

1 **Restoring local climate refugia to enhance the capacity for dispersal-limited species to**  
2 **track climate change**

3  
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5  
6 **Abstract**

7 Climate refugia are areas where species can persist through climate change with little to no  
8 movement. Among the factors associated with climate refugia are high spatial heterogeneity,  
9 such that there is only a short distance between current and future optimal climates, as well as  
10 biotic or abiotic environmental factors which buffer against variability in time. However, climate  
11 refugia may be declining due to anthropogenic homogenization of environments and degradation  
12 of environmental buffers. To quantify the potential for restoration of refugia-like environmental  
13 conditions to increase population persistence under climate change, we simulated a population's  
14 capacity to track increasing temperatures over time given different levels of spatial and temporal  
15 variability in temperature. To determine how species traits affected the efficacy of restoring  
16 heterogeneity, we explored an array of values for species' dispersal ability, thermal tolerance,  
17 and fecundity. We found that species were more likely to persist in environments with higher  
18 local heterogeneity and lower environmental stochasticity. When simulating a management  
19 action that increased the local heterogeneity of a previously homogenized environment, species  
20 were more likely to persist through climate change, and population sizes were generally higher,  
21 but there was little effect with mild temperature change. The benefits of heterogeneity restoration  
22 were greatest for species with limited dispersal ability. In contrast, species with longer dispersal  
23 but lower fecundity were more likely to benefit from a reduction in environmental stochasticity  
24 than an increase in spatial heterogeneity. Our results suggest that restoring environments to  
25 refugia-like conditions could promote species' persistence under climate change in addition to  
26 conservation strategies such as assisted migration, corridors, and increased protection.

27  
28 **Keywords:** climate change; climate refugia; dispersal; environmental stochasticity;  
29 heterogeneity; metapopulations; population modeling; restoration

## 30 **Introduction**

31 Many species are tracking climate change by shifting their ranges to higher latitudes and  
32 elevations (Parmesan et al. 1999, Chen et al. 2011). Species that are adapted to a narrow range of  
33 climate conditions that cannot shift to analogous climates quickly enough could be at risk of  
34 extinction (Pearson 2006, Urban 2015). Traits that could limit a species' ability to track climate  
35 change include short dispersal, narrow climate tolerance, or low fecundity (Pearson 2006, Urban  
36 2015). The ability to track climate change also depends on characteristics of the environment, as  
37 variation in spatial heterogeneity and topography mean that local climate will change at different  
38 speeds in different areas across multiple scales (Ashcroft et al. 2009).

39 Areas that are expected to face relatively limited climate change represent "climate  
40 refugia" where species might persist with little to no movement (Dobrowski 2011, Morelli et al.  
41 2016). Paleocological research suggests that many dispersal-limited tree species survived past  
42 rapid climate change events in climate refugia because physical geographic characteristics, such  
43 as topography, buffered against rapid shifts in climate (Gavin et al. 2014). Though climate  
44 refugia often arise from physical characteristics such as topography (Dobrowski 2011), snowmelt  
45 (Millar et al. 2015), hydrology (McLaughlin et al. 2017), or upwelling in coral reefs (Chollett &  
46 Mumby 2013), climate refugia could also be the result of biological characteristics such as  
47 community composition and canopy cover (Lloret et al. 2012; De Frenne et al 2013).

48 Preserving climate refugia could support the persistence of climate-vulnerable  
49 populations (Morelli et al. 2016). This management approach holds potential for species that  
50 already live in areas that already contain climate refugia, which could include many climate-  
51 vulnerable species (Harrison & Noss 2017). However, because many common methods for  
52 identifying climate refugia rely on paleocological records that do not reflect recent landscape

53 changes, they may have limited utility in making predictions for modern climate change (Keppel  
54 et al. 2012). In particular, human development in biodiversity hotspots and climate refugia could  
55 reduce the availability of climate refugia for species that live within them (Cincotta et al. 2000).  
56 Climate-vulnerable species that do not currently live near or within climate refugia might then  
57 require alternative conservation strategies (Roberts & Hamann 2016), such as restoring the  
58 environmental conditions that might have previously supported refugia.

