ((Wisz et al., 2013; Boulanger and Puigdevall, 2021; Micheletti et al., 2021)). The indirect climate effects alter the vegetation and wildfire, which cause changes in habitat. Impacts could be also direct characterized by immediate effects that are exerted by climate and meteorological conditions that are not related to vegetation (Micheletti et al., 2021). The two climate-induced effects must be seen as complementary when studying their implications on ecosystem functionality. For example, the inclusion of climatic variables reflects other aspects than just those related to forest landscapes. To preserve ecosystem services, it is important to quantify the magnitude of climate-induced changes in biodiversity following both direct indirect pathways. Such a strategy would help to identify best conservation actions when these are needed. If habitat-based climate change is projected to decrease species occupancy, for example, land management actions could be adapted by targeting vegetation restoration. Species translocation actions could be adopted if direct changes are anticipated to cause a decline in species occupancy (Micheletti et al., 2021).

Future alterations in forest structure are not only influenced by climate-induced changes on stand dynamics and natural disturbances, but also by anthropogenic disturbances such as harvest activities (Boulanger et al., 2017). Climate and landuse changes may amplify changes in wildlife habitat (Bentz et al., 2010; Tremblay et al., 2018). For example, an increase in disturbance rate due to warmer conditions could favour the regeneration of warm-adapted, pioneer tree species (Brice et al., 2020; Boulanger and Puigdevall, 2021). The synergistic effects of anthropogenic disturbances and climate change could alter species assemblages, and, therefore, biodiversity. Considering the interactive and cumulative impacts of climate change and anthropogenic disturbances on forest landscapes and, hence, projections of future biodiversity are paramount. Yet, very few studies have considered such impacts on several and diversified taxa (but see Cadieux et al. (2020)).

In this work, we investigated future climate-induced variations in bird and beetle assemblages in Québec's boreal forest. We assessed effects of future climate conditions on these assemblages by comparing forest landscapes that are simulated under two anthropogenic radiative-forcing scenarios, i.e., Representative Concentration Pathway (RCP) 4.5 and RCP 8.5 (van Vuuren et al., 2011) with landscapes that are simulated

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

under average historical (baseline) climate conditions. We further assessed how forest management affects future assemblages by simulating future species occupancy under two forest management levels: no harvest activities and high harvest level. We analyze the effects of climate change in two ways: (1) indirectly, i.e., habitat-based climate change (Wisz et al., 2013; Boulanger and Puigdevall, 2021; Micheletti et al., 2021) and (2) by combining indirect and direct effects, i.e., those stemming from climate variables per se (Thuiller et al., 2018). This distinction is made to quantify the effects of those pathways on biodiversity, which requires different conservation actions (Micheletti et al., 2021). We aimed to project how species community composition would change following anthropogenic and natural disturbances that are based upon two climate-induced pathways: immediate and lagged. We also wanted to determine the main drivers of assemblage dissimilarity following the two pathways.

We opted for a species distribution modelling (SDM) approach (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Peterson et al., 2011) to model the single-species occurrence probability based on extensive field surveys of beetles and birds. We analyzed the assemblage structure based on continuous occurrence probabilities (probability-based) (Guisan and Thuiller, 2005; Grenié et al., 2020) to avoid overprediction risks (Gelfand et al., 2005; Dubuis et al., 2011; Grenié et al., 2020). It has been previously demonstrated that the probability-based richness provided a better fit of the actual richness than would the threshold-based approach (Grenié et al., 2020). We computed dissimilarity measures (Baselga, 2010; Albouy et al., 2012; Baselga, 2013) between different climate scenarios over the two harvesting levels. In this context, we adapted continuous-based decomposition in the context of occurrence probabilities to detail the two components of *β-diversity*: *balanced variation in species abundances* and *abundance gradient*, which are generalizations of turnover and nestedness (Baselga, 2013). Quantifying the main causes of change in biodiversity could be very helpful in assessing the potential underlying determinants because species replacement and nestedness, for example, are two different ways of generating assemblage dissimilarity (Baselga, 2013).

2 Material and methods

2.1 Study area and occurrence data

The study area is located in the Côte-Nord region of Québec, Canada ($48°N$ to $53°N$, $65°W$ to $71°W$), within an area of 114118km^2 (Fig. 1). The northern part of the study area belongs to the black spruce-feather moss bioclimatic domain, and is dominated by black spruce (*Picea mariana* [Mill.] BSP) and balsam fir (*Abies balsamea* [L.] Mill.). Wildfires are the major natural disturbances in areas that have yet to be

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

logged (Boucher et al., 2017). The southern part of the study area belongs to the eastern balsam fir - white birch (*Betula papyrifera* Marsha.) subdomain, mostly dominated by balsam fir and white spruce (*Picea glauca* [Moench] Voss) mixed with white or paper birch. Forest harvesting had been the main source of forest disturbance since the late 1990s in this latter area (Bouchard and Pothier, 2011). In Québec, logging affected around 0.8% of public forest annually (Bureau du Forestier en chef, 2010). This part of the territory also has been affected by an outbreak of the SBW that began in 2006 and which is still ongoing. Tree mortality began around 2015 and has subsequently increased.

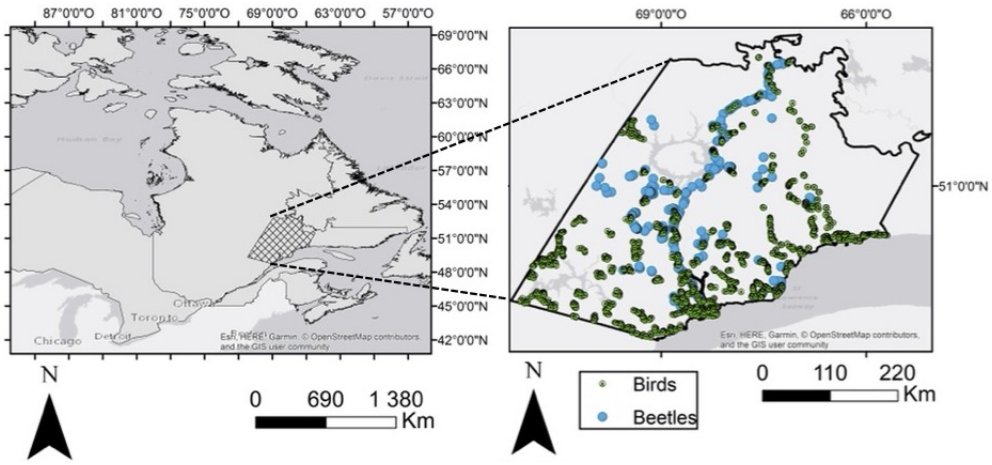

Figure 1: Study area with the presence-absence distribution of the two taxa.

We used presence-absence data that were collected between 2004 and 2018 to model species distributions. Given that we were mainly focusing on the impacts of fire and harvesting, we wanted to remove sites that were located in stands heavily damaged by the SBW outbreak (Ministère des Forêts de la Faune et des Parcs, 2018) by using a cumulative index of defoliation severity from 2007 to 2018 (Labadie et al., 2021). Annual defoliation severity was based on aerial surveys characterizing damage that was incurred by SBW since 2006 (Ministère des Forêts de la Faune et des Parcs, 2018) and was classified between 0 and 3, with 3 indicating the highest level of defoliation. The cumulative severity of the outbreak was obtained by summing the annual severity in Labadie et al. (2021). Sites with cumulative severity values of 10 and above were discarded from analyses.

We used the data from the Atlas of Breeding Birds (Atlas des oiseaux nicheurs du Québec, 2018), which were based on species occurrences that were detected using unlimited distance 5-minute point counts (Bibby et al., 2000), which were collected during the breeding season from late May to mid-July, between 2010 and 2018. For beetles, we merged different databases that had been collected in 2004, 2005, 2007 and 2011 (Janssen et al., 2009; Légaré et al., 2011; Bichet et al., 2016). In addition, we used data from 54 sites

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

that were sampled in 2018 in the northern part of the territory, along the northeast principal road going to Labrador. The sampling protocols were characterized by one multidirectional flight-interception trap per site, sampling flying beetles, and four meshed pitfall traps per site, sampling epigean beetles during their peak period of activity (June-August) (Janssen et al., 2009; Bichet et al., 2016). For beetles, we used species-level identifications where possible; otherwise, we standardized the identification to the genus level (around 92% initial identifications were considered at the species level).

