

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

4 IMMEDIATE

5 **Abstract**

6 Projecting distributions under climate change requires going beyond climate suitability
7 models. Assessing species persistence should account for the spatial arrangement and
8 the size of suitable habitats, which are often characterized by vegetation or other biotic
9 constraints. We propose that metapopulation theory can be used to leverage species distribution
10 models and account for the complexity arising from biotic interactions, demography,
11 and landscape structure. We review the theory for distribution shifts in response to climate
12 change and derive three concepts that contrast with classical approaches: i) habitat-climate
13 mismatch can generate non-equilibrium dynamics, ii) linear change in habitat occupancy
14 generates nonlinear distribution change, and iii) the effect of environmental change on
15 habitats can propagate up and have counterintuitive effects on higher trophic levels. We
16 illustrate the theory through a study of habitat suitability within the Bicknell's Thrush
17 (*Catharus bicknelli*) distribution, a threatened bird whose patchy distribution is restricted
18 to dense balsam fir forests generally found at high elevation. Under climate warming, we
19 observe from the effect of climate alone a northward expansion associated with an important
20 southern range contraction. In contrast, the distribution of associated vegetation
21 remains geographically stable despite warming. An arising mismatch between climate and
22 vegetation drives important changes to the spatial structure of suitable habitat patches.

23 Patch area, connectivity, and habitat amount can be differently affected by climate change,
24 which influence species persistence, suggesting that habitat amount alone is not enough
25 to characterize regional distribution changes. Our results support the importance of inte-
26 grating both habitat amount (biotic and abiotic) and landscape spatial structure in the
27 assessment of persistence for which the metapopulation theory may be an ideal framework.

28 1 Introduction

29 Climate change has already prompted species to shift their range toward higher latitudes and
30 elevations (Chen et al. 2011, Parmesan 2006, Virkkala and Lehikoinen 2014). Species persistence
31 in response to climate change may critically depend on their ability to expand their range
32 and track suitable environments. While most current predictive approaches ignore important
33 biological mechanisms such as demography, dispersal, and biotic interactions, these play key
34 roles in species response to environmental change (Urban et al. 2016). In response, several calls
35 have been made for models to incorporate the processes mediating species response (Stralberg
36 et al. 2019, 2015, Fordham et al. 2013) and mechanistic approaches have been developed to
37 improve the realism of projections. Some recently developed models (e.g., dynamic range models
38 and forest landscape models) already improve projections, but more work is required to increase
39 accuracy and usability as they remain rarely employed in conservation planning when compared
40 to correlative species distribution models (SDMs, Guisan and Thuiller 2005, Franklin and Miller
41 2009, Guisan et al. 2013). The challenge now lies in the development of approaches that are
42 accessible, customizable and integrate multiple processes and their interplay (Urban et al. 2016,
43 Thuiller et al. 2013, McIntire et al. 2022). A strong theoretical background is necessary to take
44 on this challenge and guide the development of approaches to balance complexity and tractability
45 in species distribution modelling (Thuiller et al. 2013).

46 Explicit modelling of the processes that underlie distribution dynamics is challenging (Hefley et
47 al. 2017, Briscoe et al. 2021). Dynamic range models provide a successful example of incor-
48 porating demographic processes and dispersal to improve the accuracy of species distribution
49 projections (Briscoe et al. 2021). They are based on niche theory, assuming that species occur
50 at locations where the environment allows positive growth rates (Hutchinson 1957, Godsoe et al.
51 2017). However, such models are often difficult to parameterize because measuring growth rate
52 is challenging (McGill 2012) and requires very specific data on species response to abiotic condi-
53 tions. Indeed, on top of being computationally intensive (Snell et al. 2014), the data required to
54 parameterize these models are rarely available (Urban et al. 2016). Furthermore, local demog-

55 raphy on its own may be insufficient to explain broad-scale species distribution, suggesting that
56 processes at broader scales must also be considered (Le Squin et al. 2021), including dispersal
57 limitations, disturbances, and biotic interactions (Urban et al. 2016, Stephan et al. 2021).

58 Another approach recently proposed is derived from metapopulation theory. Metapopulations
59 are expected to persist in heterogenous landscapes if colonization is sufficient to balance local
60 extinctions (Hanski and Ovaskainen 2000). The environment may constrain these two processes
61 and limit metapopulation persistence. Distribution limits eventually emerge over environmental
62 gradients at this location where persistence becomes critical. Furthermore, distributions may be
63 constrained by the amount of suitable conditions in a region. As a result, a species may be absent
64 from a region, or a portion of a gradient, despite the occurrence of suitable conditions if these
65 are not abundant enough or if extinction is too high relative to colonization. Metapopulation
66 theory also makes an ideal framework to incorporate several elements of complexity such as
67 landscape heterogeneity, dispersal, and biotic interactions. Realistic landscape structures can
68 be represented with spatially explicit patch occupancy models (Hanski 1999a, Ramiadantsoa et
69 al. 2018). An incidence function is used to scale colonization to patch isolation and extinction
70 risk to patch area (MacArthur and Wilson 1967, Hanski 1999a, Schnell et al. 2013, Huang et
71 al. 2019). Colonization and extinction rates can also be modulated to represent competitive,
72 mutualistic or antagonistic interactions (Hanski 1999a, Gravel et al. 2011, Vissault et al. 2020,
73 Fordham et al. 2013). The metapopulation framework may thus be understood as a flexible
74 approach to integrate fundamental processes driving distribution dynamics.

75 Landscapes are highly heterogeneous and dynamic. They are continuously affected by changes
76 that can be slow or fast. Disturbances, environmental changes, and biotic interactions are
77 processes that may cause species distribution to be constantly out of equilibrium with their
78 niche (Ovaskainen and Hanski 2002, Svenning et al. 2014, Boulangeat et al. 2018). Non-
79 equilibrium dynamics are especially marked in plants that are limited by slow demography and
80 restricted dispersal (Svenning and Sandel 2013, Savage and Vellend 2015, Talluto et al. 2017,
81 Vissault et al. 2020). Representing this reality requires an adapted approach and metapopulation

82 theory offers the opportunity to model non-equilibrium dynamics (Hanski and Simberloff 1997,
83 Ovaskainen and Hanski 2002). Recent studies have indeed documented species distributions
84 that do not match the distribution of their favourable climate and that present extinction debts
85 and colonization credits (Savage and Vellend 2015, Talluto et al. 2017). Metapopulation models
86 have shown the trailing edge of current tree distribution to be persisting despite unfavourable
87 climatic conditions as slow demography delays the extinction of populations. At the leading edge,
88 dispersal limitations and competition prevent trees from colonizing favourable habitats (Talluto
89 et al. 2017). The ability of metapopulation models to study and describe dynamic landscapes
90 therefore makes them particularly suitable to study persistence under changing climate.

91 In this paper, we show how metapopulation theory can be used to model and thus complement
92 the interpretation of species distribution in a changing environment. In addition, we illustrate
93 how metapopulation theory can be used to leverage species distribution models by accounting
94 for the complexity arising from biotic interactions, demography, and landscape structure. To
95 achieve this goal, we first review the theory to account for these key ecological processes in
96 distribution modelling and present associated sources of complexity. We then illustrate the
97 effect and importance of these processes on persistence and distribution dynamics using the
98 Bicknell's Thrush (*Catharus bicknelli*) as a case study. The Bicknell's Thrush is a threatened
99 species in Canada with restricted distribution. We conclude that metapopulation theory can
100 improve the interpretation and the use of habitat projections, notably under increasing climate
101 warming by accounting for the spatial arrangement of habitats.