59         One potential source of climate refugia that could be impacted by anthropogenic  
60 landscape change is heterogeneity in climatic conditions over space (Hampe & Jump 2011;  
61 Ashcroft et al. 2012). High climate heterogeneity can reduce the distance a species needs to  
62 move to reach analogous habitats, allowing species to track climatic change by dispersing locally  
63 rather than dispersing across large latitudinal distances (Fig. 1e; Brito-Morales et al. 2018).  
64 However, anthropogenic homogenization of landscapes has decreased biodiversity across  
65 terrestrial (McKinney & Lockwood 1999; Groffman et al. 2014), freshwater (Scott & Helfman  
66 2001), and marine (Thrush et al. 2006) ecosystems, leading to conservation proposals to restore  
67 local-scale heterogeneity and restore the natural processes that historically supported biodiversity  
68 in these locations (Palmer et al. 2010; Morelli et al. 2016). Restoring heterogeneity might  
69 therefore buffer against the effects of climate change, but restoring climate heterogeneity might  
70 negatively impact some species, such as those with niche specialization in the microclimate most  
71 prevalent in the homogenized environment (Allouche et al. 2012).

72         Another source of climate refugia impacted by anthropogenic activities are processes that  
73 buffer local interannual climate variability (Hampe & Jump 2011). Protected species'  
74 distributions are often more accurate at predicting suitable conditions for species when they  
75 account for interannual variation (Zimmermann et al. 2009; Briscoe et al. 2016). In future

76 projections, higher environmental stochasticity increases the likelihood of population extinction  
77 (Lande 1993), and higher interannual variation and frequency of extreme weather events during  
78 climate change could increase this extinction risk (Jentsch et al. 2007; Wernberg et al. 2013).  
79 Anthropogenic disturbance in locations with properties that buffer interannual climate variation  
80 could then reduce the availability of critical climate refugia, as might anthropogenic impacts that  
81 affect abiotic or biotic buffers (e.g., impacts that reduce canopy cover; De Freene et al. 2013).

82 Here, we quantify the potential for restoring human-altered environments to past levels of  
83 spatial heterogeneity or environmental stochasticity to create climate-refugia-like conditions that  
84 promote species persistence under climate change. Specifically, we use a metapopulation model  
85 to explore how local climate heterogeneity and environmental stochasticity affect a species'  
86 ability to persist through climate change. The model cycles through reproduction, dispersal, and  
87 density dependence, where variation in temperature from spatial heterogeneity, environmental  
88 stochasticity, and climate change affect reproduction. By exploring a range of values for biotic  
89 parameters (dispersal distance, thermal tolerance breadth, and fecundity) and abiotic parameters  
90 (magnitude of temperature heterogeneity over space and temperature stochasticity over time), we  
91 determine which types of species are likely to persist in which types of environments. We  
92 simulate the management actions of increasing heterogeneity or decreasing stochasticity to  
93 quantify their effect on persistence likelihood and population size in a changing climate.

94

## 95 **Methods**

96 To understand how spatio-temporal variation affects species' abilities to track climate  
97 change along a temperature gradient, we built a stochastic metapopulation model simulating a  
98 species dispersing across an environment with changing temperatures (adapted from Backus &

99 Baskett 2021; Backus et al. 2022). We represent a species as a discrete population over a series  
100 of connected patches on a one-dimensional temperature gradient (e.g., latitudinal or elevational  
101 gradient). To represent spatio-temporal heterogeneity in temperature, each patch contains several  
102 subpatches with unique temperatures that change stochastically over time at a designated level of  
103 variability. During each time step, the population cycles through reproduction, dispersal, and  
104 density-dependent survival. Species differ by dispersal ( $\gamma$ ), thermal tolerance breadth ( $\sigma$ ), and  
105 fecundity ( $\rho$ ). Each environment is defined by the standard deviation in interannual  
106 environmental stochasticity ( $S$ ) and the standard deviation in local climate heterogeneity ( $H$ ). We  
107 randomized these five parameters for each simulation to explore how each influences species'  
108 persistence and population size. We then implemented changing spatial heterogeneity or  
109 environmental stochasticity to simulate management actions that restore refugia.