2.2 Predictor variables

To predict species occurrence, we used climate and land cover variables that were grouped in two classes of models: Climate-Habitat-Based (CHBMs) and Habitat-Only-Based (HOBMs). These two model classes were designed to study the climate-induced effects, as follows: CHBMs for the mixed effects; and HOBMs for the indirect climate effects. Initially, we generated 22 potential climate variables at a 250-m resolution using the BioSim platform (Régnière et al., 2017), including the annual average of temperature, precipitation and water deficit between 2004 and 2018 (see Tab. SI1 for the description of all potential predictor variables). BioSIM simulates daily maximum and minimum temperatures (°C), precipitation (mm), water deficit, mean daily relative humidity and wind speed by matching georeferenced sources of daily weather data to spatially georeferenced points. BioSIM uses spatial regression to adjust weather data for differences in latitude, longitude, and elevation between the sources of weather data and each field location (see (Boulanger et al., 2018a) for more details). In our case, the spatially referenced points were 15 000 points that were randomly located across the entire province of Québec, whereas weather data were daily data originating from discrete weather stations that were located within the province. We generated climate variables at a 250 m scale by spatially interpolating data from the 15 000 random points using kriging and elevation as a drifting variable. Land cover maps from the Canadian National Forest Inventory (NFI) were used to generate land cover variables based on k-nearest-neighbour interpolation at a 250-m resolution that was referenced to the year 2001 (Beaudoin et al., 2014). To estimate forest composition, we used the relative importance of tree species groups (conifer and deciduous species), treed land and tree canopy-closure maps from these NFI data to generate five natural land cover classes: closed-canopy conifer forest; open-canopy mature conifer forest; mixed forest; open area; and others (Labadie et al., 2021) (see Tab. SI2 for more details). The last category was not included in the models to avoid collinearity. For the disturbed stands (by fire or harvest), we subdivided them into three age-classes: $[0, 10]$, $]10, 20]$ and $]20, 50]$ years. In addition, we also considered stand age and distance to the nearest burned area also as potential predictor variables. Stand age maps were based on the year 2001 (Beaudoin et al., 2014) with an update according to the registered fire and harvest

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

disturbances between 2004 and 2018. All predictor variable maps were projected into common framework (UTM) with a spatial resolution of 231 m. Furthermore, it was mentioned in Bichet et al. (2016) and Zhao et al. (2013) that the influence of the landscape varied between 400 m for beetles to 1000 m for birds. Consequently, we used a matrix of 21 pixels centred on the focal pixel (i.e., an approximate circle of 577.5 m radius) to calculate frequencies of the land cover (see Tab. SI1 for a description of the 10 land cover variables that were used in the study).

2.3 The modelling strategy

We used two classes of models, i.e., Habitat-Only-Based models (HOBMs) and Climate-Habitat-Based models (CHBMs), to study indirect climate effects and mixed climate effects, respectively (see filled arrows in Fig. 2). We divided our modelling strategy into five steps (see Fig. 3). The modelling procedure that is described here was repeated for the two model classes (CHBMs and HOBMs) according to potential predictor variables under each class. We standardized the variables to facilitate model convergence (MacKenzie et al., 2017) prior to model calibration that was based on the corresponding database. Steps 2 and 3 correspond to a cross-validation loop, in which we split the date into 10 folds of relatively equal size, so at each step, 9 folds were used for training and the one remaining fold was for testing.

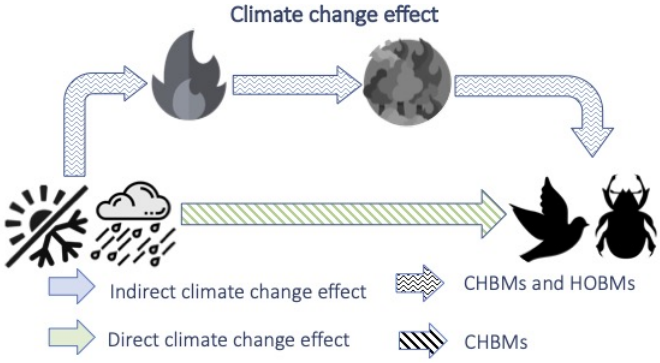

Figure 2: Framework used for the study. The indirect effects were generated through the change in forest composition and the direct effects included the immediate climate effects of temperature, precipitation and water deficit. Abbreviations: Climate-Habitat-Based Models (CHBMs), Habitat-Only-Based Models (HOBMs).

2.3.1 Step 1: Data pre-processing

We used the following procedure for preparing the two databases: (1) all raster files were aligned to the same extent and resolution (Elith et al., 2020); (2) we removed all the sites that were strongly impacted by the spruce budworm outbreak; and (3) we included only the more common species, with a minimum record of 1% and 5% presence among sites for birds and beetles, respectively.

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

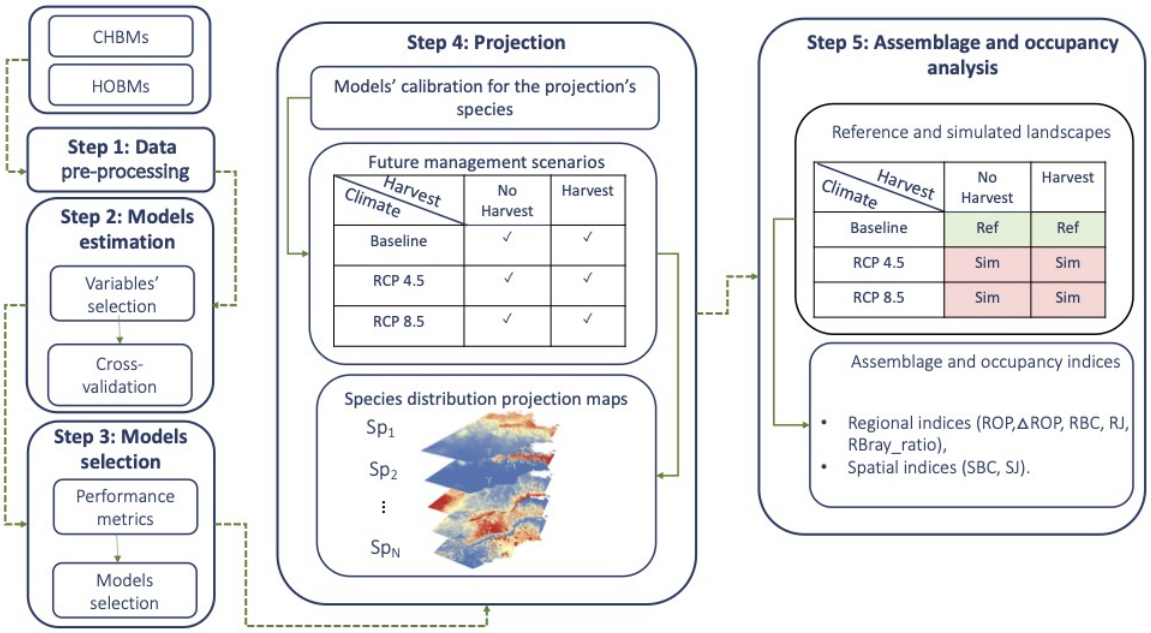

Figure 3: The modelling strategy.

2.3.2 Step 2: Model estimation

Selection of variables First, we removed the highly correlated variables, based on pairwise Pearson correlation coefficient (r), and kept the 5 most important predictor variables (Zurell et al., 2020). To do so, we fitted a univariate Generalized linear model (GLM) with linear and quadratic terms for each variable; we ranked the predictors according to their importance, using the Akaike information criterion (AIC); and removed the highly correlated variables ($|r| > 0.60$). To reduce the separation in the regressions, we removed any predictor with a standard deviation value greater than 50 through a stepwise procedure.

Cross-validation inference and computation of the occurrence probabilities We started with a generalized linear mixed model (GLMM) (package 'lme4', (Bates et al., 2015)) with a random intercept to account for differences between sampling years. We developed six and three full potential models differing only in the fixed effects for CHBMs and HOBMs model classes, respectively (see Tab. SI3). We used interaction terms between the best temperature variable (where the AIC criterion of the corresponding univariate regression is the lowest among all selected temperature variables) with distance to the nearest burned stand and with stand age variables to include the effect of latitudinal variation.

The best models were selected based on each full-model under 10-fold cross-validation by minimizing the AIC criterion (package 'MuMIn', (Barton, 2015)) under the following conditions: (1) limiting the number of

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

terms in the model between 1 and $\lceil min(N_{Pre}, N_{Abs})\rceil/5$ without counting the intercept by specifying 1 in 5 rule, where N_{Pre} and N_{Abs} represented the number of respective presence and absence records, to avoid overparameterized models; and (2) respecting the principle of marginality when the interaction terms were included in the model. For each species and for each test dataset, we calculated the occurrence probabilities matrix for the calibrated models. In total, we retained six models for CHBMs and three for the HOBMs.

2.3.3 Step 3: Models selection

Computation of the performance metrics Once the occurrence probabilities were computed for the complete dataset for each species, we calculated the following performance metrics: (1) specificity; (2) sensitivity; (3) the area under the curve AUC; and (4) the true skill statistic TSS (Araújo et al., 2005; Allouche et al., 2006). The package 'AUC' (Ballings and Van den Poel, 2013) was used to calculate the Receiver operating characteristic and the AUC; we used the package 'PresenceAbsence' (Freeman and Freeman, 2012) for the other performance metrics.

Models selection Species were excluded if no model yielded $AUC \geq 0.7$ (Araújo et al., 2005; Hosmer et al., 2013). For the selected species, we used the model with the highest AUC for projections.

2.3.4 Step 4: Projection

We estimated the parameters of the final model for the selected species based on the full dataset using the same procedure that was described for cross-validation. We subsequently used the simulated predictor variable maps for the six study scenarios and computed the occurrence probability maps.