102 **2 Key Concepts Arising From Metapopulation Theory**

103 We first review the theoretical framework to incorporate key ecological processes into a mechanistic
104 approach of range dynamics. We frame these processes in the context of a bottom-up system
105 where the distribution of a focal species (e.g., a predator, a habitat specialist or a mutualist) is
106 contingent on the distribution of a trophically lower-level species (e.g., a prey, a vegetation type
107 or a host). Our approach thus integrates dispersal, demography, and biotic interactions. We

108 study distribution dynamics under climate warming and the associated sources of complexity
109 brought by landscape structure. We then contextualize the various effects of climate change on
110 persistence using a conceptual habitat specialist species as an example. The resulting changes to
111 the species' range support the emergence of distribution changes of greater complexity than pre-
112 dicted by correlative approaches and show that accounting for spatial arrangement of habitats
113 is necessary to capture distribution changes.

114 **2.1 Model description**

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

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

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

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

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

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

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

138 2.2 Graphical representation of range limits

139 We provide three examples below illustrating how metapopulation theory can reveal some of the
 140 complexities of distribution dynamics under a changing climate.

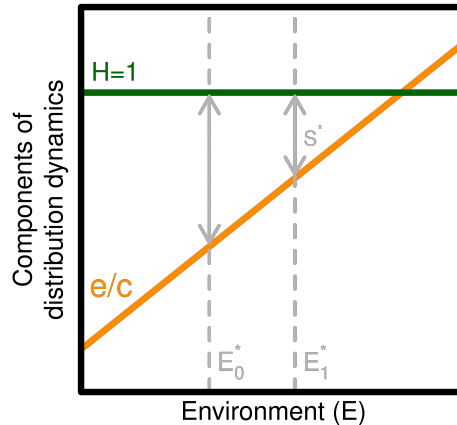


Figure 1: Graphical interpretation of the system's distribution dynamics. The distribution of the habitat specialist is defined by its intrinsic response to the environment $\frac{e}{c}$ (orange line) and by habitat occupancy ($H(E)$, green line). The habitat specialist's occupancy S^* declines with less favourable environmental conditions E_0^* and E_1^* .

141 A specialist's persistence and therefore occupancy is jointly affected by abiotic conditions and
 142 habitat availability (occupancy) such that it can be represented graphically with $\frac{e}{c}$ and $H(E)$
 143 curves. For simplicity, let's assume linear relationships. Distribution limit occurs at the position
 144 along the environmental gradient where the habitat occupancy curve (green line) crosses the
 145 extinction to colonization ratio. An example is illustrated in Figure 1. For a landscape composed
 146 of suitable habitat patches, the habitat occupancy is 1 and does not vary with environmental
 147 conditions. The specialist's intrinsic response is less favourable with increasing environmental
 148 conditions. Its occupancy for given environmental conditions is defined by the difference between
 149 habitat availability and the extinction to colonization ratio curves ($S^* = H - \frac{e}{c}$). The effect of
 150 environmental conditions on its occupancy can be graphically represented at E_0^* and E_1^* . The
 151 difference between habitat availability and the extinction to colonization ratio curves (S^* ; shown
 152 by the arrows in Figure 1) is reduced with increasing environmental conditions, illustrating a
 153 decrease in the specialist's occupancy and persistence ($S(E_0^*) > S(E_1^*)$).

154 2.2.1 Interaction of the specialist and of its habitat's response can cause indirect 155 distribution dynamics

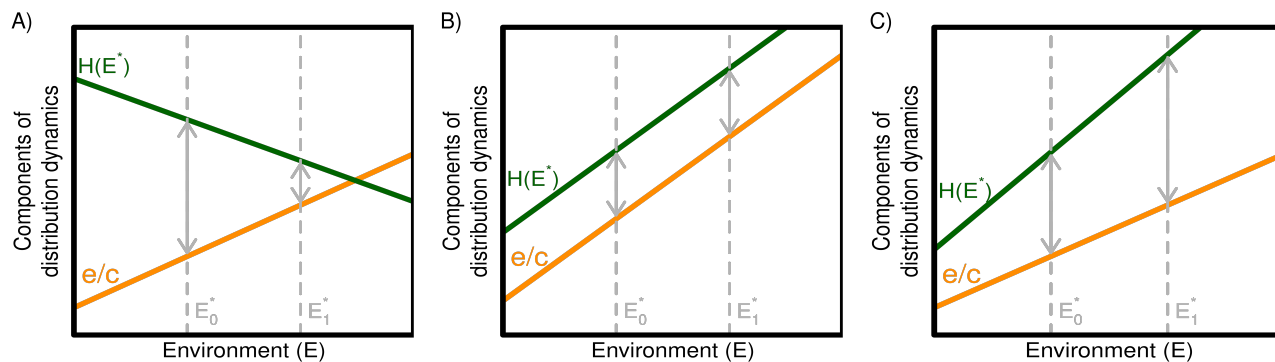


Figure 2: Change in occupancy (and persistence as shown by the grey arrows) of the habitat specialist depends on its intrinsic response to the environment $\frac{e}{c}$ (orange line) and of the habitat's response $H(E^*)$ (green line).

156 In a bottom-up system such as predator-prey or a habitat specialist, the response to environmen-
 157 tal change does not only depend on the focal species but also on the response of the associated
 158 one. The covariation in the response to the environment between the two levels is therefore of

159 critical importance. For instance, the net effect of less favourable environmental conditions to
 160 a specialist could be detrimental, without effect, or favourable depending on the effect of the
 161 environment to its habitat (Figure 2). Figure 2 A illustrates that specialist occupancy decrease
 162 (S) is amplified as environmental conditions harm simultaneously the specialist and its habitat.
 163 Conversely, stable specialist occupancy is caused by an equivalent increase of habitat availabil-
 164 ity or as one level benefits as much as the other suffers (Figure 2 B). An increase in specialist
 165 occupancy despite less favourable environmental conditions may occur if one level benefits more
 166 than the other suffers (Figure 2 C). Thus, the interaction between levels may have indirect (and
 167 counterintuitive) effects on specialist response.

168 2.2.2 Habitat mismatch affects species distribution shifts

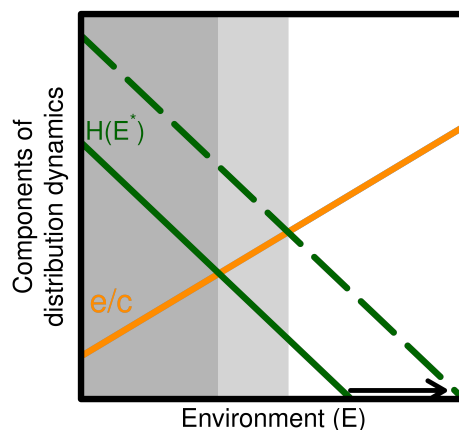


Figure 3: The distribution of the habitat specialist (grey area) is impacted by the functions relating the intrinsic response to the environment (orange line) to habitat occupancy ($H(E)$, full and dashed green lines).