110

### 111 *Environmental structure*

112 We represent local temperature variation across space with the local climate  
113 heterogeneity parameter,  $H$  (Fig. 1e). Space in this model is a one-dimensional temperature  
114 gradient of  $L$  patches, representing large-scale latitudinal or elevational change (Urban et al.  
115 2012). Each patch  $x$  contains  $W$  subpatches, representing small-scale variability in  
116 microclimates without an explicit spatial structure. Local subpatch ( $w$ ) temperature is  $T(x, w, t)$   
117 with a mean patch temperature of  $\bar{T}(x, t) = \sum_{w=1}^W T(x, w, t)$  at time  $t$ . We set the local climate  
118 heterogeneity so that each patch has a standard deviation in local temperatures of

$$H = \sqrt{\frac{\sum_{w=1}^W (T(x, w, t) - \bar{T}(x, t))^2}{W - 1}}. \quad (1)$$

119 We represent temperature variation over time with the environmental stochasticity

120 parameter,  $S$  (Fig. 1d). Each time step, all patches change in temperature by an average value of  
121  $\tau$ , with a stochastic component with autocorrelation  $\kappa$ , and standard deviation  $S$  around white  
122 noise  $\omega(t)$ . The stochastic component of yearly temperature change is  $\epsilon(t + 1) = \kappa\epsilon(t) +$   
123  $\omega(t)\sqrt{1 + \kappa^2}$ , with the square root term to remove the effect of autocorrelation on the variance  
124 (Wichmann et al. 2005). Altogether, the temperature in patch  $x$ , subpatch  $w$ , changes over time  
125 is

$$T(x, w, t + 1) = T(x, w, t) + \tau + S\epsilon(t). \quad (2)$$

126

### 127 *Population dynamics*

128 Simulated species have a population size of  $n(x, w, t)$  individuals in patch  $x$ , subpatch  $w$ ,  
129 at time  $t$ . All individuals reproduce simultaneously at the beginning of each time step with a  
130 reproductive output  $b(T(x, w, t))$  as a function of time- and location-dependent temperature  
131  $T(x, w, t)$  (Fig. 1a). The ecological performance of many species, especially ectotherms, is skew-  
132 normal depending on temperature, with peak performance at a thermal optimum, a gradual  
133 decrease below the optimum, and a sharp decrease above the optimum (Huey & Kingsolver  
134 1989; Norberg 2004). Therefore, the species' temperature-dependence is skew-normal, given  
135 skewness constant  $\lambda$  with the highest values around the thermal optimum  $\zeta$  and a sharp decrease  
136 above  $\zeta$ . Given thermal tolerance breadth  $\sigma$  and fecundity  $\rho$ , the reproductive output is

$$b(T(x, w, t)) = \exp\left(\rho \left\{ \exp\left[-\left(\frac{T(x, w, t) - \zeta}{\sigma}\right)^2\right] \cdot \left[1 + \operatorname{erf}\left(\lambda \frac{T(x, w, t) - \zeta}{\sigma}\right)\right] - 1\right\}\right) \quad (3)$$

137 (Urban et al. 2012). To incorporate demographic stochasticity, the number of propagules  
138 produced in patch  $x$ , subpatch  $w$  is a Poisson random variable with mean equal to  $b(T(x, w, t))$ ,  
139 or  $n^*(x, w, t) \sim \text{Poisson}\left(n(x, w, t) b(T(x, w, t))\right)$  (Melbourne & Hastings 2008).

