

# Spatial Structure is More Than Habitat Amount: A Metapopulation Approach is Necessary to Project Distributions Under Climate Change

IMMEDIATE

## Abstract

Projecting species distributions under climate change requires going beyond climate suitability models. We propose that metapopulation theory can be used to leverage species distribution models while accounting for landscape spatial structure, biotic interactions and demography. While reviewing how metapopulation theory reacts to climate-induced distribution shifts, we found that habitat-climate mismatch can generate non-equilibrium dynamics, linear change in habitat occupancy generates non-linear distribution change, and the effect of environmental change on habitat can have counterintuitive effects on higher trophic levels. We illustrated our findings by developing habitat suitability models for the Bicknell's Thrush (*Catharus bicknelli*) a red-listed bird species confined to perturbed balsam fir forests. Under climate warming, the Bicknell's Thrush distribution shifts northwards from the effect of climate alone while the distribution of its associated vegetation remains stable despite warming. The arising mismatch between climate and vegetation changes patch size, connectivity, and habitat structure potentially to different extent, influencing species persistence and suggesting that habitat alone is not enough to characterize regional distribution changes. Our results emphasize the importance of both habitat and landscape spatial structure in assessing persistence for which metapopulation theory is an ideal framework to further advance our understanding of species distribution.

# 1 Introduction

Climate change has already prompted species to shift their range toward higher latitudes and elevations (Chen et al. 2011, Parmesan 2006, Virkkala and Lehikoinen 2014). Species persistence in response to climate change may critically depend on their ability to expand their range and track suitable environments. While most current predictive approaches ignore important biological mechanisms such as demography, dispersal, and biotic interactions, these play key roles in species response to environmental change (Urban et al. 2016). In response, several calls have been made for models to incorporate the processes mediating species response (Fordham et al. 2013, Stralberg et al. 2015, 2019) and mechanistic approaches have been developed to improve the realism of projections. However, more work is required to increase accuracy and usability of mechanistic models as they remain rarely employed in conservation planning when compared to correlative species distribution models (SDMs, Guisan and Thuiller 2005, Franklin and Miller 2009, Guisan et al. 2013). The challenge now lies in the development of approaches that are accessible, customizable and integrate multiple processes and their interplay (McIntire et al. 2022, Thuiller et al. 2013, Urban et al. 2016).

Explicit modelling of the processes that underlie distribution dynamics is challenging (Briscoe et al. 2021, Hefley et al. 2017). Dynamic range models provide a successful example of incorporating demographic processes and dispersal to improve the accuracy of species distribution projections (Briscoe et al. 2021). They are based on niche theory, assuming that species occur at locations where the environment allows positive growth rates (Godsoe et al. 2017, Hutchinson 1957). However, such models are often difficult to parameterize because measuring growth rate is challenging (McGill 2012) and requires very specific data on species response to abiotic environmental conditions. Indeed, on top of being computationally intensive (Snell et al. 2014), the data required to parameterize these models are rarely available (Urban et al. 2016). Furthermore, local demography on its own may be insufficient to explain broad-scale species distribution, suggesting that processes at broader scales must also be considered (Le Squin et al. 2021), including dispersal limitations, disturbances, and biotic interactions (Stephan et al.

50 [2021](#), Urban et al. [2016](#)).

51 Another approach recently proposed is derived from metapopulation theory. Metapopulations  
52 are expected to persist in heterogenous landscapes if colonization is sufficient to balance local  
53 extinctions (Hanski and Ovaskainen [2000](#)). The environment may constrain these two processes  
54 and limit metapopulation persistence. Distribution limits eventually emerge over environmental  
55 gradients at this location where persistence becomes critical. Furthermore, distributions may  
56 be constrained by the amount of suitable conditions in a region. As a result, a species may be  
57 absent from a region, or a portion of a gradient, despite the occurrence of suitable conditions if  
58 these are not abundant enough or if extinction is too high. Metapopulation theory also makes an  
59 ideal framework to incorporate several elements of complexity such as landscape heterogeneity,  
60 dispersal, and biotic interactions as it is flexible enough to integrate fundamental processes  
61 driving distribution dynamics.

62 Disturbances, environmental changes, and biotic interactions are processes that may cause  
63 species distribution to be constantly out of equilibrium with their niche (Boulangeat et al. [2018](#),  
64 Ovaskainen and Hanski [2002](#), Svenning et al. [2014](#)). Non-equilibrium dynamics are especially  
65 marked in plants that are limited by slow demography and restricted dispersal (Savage and Vel-  
66 lend [2015](#), Svenning and Sandel [2013](#), Vissault et al. [2020](#)). Representing this reality requires an  
67 adapted approach and metapopulation theory offers the opportunity to model non-equilibrium  
68 dynamics (Hanski and Simberloff [1997](#), Ovaskainen and Hanski [2002](#)). Metapopulation models  
69 have shown the trailing edge of current tree distribution to be persisting despite unfavourable cli-  
70 matic conditions as slow demography delays the extinction of populations. At the leading edge,  
71 dispersal limitations and competition prevent trees from colonizing favourable habitats (Talluto  
72 et al. [2017](#)). The ability of metapopulation models to study and describe dynamic landscapes  
73 therefore makes them particularly suitable to study persistence under changing climate.

74 In this paper, we show how metapopulation theory can be used to model and thus complement  
75 the interpretation of species distribution in a changing environment. In addition, we illustrate

how metapopulation theory can be used to leverage species distribution models by accounting for the complexity arising from biotic interactions, demography, and landscape structure. After reviewing the theory to account for these key ecological processes in distribution modelling and present associated sources of complexity, we illustrate the effect and importance of these processes on persistence and distribution dynamics using the Bicknell’s Thrush (*Catharus bicknelli*), a red-listed bird species, as a case study (IUCN 2020).

## 2 Key Concepts Arising From Metapopulation Theory

### 2.1 Model description

The classic metapopulation model describes species distribution over a set of suitable patches of habitat connected by dispersal (Levins 1970, 1969). Regional dynamics are driven by colonization and extinction events, which corresponding rates depend on local environmental conditions. Together they define the species distribution limits. The dynamics may be complexified with the representation of several trophic levels, where high-trophic level species occur exclusively at locations occupied by lower-level species (Fordham et al. 2013). We adopt the specialist-habitat terminology throughout this study to lighten the text and fit the example, even if the results are more general and can apply to any bottom-up system (e.g., predator-prey or host-mutualist).