169 Range limits of a habitat specialist is jointly affected by abiotic conditions and the availability
 170 (occupancy) of its habitat. Range shift in response to environmental changes is therefore not
 171 only determined by its intrinsic response to the environment, but also by the response of the
 172 habitat. As a result, a mismatch between the species response to the environment and its realized
 173 distribution may arise, in particular when different trophic levels are not responding at the same
 174 rate to environmental change. An example is illustrated in Figure 3. The distribution may
 175 shift in the geographic space, for instance toward the north, but it should stay the same in the

176 environmental space if both levels respond similarly (Figure 3, dark shaded area). That said, if
177 a delay or any other factor prevents the habitat from tracking the new environmental conditions,
178 then the habitat curve will shift (Figure 3, green dashed line), and so will the distribution limit
179 (light shaded area). Such mismatch could either benefit or harm the specialist distribution; in
180 this example, the specialist expands to less favourable environmental conditions. The response
181 of the habitat to changing abiotic conditions does influence the specialist distribution, both in
182 extent and in the position of its distribution limits in both the environmental and geographical
183 space.

184 2.2.3 Metapopulation dynamics may precipitate species decline

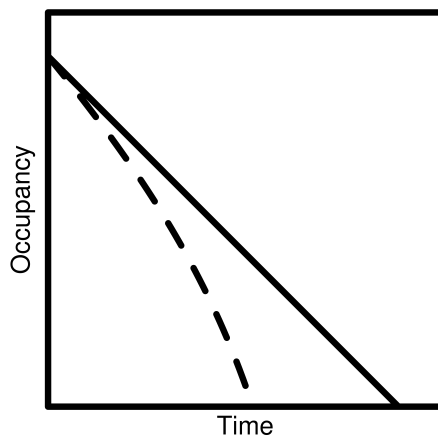


Figure 4: The response of a habitat specialist to a linear environmental change in time as it would be expected with a correlative SDM (linear response; full line). Metapopulation dynamics may precipitate - or alternatively delay - the extinction of the species in a metapopulation even if there are suitable conditions (dashed line).

185 The projection of range shifts with correlative SDMs assumes an instantaneous response to
186 environmental change. An implicit assumption is also that a reduction in habitat occupancy
187 translates into an equivalent reduction in the specialist's range, leading to extinction (Thomas et
188 al. 2004). Metapopulation dynamics may, however, precipitate the decline of a species before the
189 complete disappearance of suitable conditions. Consider a landscape where abiotic conditions
190 are spatially heterogeneous, such as temperature in a mountainous area. The progressive change
191 in this environment, like climate warming, will have two effects on the distribution of suitable
192 patches: the first direct consequence is a reduction in habitat occupancy $H(E)$, and indirectly

193 follows the increase of the extinction rate with the shrinking of suitable patches. Some favourable
194 patches may also disappear, thereby reducing the landscape connectivity. A non-linear decline
195 of occupancy therefore arises from a linear change in environmental conditions as the ratio $\frac{e(E)}{c(E)}$
196 within the specialist's persistence function increases (Figure 4). This metapopulation effect may
197 not be important at first while suitable habitat is abundant and patches are large, but increases
198 as habitat occupancy decreases, supporting an acceleration of metapopulation prevalence loss
199 to a constant abiotic environmental shift (Hanski and Ovaskainen 2000, Ovaskainen and Hanski
200 2002).

201 **2.3 Spatially explicit landscapes**

202 Analytical tools from metapopulation theory can be used to interpret range limits in spatially
203 explicit heterogeneous landscapes. Metapopulation capacity can be evaluated for realistic land-
204 scapes where patch coordinates and size are considered. Metapopulation capacity is measured
205 as the first eigenvalue of the landscape matrix M , where elements $m_{ij} = \exp(-\alpha d_{ij})A_iA_j$ for
206 $j \neq i$ and $m_{ii} = 0$ (Hanski and Ovaskainen 2000). $\frac{1}{\alpha}$ describes the average dispersal distance,
207 d_{ij} is the distance between patch i and j , and A_i is the area of patch i (refer to Hanski and
208 Ovaskainen (2000) for the full description). Metapopulation capacity is a measure of a species'
209 ability to maintain itself regionally as a function of connectivity and local extinctions. It pro-
210 vides the means to evaluate conditions for persistence given the spatial arrangement of patches
211 and their size.

212 Climate change can profoundly alter landscapes as experienced by species; not only does it influ-
213 ence the amount of suitable habitats, but also the capacity of species to persist when colonization
214 and extinction prevail. Consider a mountainous landscape inhabited by a high elevation habitat
215 specialist. The landscape is marked by a steep elevational gradient in temperature where warm
216 temperatures at low elevations exceed the species' tolerance. The landscape would therefore
217 be divided between suitable cold habitats on mountain tops and unsuitable warmer habitats at
218 the bottom. The topography will not only determine the total surface of suitable conditions,

219 but also the frequency distribution of patch sizes and of distances among mountain tops. As a
220 result, it will influence the connectivity of the landscape and the distribution of patch specific
221 extinction rates.

222 A schematic example is provided in Figure 5, inspired by the case study that will follow in the
223 next section. Fixing a lower climatic range limit in a hypothetical mountainous landscape, we
224 find nine suitable habitat patches of various sizes, distributed at various distances one from
225 another (Figure 5, left panel). Habitat patches here represent high elevation mountain tops.
226 The warming of climatic conditions causes an elevational shift of lower range limits resulting in
227 the contraction of habitat patches. An equal contraction between patches produces important
228 changes to the landscape's structure (Figure 5, right panel). The number of patches declines to
229 six for a 63% reduction of total habitat area. Patches become generally smaller from contraction
230 and fragmentation, and the smallest patches go extinct. Further, not only smaller patches are
231 assumed to support smaller population sizes, have superior extinction risks, and produce fewer
232 colonizers (Hanski and Ovaskainen 2000), but the loss and the fragmentation of patches alter
233 species dispersal ability through the loss of connectivity (Huang et al. 2019). As a result, the
234 metapopulation capacity declines by 82%.

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

239 **3 Case Study: Bicknell's Thrush in North-Eastern Amer-** 240 **ica**

241 We illustrate the concepts presented in the previous section with a case study of the Bicknell's
242 Thrush (*Catharus bicknelli*), a threatened bird species in Canada (COSEWIC 2009). Bicknell's
243 Thrush is the smallest Nordic thrush within the *Catharus* genus and is visually similar to the

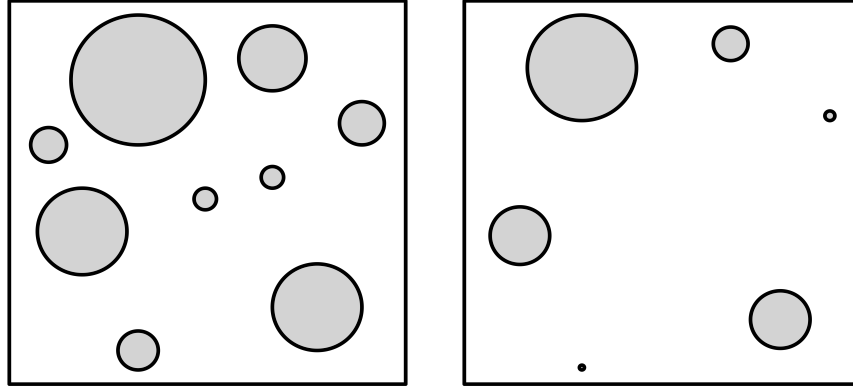


Figure 5: Species persistence is affected by changes to landscape connectivity as well as habitat amount. Black circles filled in grey delimit suitable habitat patches. The left panel presents a hypothetical mountainous landscape where suitable patches represent high elevation mountain tops and right panel the same landscape where patches 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%.