2.3.5 Step 5: Assemblage and occupancy analysis

We used the following indices to compare species assemblages between scenarios:

The regional occupancy probability (ROP)**:** ROP was calculated as the regional average of the occurrence probabilities for the study area (Bichet et al., 2016). We also used the percentage of change in ROP between the reference (Ref) and the simulated (Sim) scenarios (see step 5 in Fig. 3 for the definitions of Ref and Sim scenarios): $\Delta\overline{ROP}_{Sim,Ref} = \left(\frac{\overline{ROP}_{Sim} - \overline{ROP}_{Ref}}{\overline{ROP}_{Ref}}\right) \times 100$, where $\overline{ROP}_s$ represented the average of the ROP over all species under the scenario s given by:

$$\begin{cases} \overline{ROP}_s = \dfrac{1}{N_{species}} = \sum_{i=1}^{N_{species}} ROP_{i,s} \\ ROP_{i,s} = \dfrac{1}{N_{pixel}} = \sum_{j=1}^{N_{pixel}} P_{s,i,j} \end{cases} \tag{1}$$

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

where $N_{species}$, N_{pixel} and $P_{s,i,j}$ represented respectively the species number, the number of pixels in the study area and the occurrence probability of the species i for the scenario s at the cell j.

Dissimilarity measures: Jaccard Index of Dissimilarity was used to assess climate change effects on species assemblage (Baselga, 2010, 2013; Legendre, 2014; Bichet et al., 2016; Barton et al., 2016; Belliard et al., 2018; Scherrer et al., 2020). We computed two different Jaccard indices, both based on Bray-Curtis dissimilarity measure, regional (RJ) and spatial (SJ) Jaccard indices computed as follows:

$$\begin{cases} RBC_{Sim,Ref} = \sum_{i=1}^{N_{species}} \frac{|ROP_{Sim,i} - ROP_{Ref,i}|}{\sum_{i=1}^{N_{species}} (ROP_{Sim,i} + ROP_{ref,i})} \\ SBC_{Sim,Ref,j} = \sum_{i=1}^{N_{species}} \frac{|P_{Sim,i,j} - P_{Ref,i,j}|}{\sum_{i=1}^{N_{species}} (P_{Sim,i,j} + P_{Ref,i,j})} \\ RJ_{Sim,Ref} = \frac{2RBC_{Sim,Ref}}{1+RBC_{Sim,Ref}},\ SJ_{Sim,Ref,j} = \frac{2SBC_{Sim,Ref,j}}{1+SBC_{Sim,Ref,j}} \end{cases} \tag{2}$$

$RBC_{Sim,Ref}$ and $SBC_{Sim,Ref,j}$ represented respectively the regional Bray-Curtis dissimilarity between the scenarios Sim and Ref, the spatial Bray-Curtis at the cell j selected randomly.

From Fig. 4, we compared the performance of the Jaccard index that was based on our continuous output (SJ_{OP}) and the traditional Jaccard that was based based on the presence-absence transformation ($SJ_{Incidence}$). From the simulation results, the SJ_{OP} yield results that were close to $SJ_{Incidence}$ and performance increased with the number of species that were analyzed (see Fig. 4I). Furthermore, we added two situations with weaker binarization (Bad and Medium cases in Fig. 4) to illustrate that a gap can be generated between the two indices that is due mainly to binarization error.

Beta ratio: We separated the Bray-Curtis dissimilarity index into two additive components: (1) the occurrence gradient (BC_grad); and (2) balanced variation in species occurrence (BC_bal) to quantify the main drivers in assemblage dissimilarity. We used these notations instead of the abundance gradient and balanced variation in species abundance (Baselga, 2013) because we worked with occurrence and occupancy probabilities. We presented a detailed explanation of each component, as follows:

- If $BC_grad_{Sim,Ref} = 0$ ($BC_{Sim,Ref} = BC_bal_{Sim,Ref}$), means a **total** absence of differences in occurrences between the two scenarios. Furthermore, if $BC_{Sim,Ref} \simeq 0$, the assemblage structure remained almost the same. If $BC_{Sim,Ref} \simeq 1$, the occurrence of species in one scenario was almost perfectly balanced by the occurrence of species in the other scenario.

- If $BC_bal_{Sim,Ref} = 0$ ($BC_{Sim,Ref} = BC_grad_{Sim,Ref}$), this means that all species occurrence changes from one scenario to the next were in **the same direction**. If $BC_{Sim,Ref} \simeq 1$, this im-

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

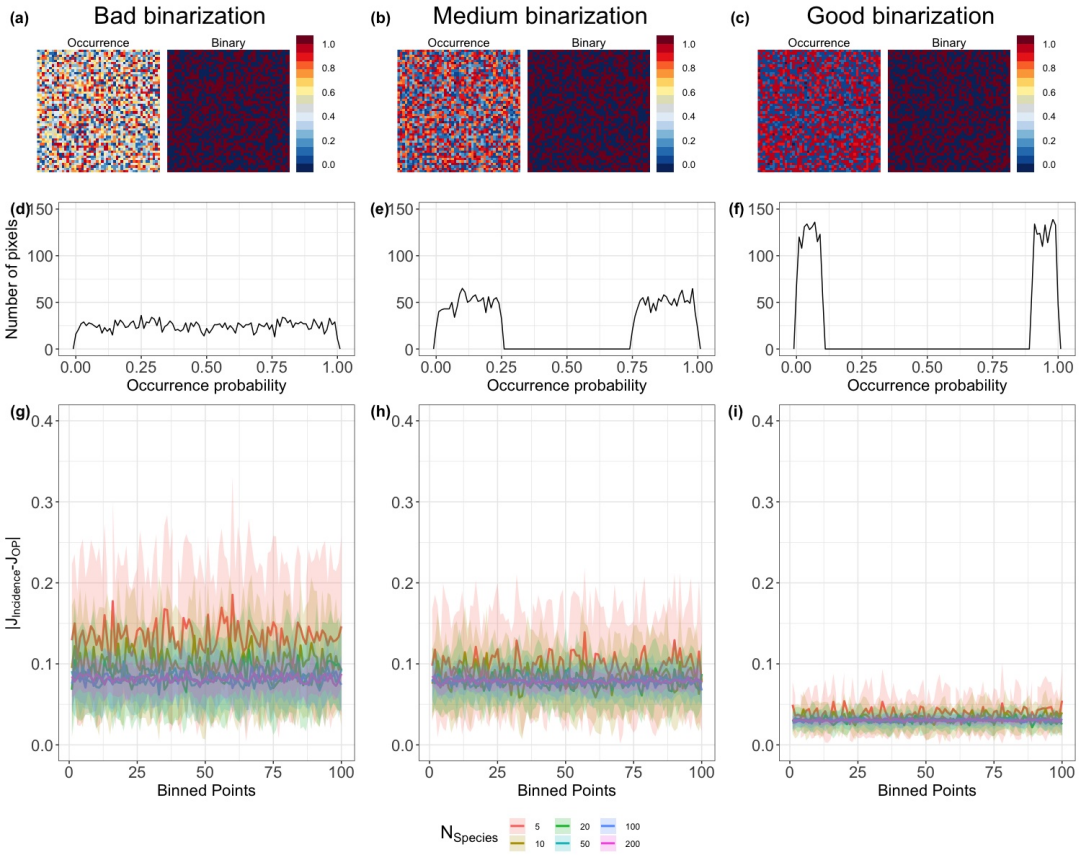

Figure 4: A generic Incidence-based VS Occurrence Probabilities Jaccard dissimilarity. The three levels of binarization concerned the rank choice of the occurrence probabilities that were simulated from a mixture of uniform distributions under constraints. **A-B-C** represented the three simulated occurrence probabilities and the corresponding binarized maps with 0.5 threshold for one species and under one scenario. **D-E-F** showed the frequency of the occurrence probability at the different pixels. **G-H-I** concerned the absolute difference between Jaccard dissimilarity based on the binarized data and the continuous version by varying the number of species.

plies that the difference in occurrence between the two scenarios is too large and in the same direction in almost all species.

To measure the fraction of each component of Bray-Curtis dissimilarity, we used the BC_ratio given by $BC_ratio_{Sim,Ref} = \frac{BC_grad_{Sim,Ref}}{BC_{Sim,Ref}}$. If $BC_ratio > 0.5$, the assisted community change was caused mostly by the occurrence gradient whereas a value smaller than 0.5 indicated a dominance of balanced change in occurrence in the assemblage dissimilarity (Albouy et al., 2012). We used the package 'betapart' (Baselga and Orme, 2012) for the assemblage analysis.

The BC_ratio and its components were illustrated by using occurrence probabilities. The same formalism was adapted regionally through the regional occupancy probabilities.

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

2.4 The study climate and forest management scenarios

We obtained future climate projections from the Canadian Earth System Model version 2 (CanESM2) for RCP 4.5 and RCP 8.5 for the period 2071-2100 and were further downscaled to a 10-km resolution using ANUSPLIN (McKenney et al., 2013). Future monthly normals at each random point that was previously used to assess baseline climate were directly assessed from changes that were observed between the 1981-2010 period and future projections in the 10-km cell in which the random point was located. Daily time series were stochastically generated for each random point from these future monthly normals using BioSIM. Future climate variables at each random point were calculated by averaging these daily values from 30 BioSIM simulations (Boulanger et al., 2018a). Climate scenarios varied depending upon the mean annual temperature that was expected to increase between 3 °C (RCP4.5) and 7.5 °C (RCP8.5) throughout the southern boreal region by 2100 (compared with 2000, see Fig. 5), while average precipitation was projected to increase between 7% and 10% regionally with relatively small differences among scenarios (Boulanger et al., 2018b; Boulanger and Puigdevall, 2021), see Fig. 5).