Consider a simplistic system composed of a specialist species tracking the spatial distribution of a dynamic favourable habitat, such as a particular type of vegetation patch providing shelter and food. The model represents the dynamics of the occupancy of three possible states: empty, occupied by the favourable habitat alone ( $H$ ) or in co-occurrence with the specialist ( $S$ ). The landscape is heterogeneous and each local patch is characterized by the abiotic environmental condition ( $E$ ). Dynamics of occupancy are given by the following system of differential equations:

$$\frac{dH(E)}{dt} = c_H(E)H(1 - H) - e_H(E)H$$

$$\frac{dS(E)}{dt} = c_S(E)S(H(E) - S) - e_S(E)S$$

Where  $c(E)$  is the function for colonization rate and  $e(E)$  for the extinction rate. Both are species-specific functions of the abiotic environment such that  $H$  and  $S$  also depend on  $E$ , the abiotic environmental conditions. A specialist persists over the landscape in a dynamic equilibrium between habitat availability (i.e., habitat occupancy over the landscape), colonization, and extinction if its occupancy  $S$  is larger than zero:

$$S(E^*) = H(E^*) - \frac{e_S(E^*)}{c_S(E^*)}$$

and the distribution limit is defined by  $S(E^*) = 0$ , such that it is located where  $H(E^*) = \frac{e_S(E^*)}{c_S(E^*)}$ . Distribution limits of a habitat specialist are therefore determined by its intrinsic response to the abiotic environment (the ratio  $\frac{e_S(E)}{c_S(E)}$ ), in conjunction with the habitat response to the abiotic environment ( $\frac{e_H(E)}{c_H(E)}$ ).

## 2.2 Graphical representation of range limits

We provide three examples to illustrate how metapopulation theory can reveal some of the complexities of distribution dynamics under a changing climate.

A specialist's persistence and therefore occupancy is jointly affected by environmental conditions and habitat availability (occupancy) such that it can be represented graphically with  $\frac{e(E)}{c(E)}$  and  $H(E)$  curves (Figure 1). Distribution limit occurs at the position along the environmental gradient where the habitat occupancy curve crosses the extinction to colonization ratio. The specialist's occupancy for given environmental conditions is defined by the difference between habitat availability and the extinction to colonization ratio curves ( $S^* = H - \frac{e}{c}$ ). The difference between habitat availability and the extinction to colonization ratio curves ( $S^*$ ; shown by the arrows in Figure 1 A) is reduced with increasing environmental conditions, illustrating a decrease

118 in the specialist's occupancy and persistence ( $S(E_0^*) > S(E_1^*)$ ).

### 119 2.2.1 Interaction of the specialist and of its habitat's response can cause indirect 120 distribution dynamics

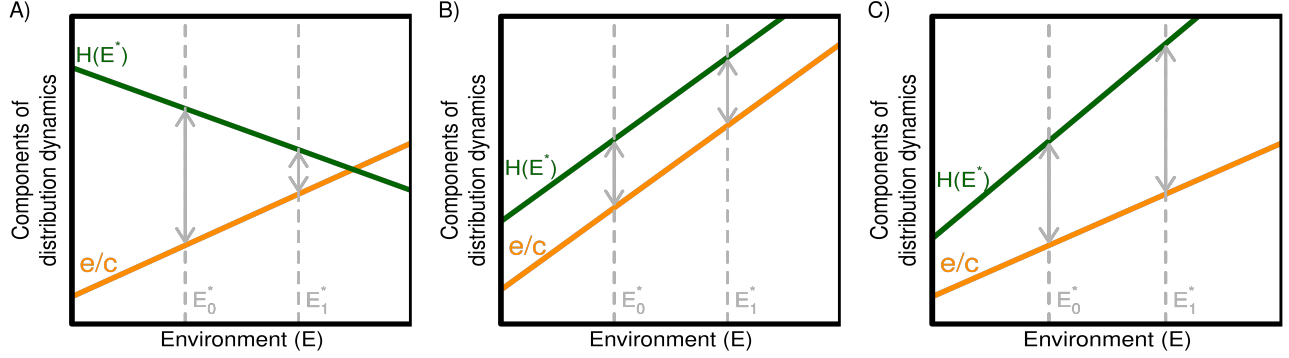


Figure 1: Change in occupancy (and persistence as shown by the grey arrows) of the habitat specialist depends on its intrinsic response to the environment  $\frac{e}{c}$  (orange line) and of the habitat's occupancy  $H(E^*)$  (green line).

121 In a bottom-up system such as predator-prey or a habitat specialist, the response to environmen-  
122 tal change does not only depend on the focal species but also on the response of the associated  
123 one. The covariation in the response to the environment between the two levels is therefore of  
124 critical importance. For instance, the net effect of less favourable environmental conditions to a  
125 specialist could be detrimental (Figure 1 A), without effect (Figure 1 B), or favourable (Figure  
126 1 C) depending on the effect of the environment to its habitat. Thus, the interaction between  
127 trophic levels may have indirect (and counterintuitive) effects on specialist response.

### 128 2.2.2 Habitat mismatch affects species distribution shifts

129 Range limits of a habitat specialist is jointly affected by environmental conditions and the  
130 availability (occupancy) of its habitat. Range shift in response to environmental changes is  
131 therefore not only determined by its intrinsic response to the environment, but also by the  
132 response of the habitat to the environment. As a result, a mismatch between the species response  
133 to the environment and its realized distribution may arise, in particular when different trophic  
134 levels are not responding at the same rate to environmental change (Figure 2). The distribution

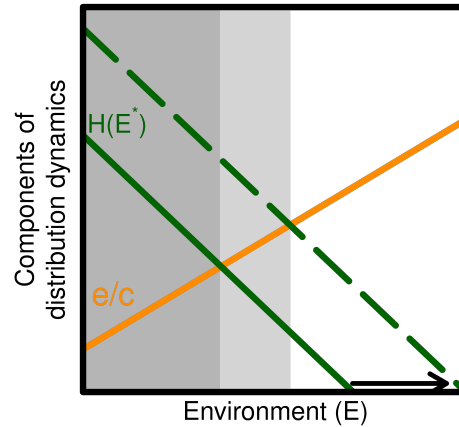


Figure 2: The distribution of the habitat specialist (grey area) is impacted by the functions relating the intrinsic response to the environment (orange line) to habitat occupancy ( $H(E)$ , full and dashed green lines). A change in the habitat occupancy at given environmental conditions (full to dashed green line) affects the specialist's persistence and shifts its distribution on the environmental gradient (dark to light grey area).

may shift in the geographic space, for instance toward the north, but it should stay the same in the environmental space if both levels respond similarly (Figure 2, dark shaded area). That said, if a delay or any other factor prevents the habitat from tracking the new environmental conditions, then the habitat curve will shift (Figure 2, green dashed line), and so will the distribution limit (light shaded area). Such mismatch could either benefit or harm the specialist distribution; in Figure 2, the specialist expands to less favourable environmental conditions. The response of the habitat to changing environmental conditions does influence the specialist distribution, both in extent and in the position of its distribution limits in environmental and geographical space.