244 Grey-cheeked Thrush (*Catharus minimus*). It migrates in Northeastern America from its win-
 245 tering grounds in the Greater Antilles and feeds on invertebrates and small fruits (Townsend et
 246 al. 2020). Populations are small and were reported to be declining in Canada (COSEWIC 2009).
 247 The dispersal of Bicknell's Thrush is not known with certainty, although it has been suggested
 248 that adults nest near the site of previous successful nesting while few yearlings are observed to
 249 come back to their site of birth (Rimmer et al. 2001, Collins 2007, Studds et al. 2012). The
 250 Bicknell's Thrush is known to be associated with very dense balsam fir (*Abies Balsamea*) forests,
 251 mostly at high elevations, resulting in a fragmented and highly restricted range (COSEWIC
 252 2009 p. @cadieux_spatially_2019). This habitat may be ephemeral, as natural disturbances,
 253 forestry and stand succession could lead to local extinctions. Furthermore, its distribution in
 254 mountainous areas is highly contingent on climate elevation gradients. Climate change could
 255 therefore pose a major threat to the persistence of this species as favourable climatic conditions
 256 within isolated habitat patches could shrink rapidly (Rodenhouse et al. 2008). Unfavourable
 257 abiotic conditions are predicted to increase at the edges of mountaintop fir forest patches with
 258 the warming of climate and the limited response capacity of boreal tree species (Talluto et al.
 259 2017, Vissault et al. 2020).

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

268 **3.1 Methods**

269 **3.1.1 Studied region**

270 The Bicknell's Thrush breeding range was projected for the region where the majority of the
271 Canadian occurrences are identified (COSEWIC 2009, Townsend et al. 2020). Populations are
272 primarily found in the province of Québec, specifically in the Appalachian Mountains in the
273 southeast and the Laurentians Mountains north of the St. Lawrence River. The landscape is
274 composed of boreal, mixed and temperate forests, with their distributions mainly driven by
275 climatic latitudinal and elevational gradients. Mean annual temperature ranges from -4.0 to
276 7.5 °C in this region, but the Bicknell's Thrush occupies locations with a more restricted range
277 because of its preference for high-elevation areas. Annual precipitation ranges from 730 to 950
278 mm.

279 **3.1.2 Data**

280 Distribution data consisted of 6,079 observations of nesting behaviour sampled from 1994 to
281 2020 and was provided by the le *Regroupement QuébecOiseaux* (SOS-POP 2021). It contains
282 observations from various sources, including scientific surveys and citizen science. The region of
283 interest was rasterized on a grid of 250 x 250 m cells, where an observation within a cell was
284 defined as a presence and the other cells were left empty. By gridding the region of interest,

285 we considered the locations where one or more observations were made as a single presence,
286 accounting for any potential effects of temporal and spatial pseudo-replication resulting, for
287 example, from multiple sightings of the one individual in the same location.

288 Temperature, precipitation, elevation, and balsam fir biomass were used to model occurrences.
289 This selection of variables was motivated by expert knowledge as best reflecting Bicknell's Thrush
290 preference for high elevation and fir dominated habitats (COSEWIC 2009, Townsend et al. 2020).
291 Mean annual temperature and total annual precipitation were interpolated from climate station
292 records for the 1981-2010 period to produce a time series of annual means (McKenney et al.
293 2013). Data from a georeferenced 10 km climate grid (McKenney et al. 2013) were projected
294 to each 250 m grid cell centroid and adjusted for differences in latitude, longitude and elevation
295 with spatial regression using BioSIM v11 (Régnière et al. 2017, Régnière and St-Amant 2007).
296 BioSIM is capable of interpolating climate parameters at specific locations given that digital
297 elevation mapping, which is used as an independent variable in the model, is provided. Forest
298 composition in individual grid cells was obtained from LANDIS-II biomass outputs at simulation
299 time = 0 (see below) which was initialized using provincial ecoforestry provincial maps and
300 temporary forest inventory plots (see Boulanger and Pascual Puigdevall 2021). Absolute fir
301 biomass was considered along with relative biomass to describe Bicknell's Thrush preference for
302 dense fir stands (Cadieux et al. 2019). Elevation data was obtained using the elevatr R package,
303 then was rasterized at a 250 m resolution (Hollister et al. 2021).

304 **3.1.3 Breeding range model**

305 We estimated the number of observations per cell of the Bicknell's Thrush using downweighted
306 Poisson regression (Renner et al. 2015); a point process model for presence only data where
307 locations of presences and of quadrature points (spatially random data points necessary to
308 estimate the species distribution) are modelled as a function of environmental variables. In
309 a downweighted Poisson regression, large weights are assigned to quadrature points and small
310 weights to observations such that presence location points comprise a very small portion of the

311 data used to estimate the model. The effect is similar to applying a spatial scaling so that the
312 response is modelled as the number of observations per cell.

313 We modelled observation records as a function of climate, elevation, and forest composition with
314 250m resolution as

$$\begin{aligned} \text{Presence Points} = & \alpha + \beta_1(\text{temperature}) + \beta_2(\text{temperature}^2) \\ & + \beta_3(\text{precipitation}) + \beta_4(\text{elevation}) + \beta_5(\text{firBiomass}) + \beta_6(\text{firRelativeBiomass}) \\ & + \beta_7(\text{firBiomass} \times \text{firRelativeBiomass}) + \varepsilon \end{aligned}$$

315 where $\varepsilon \sim \text{Poisson}(\lambda)$. Temperature was considered quadratically to describe both warm
316 and cold limits. Other variables are taught to describe broad preferences and were therefore
317 considered as linear relationships (COSEWIC 2009, Townsend et al. 2020). Absolute fir biomass
318 was also considered in interaction with relative biomass to describe both stand development and
319 composition. We randomly positioned quadrature points to cover most environmental variability
320 and to maximize the accuracy of the likelihood estimation (Renner et al. 2015). We used the
321 fitted model to predict the number of observations per cell that we then converted into the
322 Bicknell's Thrush breeding range. The breeding range consists of all cells with a predicted
323 density of observation superior to 1 individual per km^2 (i.e., 0.00625 observations per cell).

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

329 3.1.4 Scenarios

330 We projected the Bicknell's thrush breeding range at a 250 m resolution for two scenarios to
331 contrast the impacts of climate with forest composition dynamics over the 2020-2100 time period.
332 We used the Bicknell's Thrush model along with calibration conditions for the breeding range
333 projection of 2020. We then used climate and forest composition scenarios for the 2040, 2070,
334 and 2100 projections.