The forest landscapes were simulated using the spatially explicit raster-based forest landscape model LANDIS-II (Scheller and Mladenoff, 2004), which simulates stand- and landscape-scale processes, including forest succession, seed dispersal and natural (wildfires and spruce budworm outbreaks) and anthropogenic (harvest) disturbances. This model has been extensively used in Québec over the last decade and has been thoroughly validated under various forest conditions (Boulanger et al., 2017; Taylor et al., 2017; Tremblay et al., 2018; Boulanger and Puigdevall, 2021). Forest landscapes were initialized for 2000 conditions 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 two levels of harvesting scenarios according to a gradient of harvesting pressure, from no harvesting to high intensity harvesting, similar to current management practices in Québec (harvest applied to 8% of the harvestable upland area per 10 years). The Biomass Harvest extension was used to simulate forest harvests. Only stands that contained tree cohorts that were greater than 60-years-old were allowed to be harvested. Mean harvested patch size varied between 40 km^2 and 150 km^2. Harvest rates were held constant throughout the simulations unless sufficient numbers of stands did not qualify for harvest. In this latter harvesting continued proceed until stands were no longer available. Simulations were performed from 2000 to 2100 using a 10-yr time step. Climate sensitive parameters for simulations that were performed under RCP 4.5 and RCP 8.5 were set to change in 2011-2020, 2041-2050 and 2071-2080. Forest succession, wildfire, SBW outbreaks and harvesting were simulated using Biomass Succession v5.0, Base Fire v4.0, BDA v4.0 and the Biomass Harvest v5.0

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

extensions, respectively. Many more details regarding LANDIS-II simulations that were performed in this study can be found in (Labadie et al., 2022) as well as in (Boulanger et al., 2017) and (Tremblay et al., 2018).

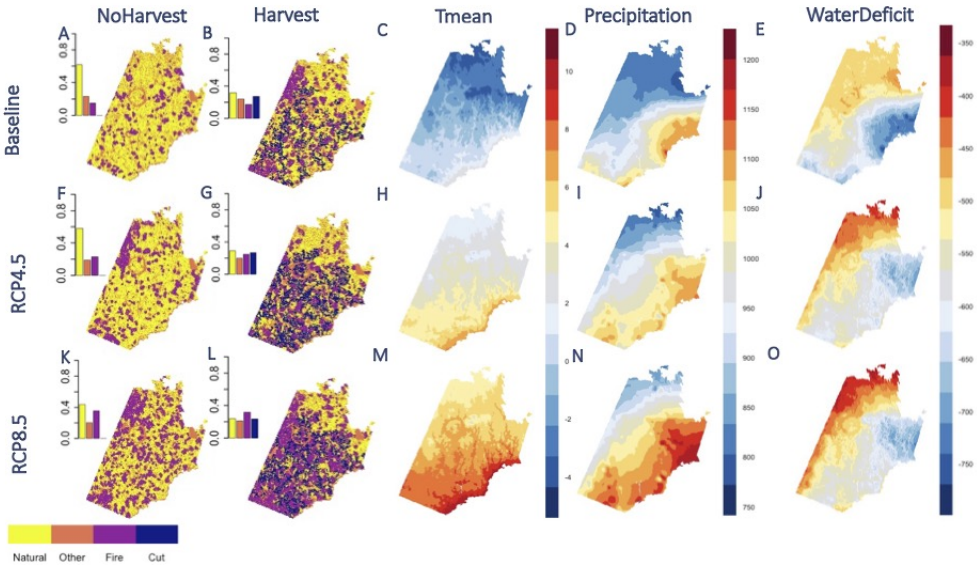

Figure 5: The distribution of the land cover and three climate variables under the simulated management scenarios in 2100. **A-B.**, **F-G.** and **K-L.** represented the distribution of land cover over the six study scenarios that were classified into four large cover classes: *Natural*, which included conifer dense, conifer open, mixed wood and open habitat; *Fire* and *Cut* for the land cover disturbed by fire and Harvest; and *Others* for the rest. The barplots represented the frequency of each class in the map. **D-F.**, **J-L.** and **P-R.** represented the distribution of mean temperature, precipitation, and water deficit for the three climate scenarios **Baseline**, **RCP4.5** and **RCP8.5**, respectively.

3 Results

Of 231 candidate species of birds and beetles, 127 and 108 species were selected for projection (with $AUC \geq 0.7$) for CHBMs and HOBMs respectively with average of AUC between 0.76 (±0.07) and 0.79 (±0.08), and TSS between 0.43 (±0.13) and 0.53 (±0.16) (mean (± SD)). For bird species, *stand age* was the most frequently selected predictor variable with 43.9% and 71% of selection in CHBMs and HOBMs, respectively, (see Fig. 6). For beetle species, mean temperature of the warmest month (*WarmMTmean*) and *stand age* were the most frequently selected variables under CHBMs and HOBMs with 33.7% and 40.3% of selection, respectively (see Fig. 6). .

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

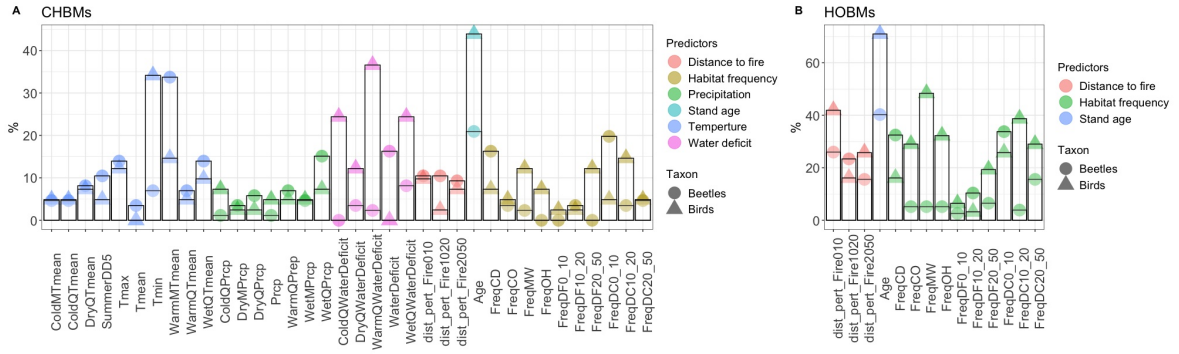

Figure 6: Percentage of the predictor variables that were included in the species regressions for the two taxa (See Tab. SI1 for the variable descriptions), **A.** for Climate-Habitat-Based Models (CHBMs) and **B.** for Habitat-Only-Based-Models (HOBMs). Land cover abbreviations: Conifer Dense (CD), Conifer Open (CO), Mixed Wood (MW), Open Habitat (OH), Disturbance by Fire (DF), and Disturbance by Cut (DC).

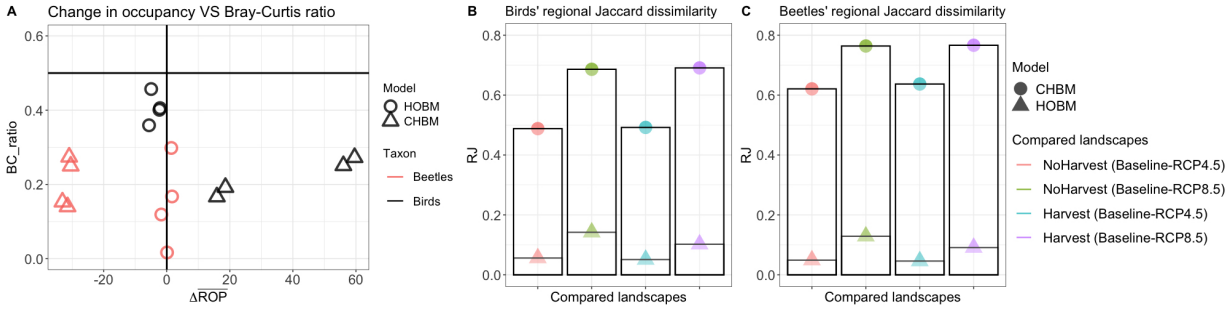

Figure 7: Regional dissimilarity and change in occupancy. **A.** the Bray-Curtis ratio (BC_ratio) with the percentage of change in the regional occupancy probability ($\Delta\overline{ROP}$) under the four compared landscapes. **B-C.** Bird and Beetle Jaccard dissimilarity measures. Abbreviations: Climate-Habitat-Based Model (**CHBM**), Habitat-Only-Based Model (**HOBM**).