### 2.2.3 Metapopulation dynamics may precipitate species decline

The projection of range shifts with correlative SDMs assumes an instantaneous response to environmental change. An implicit assumption is also that a reduction in habitat occupancy translates into an equivalent reduction in the specialist's range, leading to extinction (Thomas et al. 2004). Metapopulation dynamics may, however, precipitate the decline of a species before the complete disappearance of suitable conditions. Consider a landscape where environmental

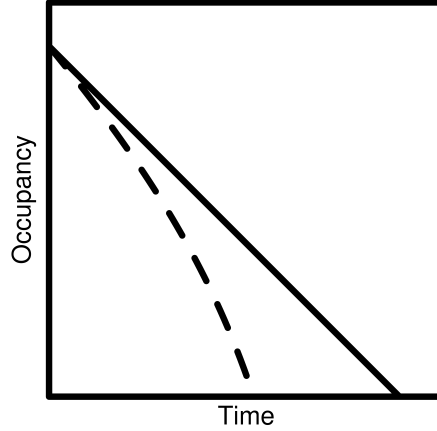


Figure 3: The response of a habitat specialist to a linear environmental change in time as it would be expected with a correlative SDM (linear response; full line). Metapopulation dynamics may precipitate - or alternatively delay - the extinction of the species in a metapopulation even if there are suitable conditions (dashed line).

conditions are spatially heterogeneous, such as temperature in a mountainous area. The progressive change in this environment, like climate warming, will have two effects on the distribution of suitable patches: the first direct consequence is a reduction in habitat occupancy  $H(E)$ , and indirectly follows the increase of the extinction rate with the shrinking of suitable patches. Some favourable patches may also disappear, thereby reducing the landscape connectivity. A non-linear decline of occupancy therefore arises from a linear change in environmental conditions as the ratio  $\frac{e(E)}{c(E)}$  within the specialist's persistence function increases (Figure 3). This metapopulation effect may not be important at first while suitable habitat is abundant and patches are large, but increases as habitat occupancy decreases, supporting an acceleration of metapopulation prevalence loss to a constant environmental shift (Hanski and Ovaskainen 2000, Ovaskainen and Hanski 2002).

## 2.3 Spatially explicit landscapes

Analytical tools from metapopulation theory can be used to interpret range limits in spatially explicit heterogeneous landscapes. Metapopulation capacity can be evaluated for realistic landscapes where patch coordinates and size are considered. Metapopulation capacity is measured as the first eigenvalue of the landscape matrix  $M$ , where elements  $m_{ij} = \exp(-\alpha d_{ij})A_iA_j$  for



166  $j \neq i$  and  $m_{ii} = 0$  (Hanski and Ovaskainen 2000).  $\frac{1}{\alpha}$  describes the average dispersal distance,  
 167  $d_{ij}$  is the distance between patch  $i$  and  $j$ , and  $A_i$  is the area of patch  $i$  (refer to Hanski and  
 168 Ovaskainen (2000) for the full description). Metapopulation capacity is a measure of a species'  
 169 ability to maintain itself regionally as a function of connectivity and local extinctions. It pro-  
 170 vides the means to evaluate conditions for persistence given the spatial arrangement of patches  
 171 and their size.

172 Climate change can profoundly alter landscapes as experienced by species; not only does it influ-  
 173 ence the amount of suitable habitats, but also the capacity of species to persist when colonization  
 174 and extinction prevail. Consider a mountainous landscape inhabited by a high elevation habitat  
 175 specialist. The landscape is marked by a steep elevational gradient in temperature where warm  
 176 temperatures at low elevations exceed the species' tolerance. The landscape would therefore  
 177 be divided between suitable cold habitats on mountain tops and unsuitable warmer habitats at  
 178 the bottom. The topography will not only determine the total surface of suitable conditions,  
 179 but also the frequency distribution of patch sizes and of distances among mountain tops. As a  
 180 result, it will influence the connectivity of the landscape and the distribution of patch specific  
 181 extinction rates.

182 A schematic example is provided in Figure 4, inspired by the case study that will follow in the  
 183 next section. Fixing a lower climatic range limit in a hypothetical mountainous landscape, we  
 184 find nine suitable habitat patches of various sizes, distributed at various distances one from  
 185 another (Figure 4, left panel). Habitat patches here represent high elevation mountain tops.  
 186 The warming of climatic conditions causes an elevational shift of lower range limits resulting  
 187 in the contraction of habitat patches and a decline in the number of patches (Figure 4, right  
 188 panel). Patches become generally smaller from contraction and fragmentation, and the smallest  
 189 patches go extinct. Further, not only smaller patches are assumed to support smaller population  
 190 sizes, have superior extinction risks, and produce fewer colonizers (Hanski and Ovaskainen 2000),  
 191 but the loss and the fragmentation of patches alter species dispersal ability through the loss of  
 192 connectivity (Huang et al. 2019).

193 The decrease in metapopulation capacity surpasses that of habitat amount, adding a spatial  
 194 structure perspective to the assumptions made by correlative approaches. The overall effect of  
 195 climate warming is not only to modify patch areas, but to change species' ability to colonize and  
 196 occupy these patches.