335 The Bicknell's Thrush breeding range distribution was first projected over time under interme-
336 diate climate change conditions using the RCP 4.5 climate forcing scenario (van Vuuren et al.
337 2011), while keeping forest composition and elevation constant. Future temperature and precip-
338 itation projections for 2021-2040, 2041-2070 and 2071-2100 periods were obtained for the RCP
339 4.5 scenario from the Canadian Earth System Model version 2 (CanESM2). Such anthropogenic
340 climate forcing is increasingly considered as one of the most likely scenarios given current and
341 pledged global climate policies (Hausfather and Peters 2020). Projections were first downscaled
342 to a 10 km resolution using the ANUSPLIN method, and then the BioSIM v11 model was used
343 to interpolate them to a 250 m resolution (Régnière and St-Amant 2007, McKenney et al. 2011).
344 BioSIM was used to project daily maximum and minimum temperatures ($^{\circ}\text{C}$), precipitation
345 (mm) by matching georeferenced sources of weather data (in this case the CanESM2 projections
346 over the 10 km Australian National University Spline grid; Hutchinson et al. 2009) to 15,000
347 random spatially georeferenced points over Quebec, adjusting the weather data for differences
348 in latitude, longitude, and elevation between the source of weather data and each random point
349 using spatial regressions. Universal kriging using elevation as a drifting variable was then used
350 to interpolate climate variables to the 250m grid. As BioSIM stochastically generate future daily
351 weather time series using 30-yr future climate normals, we averaged results from 30 BioSIM sim-
352 ulations to compute future climate variables that were assigned to the last year of the projection
353 period (e.g., 2021-2040 period became 2040).

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

356 climate variables and elevation constant in the model. Projections of forest composition for
357 the commercial forests of Québec in 2040, 2070, and 2100 were obtained from Boulanger and
358 Pascual Puigdevall (2021) which were produced using the LANDIS-II forest landscape model
359 (FLM, Scheller et al. 2007). LANDIS-II is a spatially-explicit, raster-based FLM that accounts
360 for stand (e.g., interspecies competition, mortality, establishment) and landscape-level processes
361 (e.g., disturbances, seed dispersal, and forest succession). In Boulanger and Pascual Puigdevall
362 (2021), simulations were run at a 10-year time step from the 2020 biomass initial conditions up
363 to 2150 under the RCP 4.5 climate scenario. In these simulations, climate-induced changes in
364 stand dynamics as well as in wildfires were considered. Business-as-usual harvesting as well as
365 spruce budworm outbreaks were also simulated. More details about model parameterization,
366 calibration and results can be found in Boulanger and Pascual Puigdevall (2021).

367 **3.1.5 Analyses**

368 We assessed the impacts of climate-only change and climate-induced forest change on Bicknell's
369 Thrush persistence by contrasting different aspects of landscape structure from the original
370 and forecasted landscapes. Analyses were run for the southern part of the Québec Province
371 ($410,080\text{km}^2$). Breeding range may change with respect to habitat occupancy (here, fir-stand
372 occupancy), the spatial structure of suitable patches, or the species' ability to occupy available
373 suitable patches. Isolating the effect of the different elements helps to identify the drivers and
374 their respective importance on distribution dynamics. We decomposed the landscape spatial
375 structure into three complementary elements: the number of patches, the patch areas, and the
376 inter-patch distances.

377 We further compared temporal trends in habitat amount (sensu Fahrig 2013) and persistence
378 using metapopulation capacity (Hanski 2001). We contrasted habitat amount, metapopulation
379 capacity without dispersal constraints, and metapopulation capacity with strong dispersal con-
380 straints to reveal different aspects of metapopulation response. Habitat amount alone determines
381 occupancy in the absence of metapopulation dynamics (i.e., the expectation from correlative

382 SDMs); contrasting it with metapopulation capacity under long-distance dispersal reveals the
383 effect of a reduction in patch area on extinction; metapopulation capacity under short dispersal
384 distance reveals the combined effects of reduction in patch area and change in landscape con-
385 nectivity. Without sufficient knowledge of the Bicknell’s Thrush dispersal kernel, we therefore
386 compared metapopulation capacity for extreme scenarios of dispersal within the range of plausi-
387 ble kernels. We thus evaluated metapopulation capacity for high dispersal limitations (average
388 dispersal distance of 1 km) and for long average dispersal distance (average dispersal distance
389 of 500 km).

390 **3.2 Results: Connectivity in addition to habitat amount define real-** 391 **ized range**

392 The model had high performance and accurate breeding range prediction with an AUC of 0.95.
393 Proportional fir biomass (slope \pm standard error, $\beta_6 = 3.39 \pm 0.46$) and mean annual tempera-
394 ture ($\beta_1 = 1.56 \pm 0.27$) are best predictors of the breeding range. Furthermore, the quadratic
395 temperature term is significantly negative ($\beta_2 = -0.28 \pm 0.025$) such that the model estimates
396 maximum occupancy at 2.7 Celsius (mean annual temperature). Total annual precipitation
397 ($\beta_3 = -0.0064 \pm 0.00024$) and elevation ($\beta_4 = 0.018 \pm 0.00029$) also have significant effects on
398 occupancy. Fir biomass was not a significant predictor ($\beta_5 = 0.0082 \pm 0.0081$) but its inter-
399 actions with fir relative abundance ($\beta_7 = -0.048 \pm 0.012$) and proportional fir biomass were
400 such that stands of dense fir forest are associated with greater occupancy. The model shows a
401 decrease in Bicknell’s thrush predicted occupancy at low elevations of the southern edge and of
402 the northern edge of its distribution area (Figure 6).

403 **3.2.1 Climate and habitat mismatch**

404 Our model projected varying effects of climate change on Bicknell’s Thrush breeding range within
405 the study region (Figure 6). The magnitude of change differed between climate-only and climate-
406 induced forest change scenarios. Shifts at the range edges were more pronounced than within