3.1 Occurrence and regional occupancy

The analysis of the occurrence and occupancy helped us to evaluate the direction and magnitude of potential community changes following global change. The difference between the indirect and mixed climate effects was visualized through $\Delta\overline{ROP}_{Sim,Ref}$ (Fig. 7A). The magnitude of changes in occupancy compared to the baseline reference scenario was larger when we included the climate variables (CHBMs) when compared to the models including only habitat variables (HOBMs). The change in occupancy was observed mostly for birds under HOBMs (the indirect effects) with a decrease in occupancy by comparing the climate change scenarios to the baseline. Under CHBMs, we observed that occupancy increased for birds but decreased for beetles when comparing the same radiative-forcing scenarios (RCP4.5 and RCP8.5) to the baseline (the projection maps also demonstrated this result; compare Fig. 8E to Fig. 8F and Fig. 8A to Fig. 8B). However, we observed a decrease in the percentage of winner species with climate change for the two taxa, except for birds under HOBMs with no harvest (Fig. 11; see Fig. SI1 for examples of responses of five

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

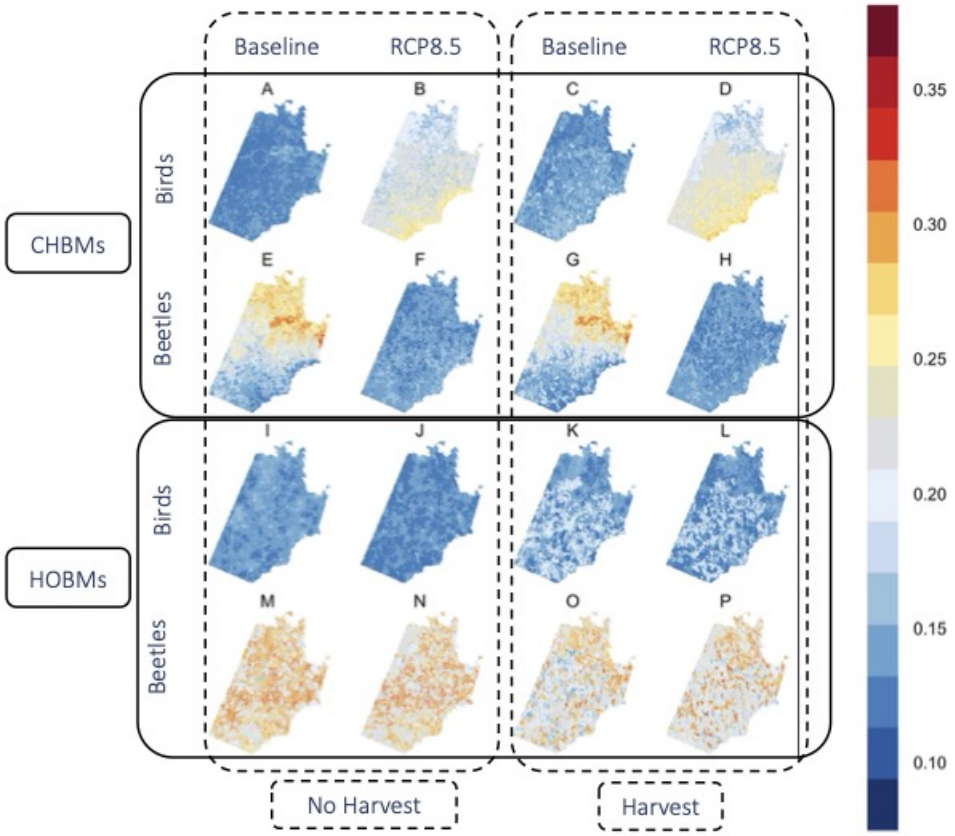

Figure 8: The average potential occurrence maps for each taxon based on four scenarios: BaselineNoHarvest (**A, E, I, M**), RCP8.5NoHarvest (**B, F, J, N**), BaselineHarvest (**C, G, K, O**) and RCP8.5Harvest (**D, H, J, P**) under the two model classes (CHBMs and HOBMs).

variable classes on eight winner and loser species).

3.2 Regional species assemblage change

An increase in assemblage dissimilarity was observed when comparing RCP4.5 and RCP8.5 to the baseline for both taxa. Based on CHBMs, regional dissimilarity from RCP4.5 to RCP8.5 increased respectively by 0.20 and 0.14 for birds and beetles under no harvest (Fig. 7B-C). Also, based on HOBMs, regional dissimilarity from RCP4.5 to RCP8.5 increasedrespectively by 0.07 and 0.08 for birds and beetles under no harvest. This regional dissimilarity was mainly incurred through balanced variation in species occupancy for both taxa ($BC_ratio < 0.5$) (see Fig. 7A).

We also observed an increase in assemblage dissimilarity from HOBMs to CHBMs for both taxa. Inclusion of the climate variables reshaped assemblage structure strongly under the two forest management levels (see differences in the Jaccard dissimilarity index between HOBMs and CHBMs, Fig. 7B-C).

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

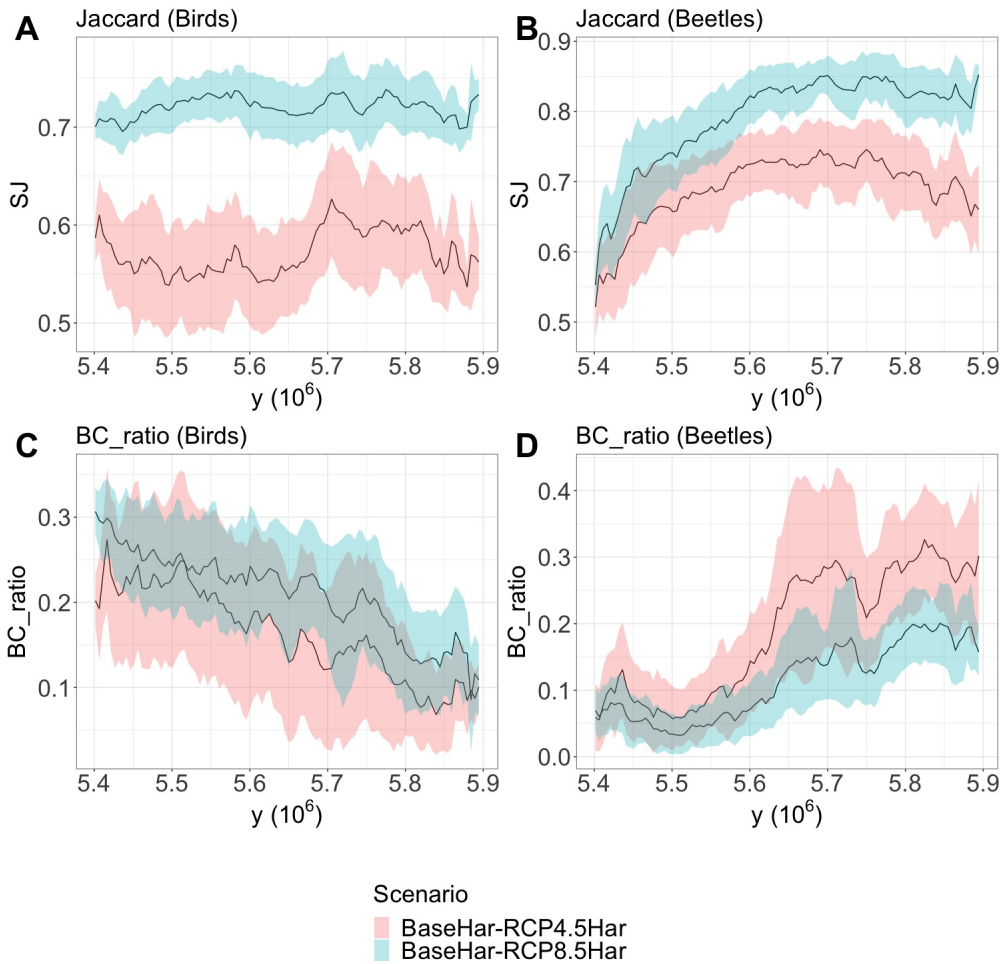

Figure 9: Spatial analysis. **A-B.** Latitudinal variation of spatial Jaccard dissimilarity of **RCP4.5Harvest** and **RCP8.5Harvest** compared to reference scenario **BaselineHarvest**. **C-D.** Latitudinal variation of spatial BC_ratio. The shaded areas represented the standard deviation.

3.3 The latitudinal change in species assemblage

The inclusion of climate variables produced a latitudinal gradient in projections of assemblage dissimilarity. We used CHBMs to analyze how latitudinal changes in temperature and other climate variables would affect assemblage structure. A clear increasing pattern was observed in assemblage dissimilarity heading north, especially for beetle species. For birds, a slight increase in dissimilarity was observed, compared to that of beetles (see the difference between Fig. 9A and Fig. 9B).