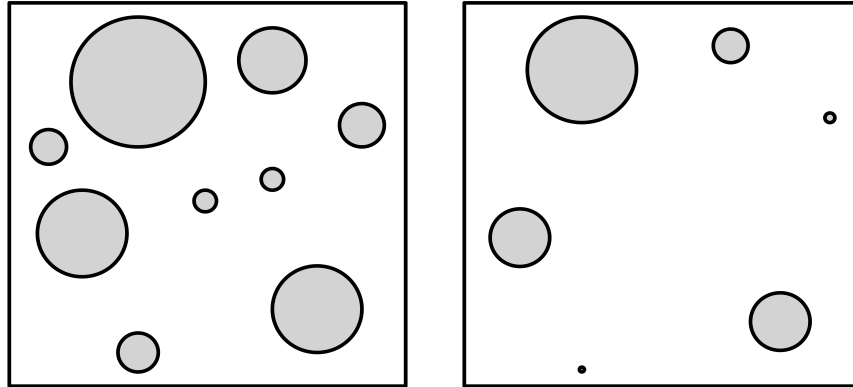


Figure 4: Species persistence is affected by changes to landscape connectivity as well as habitat amount. Circles delimit suitable habitat patches. The left panel presents a hypothetical mountainous landscape where suitable patches represent high elevation mountain tops. The right panel illustrates the same landscape where patches's radius contracted by an equal amount, simulating an elevation shift of climatic conditions on landscape suitability. Following patch contraction, metapopulation capacity declined by 82% whereas habitat amount only declined by 63%.

### 197 3 Case Study: Bicknell's Thrush in North-Eastern Amer- 198 ica

199 We illustrate the concepts presented in the previous section with a case study of the Bicknell's  
 200 Thrush (*Catharus bicknelli*), a threatened bird species in Canada (COSEWIC 2022, IUCN 2020).  
 201 Bicknell's Thrush is the smallest Nordic thrush within the *Catharus* genus and is visually similar  
 202 to the Grey-cheeked Thrush (*Catharus minimus*). It migrates in Northeastern North America  
 203 from its wintering grounds in the Greater Antilles and feeds on invertebrates and small fruits  
 204 (Townsend et al. 2020). Populations are small and were reported to be declining in Canada  
 205 (COSEWIC 2022). The dispersal of Bicknell's Thrush is not known with certainty, although it  
 206 has been suggested that adults nest near the site of previous successful nesting while few yearlings

are observed to come back to their site of birth (Collins 2007, Rimmer et al. 2001, Studds et al. 2012). The Bicknell’s Thrush is known to be associated with very dense balsam fir (*Abies Balsamea*) forests, mostly at high elevations, resulting in a fragmented and highly restricted range (Cadieux et al. 2019, COSEWIC 2022). This habitat may be ephemeral, as natural disturbances, forestry and stand succession could lead to local extinctions. Furthermore, its distribution in mountainous areas is highly contingent on climate elevation gradients. Climate change could therefore pose a major threat to the persistence of this species as favourable climatic conditions within isolated habitat patches could shrink rapidly (Rodenhouse et al. 2008). Unfavourable environmental conditions are predicted to increase at the edges of mountaintop fir forest patches with the warming of climate and the limited response capacity of boreal tree species (Talluto et al. 2017, Vissault et al. 2020).

In the following section, we project the changes to the Bicknell’s Thrush breeding range in response to climate forcing using a standard correlative approach. We then leverage the projections using the concepts developed to analyze the total amount of favourable habitat, the distribution of patch areas, their connectivity, and the metapopulation capacity. Finally, we compare Bicknell’s Thrush favourable landscapes under climate-only change and climate-induced forest change scenarios to illustrate arising climate-habitat mismatch. Thereby, we wish to reveal the joint effects of these two components of Bicknell’s Thrush’s distribution and demonstrate their importance on distribution dynamics.

## 3.1 Methods

### 3.1.1 Studied region

The Bicknell’s Thrush breeding range was projected for the province of Québec where the majority of the Canadian occurrences are found, specifically in the Appalachian Mountains in the southeast and the Laurentians Mountains north of the St. Lawrence River (COSEWIC 2022, Townsend et al. 2020). The landscape is composed of boreal, mixed and temperate forests, with their distributions mainly driven by climatic latitudinal and elevational gradients. Mean

233 annual temperature ranges from -4.0 to 7.5 °C in this region, but the Bicknell's Thrush occupies  
234 locations with a more restricted range because of its preference for high-elevation areas. Annual  
235 precipitation ranges from 730 to 950 mm.

### 236 **3.1.2 Data**

237 Distribution data consisted of 6,079 confirmed observations of nesting behavior, with geographic  
238 precision to ~30 m (1 second of latitude/longitude), sampled from 1994 to 2020. Data were  
239 provided by the Regroupement QuébecOiseaux (SOS-POP [2021](#)). It contains observations from  
240 various sources, including scientific surveys and citizen science. The region of interest was  
241 rasterized on a grid of 250 x 250 m cells, where an observation within a cell was defined as a  
242 presence. We considered the locations where one or more observations were made as a single  
243 presence, accounting for any potential effects of temporal and spatial pseudo-replication resulting,  
244 for example, from multiple sightings of the one individual in the same location.

245 Mean annual temperature, total annual precipitation, elevation, and balsam fir biomass were  
246 used to model occurrences following COSEWIC ([2022](#)) and Townsend et al. ([2020](#)). Mean annual  
247 temperature and total annual precipitation were interpolated from climate station records for the  
248 1981-2010 period to produce a time series of annual means (McKenney et al. [2013](#)). Data from a  
249 georeferenced 10 km climate grid (McKenney et al. [2013](#)) were projected to each 250 m grid cell  
250 centroid and adjusted for differences in latitude, longitude and elevation with spatial regression  
251 using BioSIM v11 (Régnière et al. [2017](#), Régnière and St-Amant [2007](#)). Forest composition in  
252 individual grid cells was obtained from LANDIS-II biomass outputs which was initialized using  
253 ecoforestry provincial maps and temporary forest inventory plots (see Boulanger and Pascual  
254 Puigdevall [2021](#)). Absolute fir biomass was considered along with relative biomass to describe  
255 Bicknell's Thrush preference for dense fir stands (Cadieux et al. [2019](#)). Elevation data was  
256 obtained using the elevatr R package, then was rasterized at a 250 m resolution (Hollister et al.  
257 [2021](#)).