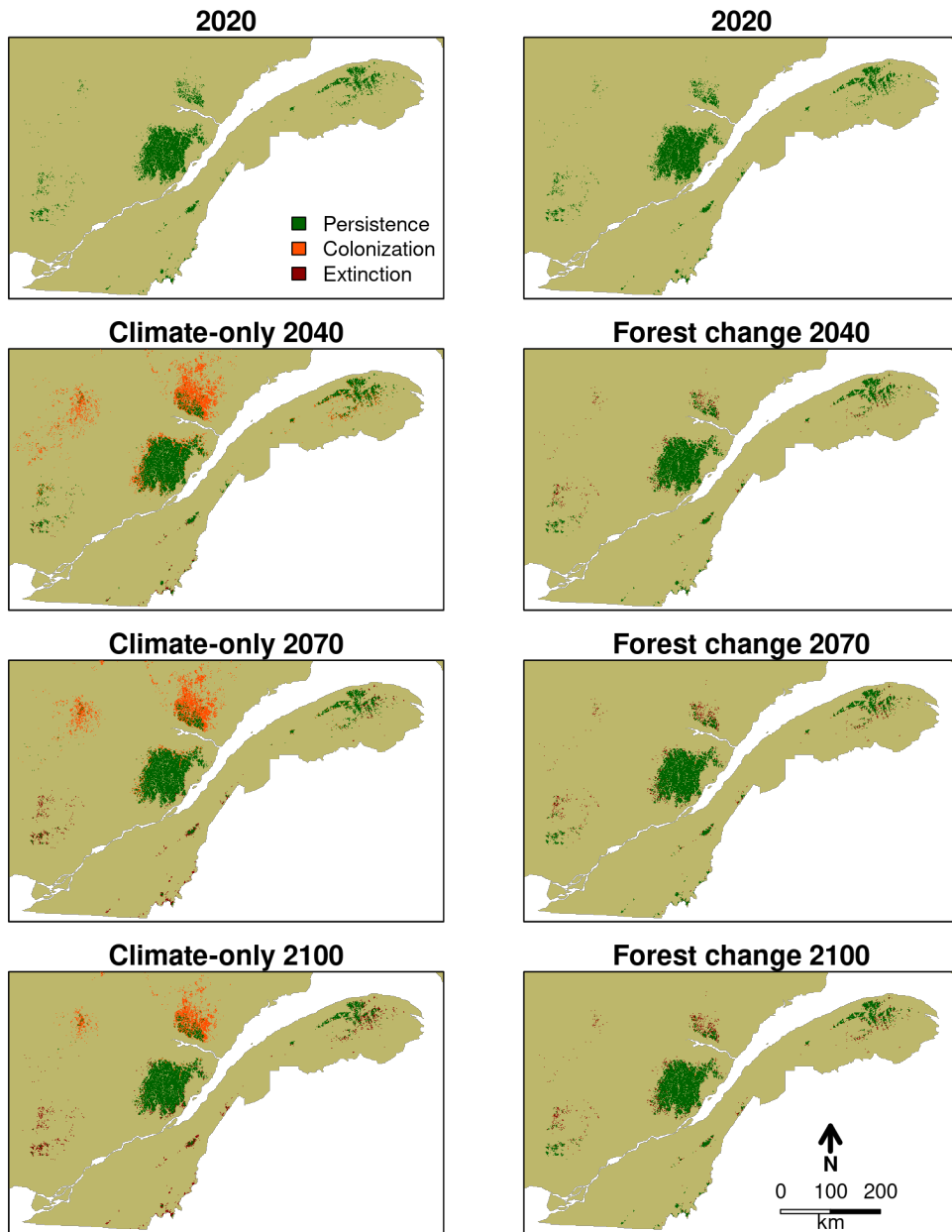


Figure 6: Projected Bicknell's thrush breeding range between 2020 and 2100 for climate-only and climate-induced forest change scenarios. Projected breeding ranges are presented as colonized, persistent, and extinct patches with 2020 initial distribution as reference. Top two panels show Bicknell's Thrush's distribution at initial conditions (2020) and therefore are identical. Lower panels show projections for 2040, 2070, and 2100.

407 the range under the climate-only scenario, with contraction at the southern edge and expansion
 408 at the northern edge. Under the climate-only scenario, extensive expansion was projected as
 409 soon as 2040 at high elevation (>600 m) and rapidly warming (up to 3 °C between 2020 and
 410 2040) regions. Multiple northward patches became momentarily suitable with climate warming
 411 at moderate elevation areas (500 to 600 m) because of the narrow range of suitable climatic
 412 conditions at these lower elevations. Important contraction was projected at the southern range
 413 edge with high elevation mountain tops insufficient to cope with temperature increase. As
 414 opposed, changes in forest composition are limited due to the slow demography and the limited
 415 dispersal of trees (Vissault et al. 2020). As a result, the projected changes to the breeding range
 416 under the forest change scenario were much more limited (Figure 6).

417 3.2.2 Changes in the spatial structure

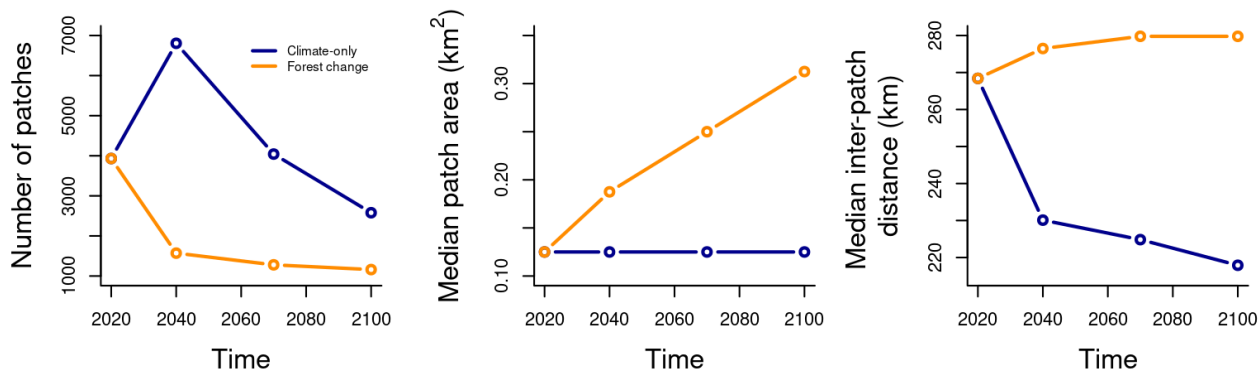


Figure 7: Change in the spatial structure of the Bicknell's Thrush breeding range between 2020 and 2100 under the climate-only (blue line) and the climate-induced changes in forest composition (orange line). The left panel presents the number of patches within the projected breeding range, the centre panel the median area of these patches, and the right panel the median distance between these patches.

418 Projections show that climate and forest changes have major consequences on the spatial struc-
 419 ture of suitable patches (Figure 7). The number of patches within the breeding range in the
 420 climate-only scenario supports the initial observation of range expansion followed by a rapid
 421 contraction with a peak in number of patches in 2040, while the climate-induced forest change
 422 scenario shows a decline in number of patches (Figure 7, left panel). Median patch area for both
 423 scenarios varied between 0.125 and 0.312 km^2 (minimum and maximum patch area = 0.0625 and

424 7805 km^2 respectively) and indicates a skewed distribution with a dominance of small patches
 425 and few very large ones (Figure 7, centre panel). On the other hand, the median inter-patch
 426 distance varied between 218 and 280 km (minimum and maximum inter-patch distance = 0.25
 427 and 809 km respectively) and shows a more balanced distribution with the landscape composed
 428 of distanced groups of regionally close patches (Figure 7, right panel). Although the distribution
 429 of patch areas in the climate-only scenario appears to remain constant through time, important
 430 decreases in the interpatch distances indicate the loss of small, isolated patches, the addition of
 431 geographically close patches, and the fragmentation of large patches (Figure 7, centre and right
 432 panels). Despite the apparent stability of the breeding range under the climate-induced forest
 433 change scenario, important changes in its spatial structure were observed. We observed a rapid
 434 decline in the number of patches and, in contrast to changes under the climate-only scenario, the
 435 median patch area constantly increased between 2020 and 2100, and the inter-patch distance
 436 marginally increased (Figure 7, centre and right panels). Results indicate that close patches
 437 became connected to form fewer, but larger patches in addition to the loss of small, isolated
 438 patches.