Our models predict that beetles would show greater sensitivity to climate variations, given that an increase in dissimilarity was observed even for a medium level of climate change, i.e., RCP 4.5 following changes in temperature between the baseline and the two forcing scenarios. In Figs 10A-B, we depicted spatial change in

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

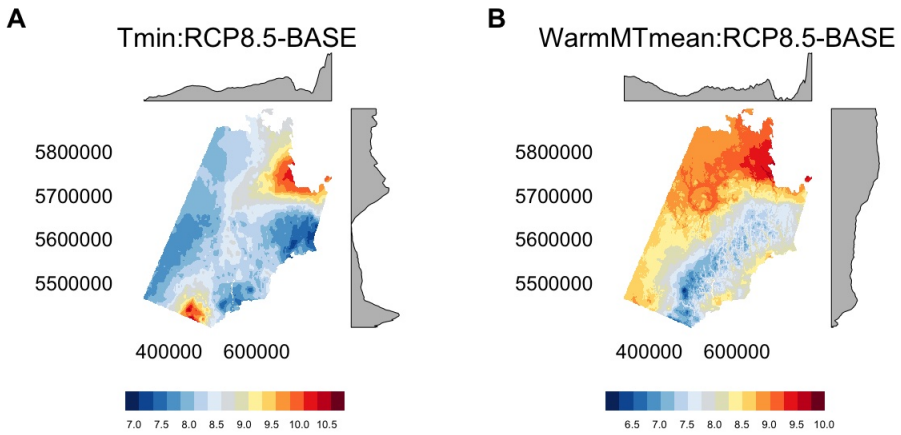

Figure 10: Temperature difference maps between RCP8.5 and baseline of annual minimum temperature (**A**) and mean temperature of the warmest month (**B**). Map scale: The dark red and the dark blue represented respectively the highest and the lowest values.

Tmin and *WarmMTmean* between RCP8.5 and baseline climate scenarios. *Tmin* and *WarmMTmean* were the most frequently selected respective predictor variables for birds and beetles (see Fig. 6A for the selection percentage). Furthermore, the observed latitudinal dissimilarity gradient was derived mainly from balanced variation in occurrence ($BC_ratio < 0.5$ in Figs. 9C-D). Yet, the two taxa behaved in a contrasting manner regarding their latitudinal variation in the occurrence gradient component of BC dissimilarity.

4 Discussion

The present study shows effects of two climate-induced pathways on animal species assemblages: (1) indirectly (i.e., through forest changes); and (2) by combining the immediate response from climate variables with the indirect effects (i.e., mixed effects). This contributes to our understanding of complex responses of animals occupancy and community compositional changes following immediate and lagged climate change effects. We showed that the two climate-induced pathways that were studied acted on species assemblage turnover. Immediate effects that were expressed through the change in climate conditions apparently strongly modified the assemblage composition more than did the lagged effects. In fact, the difference in magnitude between the two effects was due to the mismatch that was generated by rapid climate variation compared to slower vegetation change (Wu et al., 2015; Stralberg et al., 2015; Micheletti et al., 2021). Regionally, both climate effects acted on the decrease in number of winner species and on the increase in assemblage dissimilarity by ordered comparison of RCP 4.5 through RCP 8.5 to the baseline scenario. Dissimilarity was caused principally by balanced variation in species occupancy, which is considered to be a generalization of turnover for continuous outputs (Baselga, 2013). However, we observed almost an opposite feedback between

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

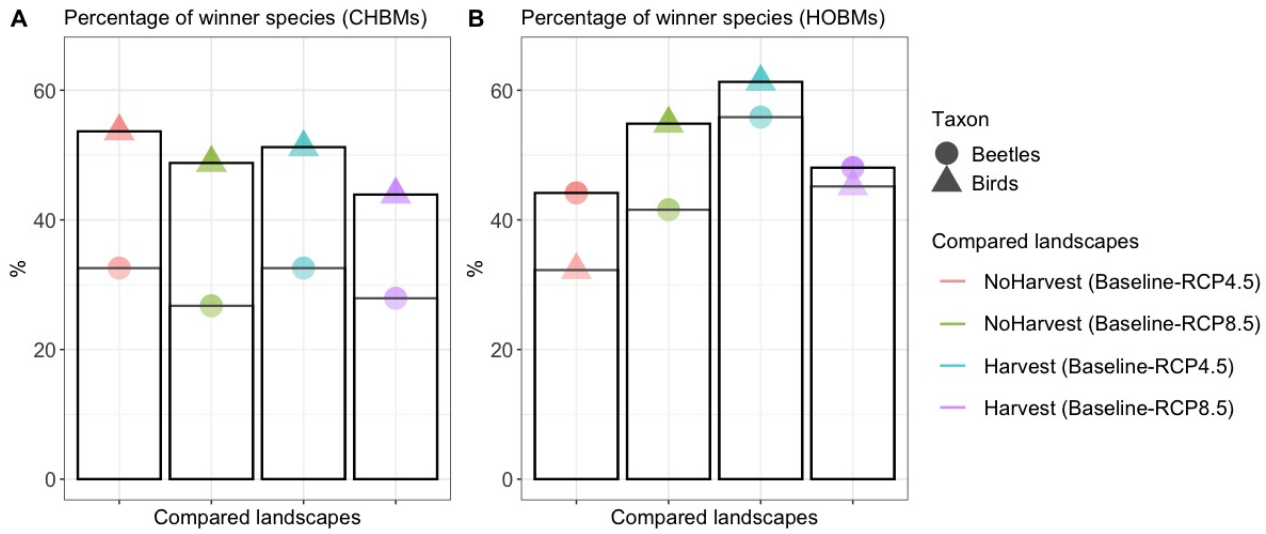

Figure 11: Percentage of winner species per taxon under the four landscapes that were compared and the two model classes (CHBMs and HOBMs). Species i was considered as winner if the regional occupancy probability under the simulated scenario was higher than under the reference scenario ($ROP_{Sim,i} > ROP_{Ref,i}$).

the two taxa regarding changes in the regional occupancy.

4.1 The implications on species assemblages and occupancy

The response of beetles and birds to climate change was predicted to be complex. We highlighted climate change projections that would likely cause pronounced variation in assemblage composition for the two study taxa by 2100 under the two harvest levels following two climate pathways. We observed a decrease in the number of winner species with increasing anthropogenic radiative forcing, i.e., between RCP4.5 and RCP8.5 (Fig. 11) under nearly all scenarios and model classes for the two taxa (except under No harvest using HOBMs for birds, Fig. 11B) (Pizzolotto et al., 2014). Moreover, the observed change in assemblage dissimilarity was mainly caused by balanced variation in occupancy for the two taxa under the two model classes.

We projected substantial differences in future biodiversity patterns, when comparing habitat-based models with those that also included climate variables. On one hand, from a habitat-based perspective (indirect effects), we observed an increase in assemblage dissimilarity by increasing anthropogenic radiative forcing compared to that of the baseline. On the other hand, we observed a slight negative effect on regional occupancy especially for birds based on the indirect effect. Yet, we estimated that only 45.2% of bird species and 48.1% of beetle species, under harvest increased their occupancy from baseline to RCP8.5 (Fig. 11B). From a climate-habitat perspective, the impact of mixed effects on biodiversity was observed to be very different compared to the indirect habitat-based effects in terms of direction and magnitude. The

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

inclusion of immediate climate effects strongly affected the turnover of biodiversity. For instance, regional dissimilarity with baseline conditions increased from 0.49 to 0.69 for birds and from 0.62 to 0.76 for beetles under RCP 4.5 and RCP 8.5, respectively. Moreover, the increase in bird occupancy as a result of the mixed combination between direct and indirect climate effects coincided globally with the *northern biodiversity paradox* that was emphasized by Matthews et al. (2004), Morin and Thuiller (2009), and Berteaux et al. (2010), which anticipated an increase in biodiversity in northern protected areas this century. For beetles, we observed a substantial decrease in regional occupancy following an increase in global warming. This outcome aligned with the global scale biodiversity trajectory predicting mostly negative effects of high emissions on biodiversity and ecosystem services (Pachauri et al., 2014). Despite the observed increase in regional occupancy for birds, the percentage of winner species decreased with climate change for the two taxa (Fig. 11A). In addition, we found that indirect effects, through climate-induced changes in habitat only, were smaller in magnitude compared to the combined indirect and direct effects for both taxa. This conclusion can be explained by the mismatch between the climate and the biota (Stralberg et al., 2015; Wu et al., 2015; Micheletti et al., 2021). For example, Brice et al. (2020) noted that under climate change the variation in climate conditions would be faster than the capacity of tree species to migrate, which creates a gap between the climatic niche and the observed distribution of species.

Moreover, differences were observed between birds and beetles regarding indirect habitat-based and mixed effects. Beetles are poikilotherms, the internal temperature of which varies according to the temperature of the environment, while birds are homeotherms, the internal temperature of which is physiologically regulated. Our results suggest the potential presence of cold-habitat beetle species in the north. With increasing radiative forcing (Fig. 8F), their occurrence probability decreases as climate conditions extend beyond their tolerance limits. This could explain the different global implications of direct climate change on beetles and birds. We can expect, therefore, a decrease in the probability of occurrence for beetles in the future, and an increase in bird occurrence in our study area. Our conclusions accord with those of other studies based on limitations to phenotypic plasticity and evolvability of critical thermal tolerances for insects (Gaston and Chown, 1999; Terblanche et al., 2007; García-Robledo et al., 2016). For instance, (García-Robledo et al., 2016) had shown the role of critical thermal temperature on insects tolerance to global warming in context of elevation, which was used as a proxy for latitude in context of global warming. The authors demonstrated that insects that were found at middle elevations and on mountain tops were less tolerant to temperature increases than were species that were restricted.