### 258 3.1.3 Breeding range model

259 We estimated the number of observations per cell of the Bicknell's Thrush using downweighted  
260 Poisson regression (Renner et al. 2015); a point process model for presence-only data where  
261 locations of presences and of quadrature points (spatially random data points necessary to  
262 estimate the species distribution) are modelled as a function of environmental variables. In  
263 a downweighted Poisson regression, large weights are assigned to quadrature points and small  
264 weights to observations such that presence location points comprise a very small portion of the  
265 data used to estimate the model. The effect is similar to applying a spatial scaling so that the  
266 response is modelled as the number of observations per cell.

267 We modelled observation records as a function of climate, elevation, and forest composition with  
268 250m resolution as

$$\begin{aligned}\log(\lambda) = & \alpha + \beta_1(\text{temperature}) + \beta_2(\text{temperature}^2) \\ & + \beta_3(\text{precipitation}) + \beta_4(\text{elevation}) + \beta_5(\text{fir biomass}) + \beta_6(\text{fir relative biomass}) \\ & + \beta_7(\text{fir biomass} \times \text{fir relative biomass})\end{aligned}$$

269 where  $\lambda$  is the number of observations that is expected to be made of the Bicknell's thrush. Tem-  
270 perature was considered quadratically to describe both warm and cold limits. Other variables  
271 are taught to describe broad preferences and were therefore considered as linear relationships  
272 (COSEWIC 2022, Townsend et al. 2020). Absolute fir biomass was also considered in interac-  
273 tion with relative biomass to describe both stand development and composition. To estimate  
274 the model, we randomly positioned quadrature points to cover most environmental variability  
275 and to maximize the accuracy of the likelihood estimation (Renner et al. 2015). We used the

276 fitted model to predict the number of observations per cell that we then converted into the Bick-  
277 nell's Thrush breeding range. The breeding range consists of all cells with a predicted density  
278 of observation superior to 1 individual per  $km^2$  (i.e., 0.00625 observations per cell).

279 We assessed model predictive performance using the area under the receiver operating charac-  
280 teristic curve (AUC, Guisan and Thuiller 2005). AUC is essentially a diagnostic tool to measure  
281 the quality of prediction of a model. A perfect prediction yields an AUC of 1 while a random  
282 prediction yields an AUC of 0.5 (the calculation of the AUC was performed with the *auc* function  
283 of the R package *pROC*, Robin et al. 2011).

#### 284 **3.1.4 Scenarios**

285 We projected the Bicknell's thrush breeding range for two scenarios to contrast the impacts of  
286 climate with forest composition dynamics over the 2020-2100 period.

287 The Bicknell's Thrush breeding range distribution was first projected over time using the RCP  
288 4.5 climate forcing scenario (van Vuuren et al. 2011), while keeping forest composition and  
289 elevation constant. Future temperature and precipitation projections for 2021-2040, 2041-2070  
290 and 2071-2100 periods were obtained for the RCP 4.5 scenario from the Canadian Earth System  
291 Model version 2 (CanESM2). Such anthropogenic climate forcing is increasingly considered as  
292 one of the most likely scenarios given current and pledged global climate policies (Hausfather  
293 and Peters 2020). Projections were first downscaled to a 10 km resolution using the ANUSPLIN  
294 method, and then the BioSIM v11 model was used to interpolate them to a 250 m resolution  
295 (McKenney et al. 2011, Régnière and St-Amant 2007). As BioSIM stochastically generate  
296 future daily weather time series using 30-yr future climate normals, we averaged results from  
297 30 BioSIM simulations to compute future climate variables that were assigned to the last year  
298 of the projection period (e.g., 2021-2040 period became 2040).

299 Second, we projected Bicknell's Thrush breeding range over time by only considering climate-  
300 induced changes in forest composition (hereafter forest change) under RCP 4.5, i.e., keeping

climate variables and elevation constant in the model. Projections of forest composition for the commercial forests of Québec in 2040, 2070, and 2100 were obtained from Boulanger and Pascual Puigdevall (2021) which were produced using the LANDIS-II forest landscape model (FLM, Scheller et al. 2007). We used tree biomass projections considering climate-induced changes in stand dynamics as well as in wildfires, business-as-usual harvesting and spruce budworm outbreaks. More details about model parameterization, calibration and results can be found in Boulanger and Pascual Puigdevall (2021).

### 3.1.5 Analyses

We assessed the impacts of climate-only change and forest change on Bicknell’s Thrush persistence by contrasting different aspects of landscape structure from the original and forecasted landscapes. Analyses were run for the southern part of the Québec Province. Breeding range may change with respect to habitat occupancy (here, fir-stand occupancy), the spatial structure of suitable patches, or the species’ ability to occupy available suitable patches. Isolating the effect of these different elements helps to identify the drivers and their respective importance on distribution dynamics. We decomposed the landscape spatial structure into three complementary elements: the number of patches, the patch areas, and the inter-patch distances.

We further compared temporal trends in habitat amount (sensu Fahrig 2013) and persistence using metapopulation capacity (Hanski 2001). We contrasted habitat amount, metapopulation capacity without dispersal constraints, and metapopulation capacity with strong dispersal constraints to reveal how accounting for metapopulation dynamics can better inform us on the Bicknell’s Thrush distribution as discussed in section 2. Note that because we do not have a good knowledge of the Bicknell’s Thrush dispersal kernel, we therefore compared metapopulation capacity for extreme scenarios of dispersal within the range of plausible kernels. We thus evaluated metapopulation capacity for high dispersal limitations (average dispersal distance of 1 km) and for long average dispersal distance (average dispersal distance of 500 km).

## 3.2 Results: Connectivity in addition to habitat amount define realized range

The model had high performance and accurate breeding range prediction with an AUC of 0.95. Proportional fir biomass (slope  $\pm$  standard error,  $\beta_6 = 3.39 \pm 0.46$ ) and mean annual temperature ( $\beta_1 = 1.56 \pm 0.27$ ) are best predictors of the breeding range. Furthermore, the quadratic temperature term is significantly negative ( $\beta_2 = -0.28 \pm 0.025$ ) such that the model estimates maximum occupancy at 2.7 Celsius (mean annual temperature). Total annual precipitation ( $\beta_3 = -0.0064 \pm 0.00024$ ) and elevation ( $\beta_4 = 0.018 \pm 0.00029$ ) also have significant effects on occupancy. Fir biomass was not a significant predictor ( $\beta_5 = 0.0082 \pm 0.0081$ ) but its interactions with fir relative abundance ( $\beta_7 = -0.048 \pm 0.012$ ) and proportional fir biomass were such that stands of dense fir forest are associated with greater occupancy. The model shows a decrease in Bicknell's thrush predicted occupancy at low elevations of the southern and the northern edge of its distribution area (Figure 5).