439 3.2.3 Persistence

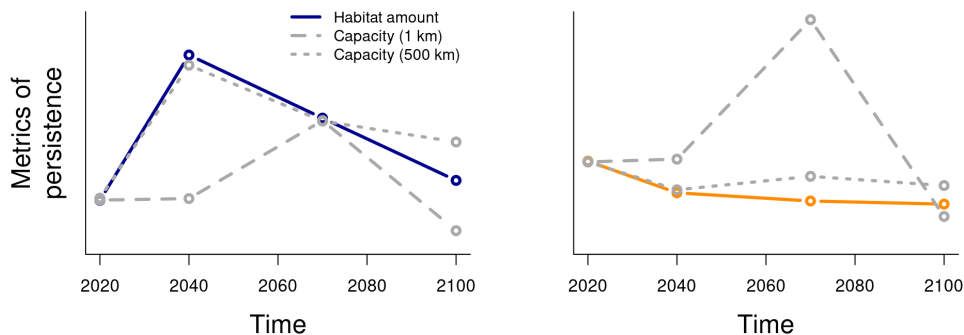


Figure 8: Changes in metrics of metapopulation persistence presented as metapopulation capacity (dashed lines) and habitat amount (full lines) from 2020 to 2100. General trends are presented for comparison. Curves are scaled and centred to the same value in 2020, their absolute value may differ. Metapopulation capacity is presented under restricted dispersal distance (1 km) and an approximation of the mean field assumption (500 km). The left panel presents climate-only scenario results and the right panel climate-induced forest change scenario.

440 We observed an initial increase of 64% (11,743 to 19,344 km^2) in habitat amount under the

441 climate-only scenario (total change of +9% between 2020 and 2100; Figure 8, full blue line)
442 while habitat amount remained almost stable with only a slight initial decrease of 11% (11,742
443 to 10,416 km^2) under the climate-induced forest change scenario (total change of -15% between
444 2020 and 2100; Figure 8, full orange line). Changes in Bicknell's Thrush metapopulation capacity
445 approximated those in habitat amount under long average dispersal distance (approximating
446 mean field assumption, Figure 8). However, we observed important divergences in the Bicknell's
447 Thrush metapopulation capacity from habitat amount when dispersal was restricted (Figure 8).
448 That is, metapopulation persistence accounting for patch size alone (long-distance dispersal) was
449 closely approximated by habitat amount but differed when accounting for both patch size and
450 connectivity (limited dispersal) when changes in the spatial structure of the breeding range were
451 not explained by habitat amount alone.

452 **4 Perspectives**

453 Using theory and a case study, we show that the climate-induced changes in distribution are
454 likely to be impacted by bottom-up interactions, demography, and landscape structure. We
455 first derived three observations from metapopulation theory. i) A specialist's range is impacted
456 by changes in habitat occupancy and a habitat-abiotic mismatch affects the range limits of the
457 specialist. ii) The interplay between habitat shrinking and connectivity loss is likely to yield
458 precipitated range contraction and could potentially lead to extinction. iii) The direction and
459 amplitude of the specialist's response to environmental change vary with the degree of environ-
460 mental response correlation between trophic levels. We projected the suitable environmental
461 conditions for a well-known bird species whose distribution is jointly affected by climate and
462 vegetation and we analyzed its spatial structure. We showed that climate-induced changes to
463 the distribution of suitable climatic conditions differed from that of its biotic habitat. Fur-
464 thermore, both the amount of habitat and the spatial structure distribution of the favourable
465 abiotic and biotic conditions are predicted to be impacted by climate change. Thus, we expect
466 the persistence of this species under climate change to be fundamentally affected by metapopu-

467 lation dynamics. We show that the metapopulation approach complements the understanding
468 of distribution changes by correlative SDMs. The metapopulation dynamics are fundamental
469 to account for changes in distributions' spatial structure and contribute to accurately capturing
470 climate-induced change in species distribution.

471 **4.1 Applications of the metapopulation approach**

472 Many studies have investigated distribution change using metapopulation theory (Schnell et al.
473 2013, Talluto et al. 2017, Huang et al. 2019, Vissault et al. 2020, Fordham et al. 2013),
474 but few have considered the complexity arising from biotic interactions and dispersal in con-
475 text of rapid environmental change. Some aspects have, however, been explored, starting with
476 the development of the theoretical basis for metapopulation dynamics on heterogeneous land-
477 scapes. Spatially realistic metapopulation theory has allowed modelling of distribution dynamics
478 in species living in fragmented landscapes (Hanski 1998, 1999b, 2001). The coupling of spatially
479 explicit metapopulation models with dynamic climate change represents a significant concep-
480 tual advancement toward realistic projections (Anderson et al. 2009). Our analysis reveals
481 distribution dynamics that previous methods fail to capture, demonstrating the importance of
482 integrating dynamic processes. A simulation study of the Iberian lynx distribution was the first
483 study to consider the interplay of climate change and trophic interactions using a metapopula-
484 tion approach (Fordham et al. 2013). It showed that these factors could be explicitly considered
485 together, exhibiting distribution dynamics of greater complexity and realism. Moreover, the
486 use of the metapopulation approach has made possible the study of non-equilibrium distribu-
487 tions by the scaling of local processes at the entire distribution (Talluto et al. 2017). Recently,
488 the approach was extended to non-equilibrium dynamics of range shift in response to climate
489 change, opening the way for the study of nonlinear dynamics of migration (Vissault et al. 2020).
490 The metapopulation framework that we propose here builds on these previous developments to
491 advance toward simultaneously projecting changes in demography and dispersal in response to
492 climate change and the multi-species effects of biotic interactions on the distribution of species.

493 The use of the metapopulation theory to inform conservation goes as far back as 1985 (Shaffer
494 1985) for species with patchy population structures and has since been adapted to account
495 for specific spatial and population dynamics (Hanski and Simberloff 1997, Huang et al. 2019,
496 Fordham et al. 2013). In response to exploitation pressure from the logging companies and
497 an extinction risk increasing rapidly, a spatially explicit metapopulation model was used to
498 define the amount of pristine forest needed to assure the survival of the northern spotted owl
499 (*Strix occidentalis caurina*) in the Northwestern United States (Shaffer 1985, Lamberson et al.
500 1993). More recently, the incidence function model has been used to study large-scale population
501 dynamics in the Glanville fritillary (*Melitaea cinxia*) whose distribution has shrunk in Europe
502 to become highly fragmented (Hanski 1994, Hanski et al. 1994). The application of these
503 models to case studies demonstrates the value of the metapopulation approach in describing the
504 distribution dynamics of species while being strongly rooted in theory and simple enough to be
505 parameterized using available ecological data (Hanski 1999a).