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

4.2 The latitudinal biodiversity drivers

For species occupying the study area and under mixed climate effects, we observed substantial changes in biodiversity with latitude with increasing radiative forcing, with almost complete replacement of the assemblage in the northern portion of the study area for beetles. This latitudinal pattern was different from Brice et al. (2019) where a northward decrease in temporal $\beta-diversity$ was observed for tree species between past (1970-1980) and present (2000-2016) periods. Our results may reflect the potential implications of direct climate effects when the situation becomes more severe, particularly for insects. This latitudinal gradient could be a result of the polar amplification that was characterized by an increase in temperature anomalies near to the pole in response to a change in global climate forcing (Holland and Bitz, 2003). However since the studied latitudinal range was relatively small, so the climatic envelope that was used for calibration could also have an impact on this trend.

4.3 Conclusion

In conclusion, based on implicit assumptions of individual species responses to climate change, our analyses identified potential repercussions of two climate-induced pathways which were based on immediate and lagged climate change, on the assemblage composition of two taxonomic groups regionally and latitudinally. We showed alteration in biodiversity both regionally and latitudinally following climate change that was derived mainly from balanced variation in species occupancy and occurrence. Moreover, we emphasized the importance of climatic variables in models to predict the occurrence of insects (beetles in our case) and birds that was distinguishable through the observed latitudinal gradient in assemblage dissimilarity. Finally, different responses between the study taxa were observed under the two climate-induced pathways, which could indicate the potential range of change for boreal species in relation to novel environmental conditions.

Acknowledgements

This work was supported by the Sentinel North program of Laval University, funded by the Canada First Research Excellence Fund. A.A., D.F., C.H., and P.D. were also supported by The Natural Sciences and Engineering Research Council of Canada (NSERC). We acknowledge Calcul Québec and Compute Canada for their technical support and computing infrastructures. We thank also the Québec Breeding Bird Atlas for supplying data. We would also like to thank the following partners: Regroupement QuébecOiseaux, Environment and Climate Change Canada and Birds Canada, as well as all of the volunteer participants who gathered data for the project. We are grateful to Louis-Paul Rivest for his valuable statistical suggestions

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

and advice. Special thanks are due to Alexandre Terrigeol for his valuable efforts regarding data collection, Georges Pelletier and Nicolas Bédard for beetle identification and to W.F.J. Parsons for his English revision.

References

Albouy, C., Guilhaumon, F., Araújo, M. B., Mouillot, D., and Leprieur, F. (2012). Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages. *Global Change Biology*, 18(10):2995–3003.

Allouche, O., Tsoar, A., and Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (tss). *Journal of Applied Ecology*, 43(6):1223–1232.

Araújo, M. B., Pearson, R. G., Thuiller, W., and Erhard, M. (2005). Validation of species–climate impact models under climate change. *Global Change Biology*, 11(9):1504–1513.

Atlas des oiseaux nicheurs du Québec (2018). Données obtenues en réponse à une demande présentée aux bureaux de l'Atlas (www.atlas-oiseaux.qc.ca). Regroupement QuébecOiseaux, Service canadien de la faune d'Environnement Canada et Études d'Oiseaux Canada. Québec, Québec, Canada.

Ballings, M. and Van den Poel, D. (2013). Package 'AUC'. `https://cran.r-project.org/web/packages/AUC`.

Barton, A. D., Irwin, A. J., Finkel, Z. V., and Stock, C. A. (2016). Anthropogenic climate change drives shift and shuffle in North Atlantic phytoplankton communities. *Proceedings of the National Academy of Sciences of the United States of America*, 113(11):2964–2969.

Barton, K. (2015). Package 'MuMIn'. `https://cran.r-project.org/web/packages/MuMIn`.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1):134–143.

Baselga, A. (2013). Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution*, 4(6):552–557.

Baselga, A. and Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity. *Methods in ecology and evolution*, 3(5):808–812.

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. `https://cran.r-project.org/web/packages/lme4`.

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Beaudoin, A., Bernier, P., Guindon, L., Villemaire, P., Guo, X., Stinson, G., Bergeron, T., Magnussen, S., and Hall, R. (2014). Mapping attributes of Canada's forests at moderate resolution through kNN and MODIS imagery. *Canadian Journal of Forest Research*, 44(5):521–532.

Belliard, J., Beslagic, S., Delaigue, O., and Tales, E. (2018). Reconstructing long-term trajectories of fish assemblages using historical data: the Seine River basin (France) during the last two centuries. *Environmental Science and Pollution Research*, 25(24):23430–23450.

Bentz, B. J., Rgnire, J., Fettig, C. J., Hansen, E. M., Hayes, J. L., Hicke, J. A., Kelsey, R. G., Negron, J. F., and Seybold, S. J. (2010). Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *BioScience*, 60(8):602–613.

Berteaux, D., Blois, S. d., Angers, J.-F., Bonin, J., Casajus, N., Darveau, M., Fournier, F., Humphries, M. M., McGill, B., Larivée, J., et al. (2010). The CC-Bio Project: studying the effects of climate change on Quebec biodiversity. *Diversity*, 2(11):1181–1204.

Bibby, C. J., Burgess, N. D., Hill, D. A., Hillis, D. M., and Mustoe, S. (2000). *Bird census techniques*. Elsevier.

Bichet, O., Dupuch, A., Hébert, C., Le Borgne, H., and Fortin, D. (2016). Maintaining animal assemblages through single-species management: the case of threatened caribou in boreal forest. *Ecological Applications*, 26(2):612–623.

Bouchard, M. and Pothier, D. (2011). Long-term influence of fire and harvesting on boreal forest age structure and forest composition in eastern québec. *Forest Ecology and Management*, 261(4):811–820.

Boucher, Y., Perrault-Hébert, M., Fournier, R., Drapeau, P., and Auger, I. (2017). Cumulative patterns of logging and fire (1940–2009): consequences on the structure of the eastern canadian boreal forest. *Landscape Ecology*, 32(2):361–375.

Boulanger, Y., Parisien, M.-A., and Wang, X. (2018a). Model-specification uncertainty in future area burned by wildfires in Canada. *International Journal of Wildland Fire*, 27(3):164–175.

Boulanger, Y. and Puigdevall, J. P. (2021). Boreal forests will be more severely affected by projected anthropogenic climate forcing than mixedwood and northern hardwood forests in eastern Canada. *Landscape Ecology*, 36(6):1725–1740.

Boulanger, Y., Taylor, A. R., Price, D. T., Cyr, D., McGarrigle, E., Rammer, W., Sainte-Marie, G., Beaudoin, A., Guindon, L., and Mansuy, N. (2017). Climate change impacts on forest landscapes along the Canadian southern boreal forest transition zone. *Landscape Ecology*, 32(7):1415–1431.

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Boulanger, Y., Taylor, A. R., Price, D. T., Cyr, D., and Sainte-Marie, G. (2018b). Stand-level drivers most important in determining boreal forest response to climate change. *Journal of Ecology*, 106(3):977–990.

Brice, M.-H., Cazelles, K., Legendre, P., and Fortin, M.-J. (2019). Disturbances amplify tree community responses to climate change in the temperate–boreal ecotone. *Global Ecology and Biogeography*, 28(11):1668–1681.

Brice, M.-H., Vissault, S., Vieira, W., Gravel, D., Legendre, P., and Fortin, M.-J. (2020). Moderate disturbances accelerate forest transition dynamics under climate change in the temperate–boreal ecotone of eastern North America. *Global Change Biology*, 26(8):4418–4435.

Bureau du Forestier en chef (2010). Bilan d'aménagement forestier durable au Québec 2000-2008. Gouvernement du Québec, Roberval, Québec, 290 p.

Bush, E. and Lemmen, D. S. (2019). Canada's Changing Climate Report. Government of Canada, Ottawa, ON, Canada, 444 p. (Editors).

Cadieux, P., Boulanger, Y., Cyr, D., Taylor, A. R., Price, D. T., Sólymos, P., Stralberg, D., Chen, H. Y., Brecka, A., and Tremblay, J. A. (2020). Projected effects of climate change on boreal bird community accentuated by anthropogenic disturbances in western boreal forest, Canada. *Diversity and Distributions*, 26(6):668–682.

Dubuis, A., Pottier, J., Rion, V., Pellissier, L., Theurillat, J.-P., and Guisan, A. (2011). Predicting spatial patterns of plant species richness: a comparison of direct macroecological and species stacking modelling approaches. *Diversity and Distributions*, 17(6):1122–1131.

Duveneck, M. J., Scheller, R. M., White, M. A., Handler, S. D., and Ravenscroft, C. (2014). Climate change effects on northern Great Lake (USA) forests: A case for preserving diversity. *Ecosphere*, 5(2):art23.

Elith, J., Graham, C., Valavi, R., Abegg, M., Bruce, C., Ford, A., Guisan, A., Hijmans, R. J., Huettmann, F., Lohmann, L., et al. (2020). Presence-only and presence-absence data for comparing species distribution modeling methods. *Biodiversity Informatics*, 15(2):69–80.