### 3.2.1 Climate and habitat mismatch

Our model projected varying effects of climate change on Bicknell's Thrush breeding range within the study region (Figure 5). The magnitude of change differed between climate-only and climate-induced forest change scenarios. Shifts at the range edges were more pronounced than within the range under the climate-only scenario, with contraction at the southern edge and expansion at the northern edge. Under the climate-only scenario, extensive expansion was projected as soon as 2040 at high elevation ( $>600$  m) and in rapidly warming (up to 3 °C between 2020 and 2040) regions. Multiple northward patches became momentarily suitable with climate warming at moderate elevation areas (500 to 600 m) because of the narrow range of suitable climatic conditions at these lower elevations. Important contraction was projected at the southern range edge with high elevation mountain tops insufficient to cope with temperature increase. Conversely, changes in forest composition are limited due to the slow demography and the limited dispersal of trees (Vissault et al. 2020). As a result, the projected changes to the



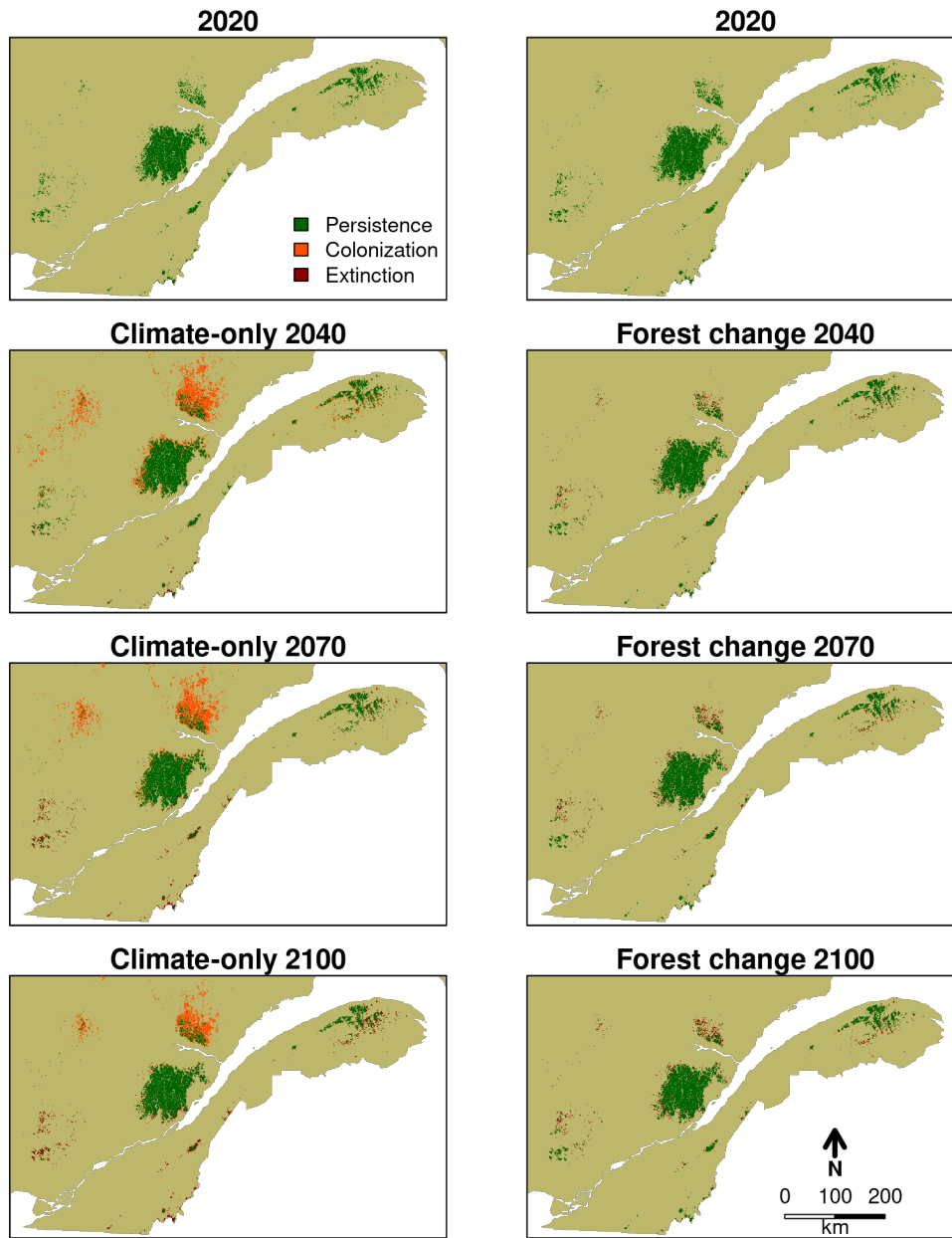


Figure 5: Projected Bicknell's thrush breeding range between 2020 and 2100 for climate-only and climate-induced forest change scenarios. Projected breeding ranges are presented as colonized, persistent, and extinct patches with 2020 initial distribution as reference.

352 breeding range under the forest change scenario were much more limited (Figure 5).

### 353 3.2.2 Changes in the spatial structure

354 Projections show that climate and forest changes have major consequences on the spatial struc-  
355 ture of suitable patches (Figure 6, Suppl. Mat. S1). The number of patches within the breeding  
356 range in the climate-only scenario supports the initial observation of range expansion followed by  
357 a rapid contraction with a peak in number of patches in 2040, while the forest change scenario  
358 shows a decline in number of patches. Overall, median patch area for both scenarios varied  
359 between 0.125 and 0.312  $km^2$  (minimum and maximum patch area = 0.0625 and 7805  $km^2$   
360 respectively) and indicates a skewed distribution with a dominance of small patches and few  
361 very large ones. On the other hand, the median inter-patch distance varied between 218 and 280  
362 km (minimum and maximum inter-patch distance = 0.25 and 809 km respectively) and shows  
363 a more balanced distribution with the landscape composed of distanced groups of regionally  
364 close patches. Although the distribution of patch areas in the climate-only scenario appears to  
365 remain constant through time, important decreases in the interpatch distances indicate the loss  
366 of small, isolated patches, the addition of geographically close patches, and the fragmentation  
367 of large patches. Despite the apparent stability of the breeding range under the climate-induced  
368 forest change scenario, important changes in its spatial structure were observed (Figure 6). We  
369 observed a rapid decline in the number of patches and, in contrast to changes under the climate-  
370 only scenario, the median patch area constantly increased between 2020 and 2100, and the  
371 inter-patch distance marginally increased. Results indicate that close patches became connected  
372 to form fewer, but larger patches in addition to the loss of small, isolated patches (Suppl. Mat.  
373 S1).