506 Metapopulation theory and models effect today how conservation priorities are defined at a
507 variety of scales. The conservation of ecological corridors is the current focus of important
508 initiatives worldwide including, but not limited to, Corridor Appalachien, Nature Conservancy
509 Canada, Yellowstone to Yukon Conservation Initiative and Western Wildway Network Priority
510 Corridor Project, while habitat fragmentation is a criterion of threat for the IUCN Red List
511 (IUCN 2021). Metapopulation theory predicts the scaling of extinction risk with increasing
512 habitat isolation, something other non-spatially explicit approaches do not consider. We further
513 show that a species' ability to access suitable habitat is a determining factor of its persistence.
514 Equally, assisted colonization and habitat restoration are brought forward as means to support
515 species persistence by increasing respectively colonization rates and habitat occupancy (Willis
516 et al. 2009, Ricciardi and Simberloff 2009, Fordham et al. 2013). Ultimately, metapopulation
517 theory's main contribution to current conservation initiatives has been to raise attention on the
518 effect of spatial structure of the landscape and dispersal on species persistence.

519 4.2 Metapopulation dynamics

520 We have shown using a metapopulation approach that a change in the occupancy of a habi-
521 tat along an abiotic environmental gradient may impact the distribution of higher levels, such
522 as predators or, here, habitat specialists. Therefore, a mismatch between the distribution of
523 the habitat and of the favourable abiotic conditions may affect the position of the specialist's
524 range edge along an environmental gradient. This is the result of local increases or decreases in
525 colonization and extinction rates from changes in habitat occupancy. Indeed, we observed the
526 Bicknell's Thrush breeding range projection from climate-induced forest change to remain stable
527 despite important climate change. Less contraction than expected from climate-only projections
528 were observed at the warm edge of southern local habitat patches, indicating the establishment
529 of a mismatch. The high elevation coniferous patches persisted into warmer abiotic conditions,
530 increasing fir occupancy under abiotic conditions where it was previously rare or absent. Further-
531 more, we observed no range expansion of the specialist where the climate-only scenario predicts
532 northern expansion, revealing a decrease in habitat occupancy for climatic conditions where
533 it was previously available. This observation is likely the result of prolonged persistence (i.e.,
534 extinction debt) of the Bicknell's Thrush where it is already observed despite less favourable
535 abiotic conditions, and the reduction of occupancy in favourable abiotic conditions where it is
536 initially observed (i.e., colonization credit). As a result, non-equilibrium dynamics in Bicknell's
537 Thrush distribution change are predicted to be an important source of complexity. Forested
538 habitat-abiotic, or resource-abiotic mismatch in response to environmental change is to be ex-
539 pected in natural systems from limitations in dispersal ability and demography (Svenning et
540 al. 2014). Conversely, habitats that shift faster than abiotic conditions may instead decrease
541 specialist persistence in its current range and favour environmental, but not geographical range
542 stability. It is clear that non-equilibrium dynamics in species distributions are key elements of
543 complexity. Hence, predictions are likely to be biased without proper models to account for it.

544 Correlative SDMs predict direct response of species' range to habitat amount variations such
545 that a decrease in habitat amount causes an equivalent contraction of the species' range. How-

546 ever, we have shown that a metapopulation framework offers complementary information to
547 extract from habitat projections. The contraction of a species' range may be accelerated (or
548 slowed) by metapopulation dynamics. Here, the effect of landscape connectivity interacts with
549 habitat occupancy to generate dynamics of greater complexity. We observed changes in the Bick-
550 nell's Thrush distribution projections in both habitat amount and in spatial structure of habitat
551 patches. Landscape connectivity was affected by newly suitable habitat patches, the extinction
552 of the smallest habitat patches, the fragmentation of the larger ones, and the dispersal distance.
553 In concordance with our intuition, changes in Bicknell's Thrush persistence were affected by
554 metapopulation dynamics. Persistence could not be explained by changes in habitat amount
555 alone contrasting with the assumption made by correlative SDMs (Figure 8). Furthermore, our
556 results support Hanski (2015) in that connectivity is fundamental to species regional distribu-
557 tion, abundance, and biodiversity in opposition to the habitat amount hypothesis (Fahrig 2013).
558 That is because the species' ability to use all available habitat is affected by dispersal, which
559 habitat amount alone does not represent.

560 More favourable abiotic conditions can have unexpected negative impacts on specialists if their
561 habitats are negatively affected. We described this phenomenon as the effect of environmental
562 response correlation between trophic levels (see *Key concepts* section). It is a concept unique to
563 process-based approaches that cannot be observed directly using a correlative SDM approach
564 as it originates from the joint effects of species-specific environmental performance and of bi-
565 otic interactions. Although we have not been able to measure it directly with the Bicknell's
566 Thrush case, we observed an important contrast between its response to climate-only change
567 and to climate-induced forest change: the habitat amount increased in the first scenario and
568 declined in the second. We showed that regionally more favourable climatic conditions to the
569 Bicknell's Thrush may have, even if only temporarily due to colonization or extinction lags, the
570 opposite effect on its habitat. Therefore, the resulting distribution dynamics from the interplay
571 between trophic levels are complex to predict. Counterintuitive dynamics can arise from species'
572 environmental correlation. Indeed, the Bicknell's thrush example illustrates the necessity of

573 documenting the response between trophic levels to a rapidly changing environment as they can
574 produce non-equilibrium dynamics when considered together. It is when the lower trophic level
575 affects the specialist's colonization and extinction rates asymmetrically that non-equilibrium
576 distribution dynamics are observed. Because metapopulation models can incorporate such dy-
577 namics on specialists' population dynamics, the resulting projections may be of greater realism.

578 **4.3 Limitations of the current approach**

579 Metapopulation models require few parameters making them relatively easy to parameterize.
580 Such models have been calibrated for mammals and trees (Talluto et al. 2017, Vissault et al.
581 2020, Fordham et al. 2013) and can also be for birds although the dispersal component may be
582 challenging to evaluate (Van Houtan et al. 2007, Studds et al. 2012). Even in the absence of a
583 calibrated model, the metapopulation approach offers tools to interpret projections outputs from
584 correlative SDMs. We showed that different aspects of the landscape's structure could easily
585 be described and studied. An integrated interpretation of distribution changes can be gained
586 from scenarios of dispersal and extinction. Such scenarios can then be used to evaluate species
587 persistence.

588 Several other factors could also impact the system's response to climate warming. The model
589 described here is best suited for habitat specialists whose presence depends on the prior estab-
590 lishment of another species that they do not impact, but it could also be generalized to other
591 types of interactions (see Gravel et al. 2011 for an example of a very general model). The
592 concepts developed in this study are more general than the specialist-habitat context in which
593 they are presented and can apply to any bottom-up system. Positive and negative effects of
594 the specialist on its habitat could influence the system's response to climate change differently.
595 For example, habitat (i.e., resource) removal by the specialist may reduce competition of habitat
596 types and decrease response lag, accelerating the specialist's decline at the scale of the landscape
597 (Vissault et al. 2020). Prolonged occupancy of the habitat by the specialist may, on the other
598 hand, increase habitat mismatch and support source-sink dynamics. In addition to biotic inter-

599 actions, metapopulation dynamics at the landscape level could be affected by the interaction of
600 climate change and natural disturbances. For instance, wildfires and insect outbreak regimes are
601 expected to be strongly altered under climate change (Boulanger and Pascual Puigdevall 2021),
602 and associated biodiversity (see Tremblay et al. (2018) for a case study). Both are important
603 drivers of forest dynamics, and our results show that modification in habitat distribution is
604 associated with the specialist response.

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

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