Freeman, E. and Freeman, M. E. (2012). Package 'PresenceAbsence'. `https://cran.r-project.org/web/packages/PresenceAbsence/`.

García-Robledo, C., Kuprewicz, E. K., Staines, C. L., Erwin, T. L., and Kress, W. J. (2016). Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

global warming for extinction. *Proceedings of the National Academy of Sciences of the United States of America*, 113(3):680–685.

Gaston, K. J. and Chown, S. L. (1999). Elevation and climatic tolerance: A test using dung beetles. *Oikos*, 86(3):584–590.

Gelfand, A. E., Schmidt, A. M., Wu, S., Silander Jr, J. A., Latimer, A., and Rebelo, A. G. (2005). Modelling species diversity through species level hierarchical modelling. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, 54(1):1–20.

Girardin, M. P., Bouriaud, O., Hogg, E. H., Kurz, W., Zimmermann, N. E., Metsaranta, J. M., de Jong, R., Frank, D. C., Esper, J., Büntgen, U., Guo, X. J., and Bhatti, J. (2016). No growth stimulation of Canada's boreal forest under half-century of combined warming and CO_2 fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, 113(52):E8406–E8414.

Grenié, M., Violle, C., and Munoz, F. (2020). Is prediction of species richness from stacked species distribution models biased by habitat saturation? *Ecological Indicators*, 111:105970.

Guisan, A. and Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8(9):993–1009.

Guisan, A. and Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135(2):147–186.

Hillebrand, H., Soininen, J., and Snoijs, P. (2010). Warming leads to higher species turnover in a coastal ecosystem. *Global Change Biology*, 16(4):1181–1193.

Holland, M. M. and Bitz, C. M. (2003). Polar amplification of climate change in coupled models. *Climate Dynamics*, 21(3):221–232.

Hosmer, D. W., Lemeshow, S., and Sturdivant, R. X. (2013). *Applied logistic regression*, volume 398. John Wiley & Sons.

Janssen, P., Fortin, D., and Hébert, C. (2009). Beetle diversity in a matrix of old-growth boreal forest: influence of habitat heterogeneity at multiple scales. *Ecography*, 32(3):423–432.

Kelly, A. E. and Goulden, M. L. (2008). Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 105(33):11823–11826.

Kumar, P. (2013). Hydrology: Seasonal Rain Changes. *Nature Climate Change*, 3(9):783–784.

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Labadie, G., Hardy, C., Boulanger, Y., Vanlandeghem, V., Hebblewhite, M., and Fortin, D. (2022). Global changes impact a threatened species through alteration of predator-prey dynamics. *To be submitted to Nature Climate Change*.

Labadie, G., McLoughlin, P. D., Hebblewhite, M., and Fortin, D. (2021). Insect-mediated apparent competition between mammals in a boreal food web. *Proceedings of the National Academy of Sciences of the United States of America*, 118(30).

Légaré, J.-P., Hébert, C., and Ruel, J.-C. (2011). Alternative silvicultural practices in irregular boreal forests: Response of beetle assemblages. *Silva Fennica*, 45(5):937–956.

Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, 23(11):1324–1334.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L., and Hines, J. E. (2017). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier.

Masson-Delmotte, V., Zhai, P., Pörtner, H.-O., Roberts, D., Skea, J., Shukla, P. R., et al. (2018). Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. Technical report, IPCC.

Matthews, S., O"Connor, R., Iverson, L. R., and Prasad, A. M. (2004). Atlas of climate change effects in 150 bird species of the Eastern United States. Gen. Tech. Rep. NE-318. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 340 p.

McKenney, D., Pedlar, J., Hutchinson, M., Papadopol, P., Lawrence, K., Campbell, K., Milewska, E., Hopkinson, R. F., and Price, D. (2013). Spatial climate models for Canada's forestry community. 89(05):659–663.

Micheletti, T., Stewart, F. E. C., Cumming, S. G., Haché, S., Stralberg, D., Tremblay, J. A., Barros, C., Eddy, I. M. S., Chubaty, A. M., Leblond, M., Pankratz, R. F., Mahon, C. L., Van Wilgenburg, S. L., Bayne, E. M., Schmiegelow, F., and McIntire, E. J. B. (2021). Assessing pathways of climate change effects in SpaDES: An application to bBoreal Landbirds of Northwest Territories Canada. *Frontiers in Ecology and Evolution*, 9(October).

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Ministère des Forêts de la Faune et des Parcs (2018). Aires infestées par la tordeuse des bourgeons de l'épinette au québec en 2018, 20 p. Technical report, Québec, gouvernement du Québec, Direction de la protection des forêts.

Morin, X. and Thuiller, W. (2009). Comparing niche-and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, 90(5):1301–1313.

Pachauri, R. K., Allen, M. R., Barros, V. R., Broome, J., Cramer, W., Christ, R., Church, J. A., Clarke, L., Dahe, Q., Dasgupta, P., et al. (2014). *Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. IPCC, Gland, Switzerland.

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M., and Araújo, M. B. (2011). *Ecological niches and geographic distributions (MPB-49)*, volume 49. Princeton University Press.

Pizzolotto, R., Gobbi, M., and Brandmayr, P. (2014). Changes in ground beetle assemblages above and below the treeline of the Dolomites after almost 30 years (1980/2009). *Ecology and Evolution*, 4(8):1284–1294.

Pureswaran, D. S., De Grandpré, L., Paré, D., Taylor, A., Barrette, M., Morin, H., Régnière, J., and Kneeshaw, D. D. (2015). Climate-induced changes in host tree–insect phenology may drive ecological state-shift in boreal forests. *Ecology*, 96(6):1480–1491.

Régnière, J., Saint-Amant, R., Béchard, A., and Moutaoufik, A. (2017). BioSIM 11: User's manual. Technical report, Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Québec, QC Canada.

Scheller, R. M. and Mladenoff, D. J. (2004). A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. *Ecological Modelling*, 180(1):211–229. Modelling disturbance and succession in forest landscapes using LANDIS.

Scherrer, D., Mod, H. K., and Guisan, A. (2020). How to evaluate community predictions without thresholding? *Methods in Ecology and Evolution*, 11(1):51–63.

Stralberg, D., Bayne, E. M., Cumming, S. G., Sólymos, P., Song, S. J., and Schmiegelow, F. K. (2015). Conservation of future boreal forest bird communities considering lags in vegetation response to climate change: A modified refugia approach. *Diversity and Distributions*, 21(9):1112–1128.

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Taylor, A. R., Boulanger, Y., Price, D. T., Cyr, D., McGarrigle, E., Rammer, W., and Kershaw, J. A. (2017). Rapid 21st century climate change projected to shift composition and growth of Canada's Acadian Forest Region. *Forest Ecology and Management*, 405:284–294.

Terblanche, J. S., Deere, J. A., Clusella-Trullas, S., Janion, C., and Chown, S. L. (2007). Critical thermal limits depend on methodological context. *Proceedings of the Royal Society B: Biological Sciences*, 274(1628):2935–2943.

Thuiller, W., Guéguen, M., Bison, M., Duparc, A., Garel, M., Loison, A., Renaud, J., and Poggiato, G. (2018). Combining point-process and landscape vegetation models to predict large herbivore distributions in space and time— A case study of *Rupicapra rupicapra*. *Diversity and Distributions*, 24(3):352–362.

Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B., and Araujo, M. B. (2011). Consequences of climate change on the tree of life in Europe. *Nature*, 470(7335):531–534.

Tremblay, J. A., Boulanger, Y., Cyr, D., Taylor, A. R., Price, D. T., and St-Laurent, M.-H. (2018). Harvesting interacts with climate change to affect future habitat quality of a focal species in eastern Canada's boreal forest. *PLOS ONE*, 13(2):1–25.

van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S. J., and Rose, S. K. (2011). The representative concentration pathways: an overview. *Climatic Change*, 109(1):5.

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., Dormann, C. F., Forchhammer, M. C., Grytnes, J.-A., Guisan, A., Heikkinen, R. K., Høye, T. T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N. M., Termansen, M., Timmermann, A., Wardle, D. A., Aastrup, P., and Svenning, J.-C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews*, 88(1):15–30.

Wu, D., Zhao, X., Liang, S., Zhou, T., Huang, K., Tang, B., and Zhao, W. (2015). Time-lag effects of global vegetation responses to climate change. *Global Change Biology*, 21(9):3520–3531.

Zhang, Y. and Liang, S. (2014). Changes in forest biomass and linkage to climate and forest disturbances over northeastern china. *Global Change Biology*, 20(8):2596–2606.

Zhao, Q., Azeria, E. T., Le Blanc, M.-L., Lemaître, J., and Fortin, D. (2013). Landscape-scale disturbances modified bird community dynamics in successional forest environment. *PLOS ONE*, 8(11):1–11.

bioRxiv preprint doi: https://doi.org/10.1101/2022.01.31.477297; this version posted February 1, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Zurell, D., Zimmermann, N. E., Gross, H., Baltensweiler, A., Sattler, T., and Wüest, R. O. (2020). Testing species assemblage predictions from stacked and joint species distribution models. *Journal of Biogeography*, 47(1):101–113.