### 374 3.2.3 Persistence

375 We observed an initial increase of 64% (11,743 to 19,344  $km^2$ ) in habitat amount under the  
376 climate-only scenario (total change of +9% between 2020 and 2100; Figure 6 A, full blue line)  
377 while habitat amount remained almost stable with only a slight initial decrease of 11% (11,742 to

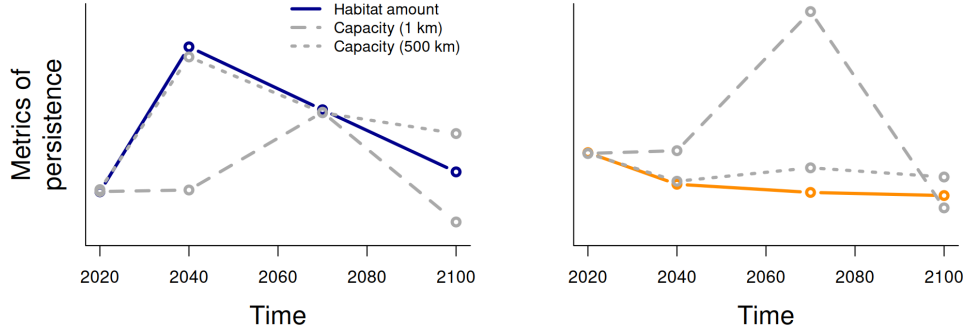


Figure 6: Changes in metrics of metapopulation persistence presented as metapopulation capacity (dashed lines) and habitat amount (full lines) from 2020 to 2100. Curves are scaled and centred to the same value in 2020 for comparison. Metapopulation capacity is presented under restricted dispersal distance (1 km) and an approximation of the mean field assumption (500 km). Panel A presents climate-only scenario results and panel B the climate-induced forest change scenario.

10,416  $km^2$ ) under the climate-induced forest change scenario (total change of -15% between 2020 and 2100; Figure 6 B, full orange line). Changes in Bicknell's Thrush metapopulation capacity approximated those in habitat amount under long average dispersal distance (approximating mean field assumption, Figure 6). However, metapopulation persistence accounting for patch size alone (long-distance dispersal) was closely approximated by habitat amount but differed when accounting for both patch size and connectivity (limited dispersal) when changes in the spatial structure of the breeding range were not explained by habitat amount alone.

## 4 Perspectives

Using theory and a case study, we show that the climate-induced changes in distribution are likely to be impacted by bottom-up interactions, demography, and landscape structure. We first derived three observations from metapopulation theory. i) A specialist's range is impacted by changes in habitat occupancy and a habitat-environment mismatch affects the range limits of the specialist. ii) The interplay between habitat shrinking and connectivity loss is likely to yield precipitated range contraction and could potentially lead to extinction. iii) The direction and amplitude of the specialist's response to environmental change vary with the degree of envi-

ronmental response correlation between trophic levels. We projected the suitable environmental conditions for a well-known bird species whose distribution is jointly affected by climate and vegetation and we analyzed its spatial structure. We showed that climate-induced changes to the distribution of suitable climatic conditions differed from that of its biotic habitat. Furthermore, both the amount of habitat and the spatial structure distribution of the favourable environmental and biotic conditions are predicted to be impacted by climate change. Thus, we expect the persistence of this species under climate change to be fundamentally affected by metapopulation dynamics. We show that the metapopulation approach complements the understanding of distribution changes by correlative SDMs. The metapopulation dynamics are fundamental to account for changes in distributions' spatial structure and contribute to accurately capturing climate-induced change in species distribution.

#### 4.1 Applications of the metapopulation approach

Many studies have investigated distribution change using metapopulation theory (Fordham et al. 2013, Huang et al. 2019, Schnell et al. 2013, Talluto et al. 2017, Vissault et al. 2020), but few have considered the complexity arising from biotic interactions and dispersal in context of rapid environmental change. Some aspects have, however, been explored, starting with the development of the theoretical basis for metapopulation dynamics on heterogeneous landscapes. Spatially realistic metapopulation theory has allowed modelling of distribution dynamics in species living in fragmented landscapes (Hanski 1998, 1999, 2001). The coupling of spatially explicit metapopulation models with dynamic climate change represents a significant conceptual advancement toward realistic projections (Anderson et al. 2009). Our analysis reveals distribution dynamics that previous methods fail to capture, demonstrating the importance of integrating dynamic processes. The metapopulation framework that we propose here proposes to simultaneously project changes in demography and dispersal in response to climate change and the multi-species effects of biotic interactions on the distribution of species.

Metapopulation theory and models influence how conservation priorities are defined at various

scales today. Metapopulation theory predicts the scaling of extinction risk with increasing habitat isolation, which non-spatially explicit approaches do not consider. We further show that a species' ability to access suitable habitat is a determining factor of its persistence. Assisted colonization and habitat restoration are proposed as means to support species persistence by increasing colonization rates and habitat occupancy, respectively (Fordham et al. 2013, Ricciardi and Simberloff 2009, Willis et al. 2009). Ultimately, metapopulation theory's main contribution to current conservation initiatives has been to highlight the effect of landscape spatial structure and dispersal on species persistence.

## 4.2 Metapopulation dynamics

We have shown using a metapopulation approach that a change in the occupancy of a habitat along an abiotic environmental gradient may impact the distribution of higher levels, such as predators or, here, habitat specialists. Therefore, a mismatch between the distribution of the habitat and of the favourable environmental conditions may affect the position of the specialist's range edge along an environmental gradient. This is the result of local increases or decreases in colonization and extinction rates from changes in habitat occupancy. Indeed, we observed the Bicknell's Thrush breeding range projection from climate-induced forest change to remain stable despite important climate change. Less contraction than expected from climate-only projections were observed at the warm edge of southern local habitat patches, indicating the establishment of a mismatch. The high elevation coniferous patches persisted into warmer conditions, increasing fir occupancy under environmental conditions where it was previously rare or absent. Furthermore, we observed no range expansion of the specialist where the climate-only scenario predicts northern expansion, revealing a decrease in habitat occupancy for climatic conditions where it was previously available. This observation is likely the result of prolonged persistence (i.e., extinction debt) of the Bicknell's Thrush where it is already observed despite less favourable environmental conditions, and the reduction of occupancy in favourable environmental conditions where it is initially observed (i.e., colonization credit). As a result, non-equilibrium dynamics in Bicknell's Thrush distribution change are predicted to be an important source of complexity.

446 Forested habitat-environment, or resource-environment mismatch in response to environmental  
447 change is to be expected in natural systems from limitations in dispersal ability and demography  
448 (Svenning et al. 2014). Conversely, habitats that shift faster than abiotic environmental condi-  
449 tions may instead decrease specialist persistence in its current range and favour environmental,  
450 but not geographical range stability. It is clear that non-equilibrium dynamics in species dis-  
451 tributions are key elements of complexity. Hence, predictions are likely to be biased without  
452 proper models to account for it.

453 Correlative SDMs predict direct response of species' range to habitat amount variations such  
454 that a decrease in habitat amount causes an equivalent contraction of the species' range. How-  
455 ever, we have shown that a metapopulation framework offers complementary information to  
456 extract from habitat projections. The contraction of a species' range may be accelerated (or  
457 slowed) by metapopulation dynamics. Here, the effect of landscape connectivity interacts with  
458 habitat occupancy to generate dynamics of greater complexity. We observed changes in the Bick-  
459 nell's Thrush distribution projections in both habitat amount and in spatial structure of habitat  
460 patches. Landscape connectivity was affected by newly suitable habitat patches, the extinction  
461 of the smallest habitat patches, the fragmentation of the larger ones, and the dispersal distance.  
462 In concordance with our intuition, changes in Bicknell's Thrush persistence were affected by  
463 metapopulation dynamics. Persistence could not be explained by changes in habitat amount  
464 alone contrasting with the assumption made by correlative SDMs (Figure 6). Furthermore, our  
465 results support Hanski (2015) in that connectivity is fundamental to species regional distribu-  
466 tion, abundance, and biodiversity in opposition to the habitat amount hypothesis (Fahrig 2013).  
467 That is because the species' ability to use all available habitat is affected by dispersal, which  
468 habitat amount alone does not represent.

469 More favourable abiotic environmental conditions can have unexpected negative impacts on spe-  
470 cialists if their habitats are negatively affected. We described this phenomenon as the effect  
471 of environmental response correlation between trophic levels (see *Key concepts* section). It is  
472 a concept unique to process-based approaches that cannot be observed directly using a cor-

relative SDM approach as it originates from the joint effects of species-specific environmental performance and of biotic interactions. Although we have not been able to measure it directly with the Bicknell's Thrush case, we observed an important contrast between its response to climate-only change and to climate-induced forest change: the habitat amount increased in the first scenario and declined in the second. We showed that regionally more favourable climatic conditions to the Bicknell's Thrush may have, even if only temporarily due to colonization or extinction lags, the opposite effect on its habitat. Therefore, the resulting distribution dynamics from the interplay between trophic levels are complex to predict. Counterintuitive dynamics can arise from species' environmental correlation. Indeed, the Bicknell's thrush example illustrates the necessity of documenting the response between trophic levels to a rapidly changing environment as they can produce non-equilibrium dynamics when considered together. It is when the lower trophic level affects the specialist's colonization and extinction rates asymmetrically that non-equilibrium distribution dynamics are observed. Because metapopulation models can incorporate such dynamics on specialists' population dynamics, the resulting projections may be of greater realism.

### 4.3 Limitations of the current approach

Metapopulation models require few parameters making them relatively easy to parameterize. Even in the absence of a calibrated model, the metapopulation approach offers tools to interpret projections outputs from correlative SDMs. We showed that different aspects of the landscape's structure could easily be described and studied. An integrated interpretation of distribution changes can be gained from scenarios of dispersal and extinction. Such scenarios can then be used to evaluate species persistence.

Several other factors could also impact the system's response to climate warming. The model described here is best suited for habitat specialists whose presence depends on the prior establishment of another species that they do not impact, but it could also be generalized to other types of interactions (Gravel et al. 2011). The concepts developed in this study are more general

499 than the specialist-habitat context in which they are presented and can apply to any bottom-up  
500 system. Positive and negative effects of the specialist on its habitat could influence the system's  
501 response to climate change differently. For example, habitat (i.e., resource) removal by the  
502 specialist may reduce competition of habitat types and decrease response lag, accelerating the  
503 specialist's decline at the scale of the landscape (Vissault et al. 2020). Prolonged occupancy of  
504 the habitat by the specialist may, on the other hand, increase habitat mismatch and support  
505 source-sink dynamics (Pulliam 1988). In addition to biotic interactions, metapopulation dynam-  
506 ics at the landscape level could be affected by the interaction of climate change and natural  
507 disturbances. For instance, wildfires and insect outbreak regimes are expected to be strongly  
508 altered under climate change (Boulanger and Pascual Puigdevall 2021), and associated biodiver-  
509 sity (see Tremblay et al. (2018) for a case study). Both are important drivers of forest dynamics,  
510 and our results show that modification in habitat distribution is associated with the specialist  
511 response.

512 We hope that biodiversity actors benefit from more accurate, yet accessible methods to estimate  
513 distribution changes. Correlative SDMs are most often used to project distribution changes,  
514 but metapopulation models allow a more accurate estimation of colonization and extinction  
515 rates with a multispecies perspective. Our estimation of the Bicknell's Thrush range projected  
516 that the biotic interactions will favour the species' persistence where it already occurs, but will  
517 limit its progression further north where firs are not as abundant despite increases in climate  
518 suitability. The resulting effect is likely to be the regional contraction of the Bicknell's Thrush  
519 range despite more favourable climatic conditions. Our study highlights the importance of  
520 demography, dispersal and biotic interactions on distribution change to rapid environmental  
521 change and the importance of spatial structure on the interpretation of projections.



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