140 Between reproduction and density-dependence, each propagule disperses from its origin  
141 (Fig. 1b), representing typical life histories of plants and many marine invertebrates. The model  
142 pools all propagules in a patch prior to dispersal, such that the total number of propagules in  
143 patch  $x$  at time  $t$  is  $N^*(x, t) = \sum_{w=1}^W n^*(x, w, t)$ . We adapt the heavy-tailed Laplace dispersal  
144 kernel to a discrete space analog, as most studies that fit empirical dispersal data to theoretical  
145 dispersal kernels show that heavy-tailed kernels (with accelerating spreading rates) outperform  
146 thinner-tailed kernels among a wide variety of species (Nathan et al. 2012). We define  $\gamma$  as the  
147 mean absolute distance (in patches) that individuals move and define the kernel parameter  $q =$   
148  $(\gamma + 1 - \sqrt{\gamma^2 + 1})/\gamma$ . Thus, the probability of moving from patch  $x$  to patch  $y$  is

$$k(x, y) = \left(\frac{q}{2 - q}\right) (1 - q)^{|x-y|} \quad (4)$$

149 (Backus & Baskett 2021; Backus et al. 2022). All propagules disperse from patch  $x$  throughout  
150 all patches with a multinomial random vector. After arriving at patch  $y$ , propagules randomly  
151 distribute among the  $W$  subpatches of patch  $y$ . The resulting number of dispersed propagules in  
152 patch  $y$ , subpatch  $w$ , at time  $t$  is  $n^{**}(y, w, t)$ .

153 Lastly, dispersed propagules compete for limited space and resources within each  
154 subpatch, given constant carrying capacity  $K$  in each subpatch (Fig. 1c). For simplicity, density-  
155 dependent survival is a variation on lottery competition (Sale 1978), where each individual has  
156 an equal probability of surviving, based on the Beverton-Holt density-dependence,

$$p(n^{**}(x, w, t)) = \left(1 + \frac{n^{**}(x, w, t)}{K}\right)^{-1}. \quad (5)$$

157 The total number of individuals that survive in patch  $x$ , subpatch  $w$ , after competition is a  
158 binomial random variable  $n(x, t + 1) \sim \text{Binomial}\left(n^{**}(x, w, t), p(n^{**}(x, w, t))\right)$  (Melbourne &  
159 Hastings 2008). Though temperature does not affect density-dependent survival, this is

160 immediately followed by reproduction that incorporates temperature-dependence (Eq. 3).

161

### 162 *Parameterization and implementation*

163 For all simulations, the number total number of patches was  $L = 512$  and the number of  
164 subpatches per patch was  $W = 8$  (giving a total of  $2^{12}$  discrete locations). The initial mean  
165 temperature across the temperature gradient varied linearly from  $\bar{T}(1,0) = 9.78^\circ\text{C}$  on the  
166 poleward edge to  $\bar{T}(L, 0) = 30.22^\circ\text{C}$  on the equatorward edge, though the species would only  
167 occupy a subset of this range. Annual temporal autocorrelation was  $\kappa = 0.767$  based on the  
168 measured combined global land-surface air and sea-surface water temperature anomalies from  
169 1880 to 1979 (GISTEMP Team 2019; Lenssen et al. 2019). The carrying capacity was a  
170 temperature-independent constant  $K = 8$  per subpatch so that each patch could carry a total of  
171 64 individuals at carrying capacity. In all simulations, we set the species' thermal optimum to  
172  $\zeta = 20^\circ\text{C}$  with a skewness  $\lambda = -2.7$  to ensure that species performance is greatest at the center  
173 of the initial temperature gradient.

174 We ran two sets of simulations with  $10^9$  replicates to quantify species persistence  
175 through gradually increasing temperatures under different species demographic values and  
176 degrees of spatio-temporal environmental variation. For each simulation, we generated a  
177 randomized environment and temporal time series based on the local temperature heterogeneity  
178 ( $H$ ) and environmental stochasticity ( $S$ ), each drawn from uniform distributions (Table 1). We  
179 generated species by drawing the mean dispersal distance ( $\gamma$ ) from a log-uniform distribution  
180 and the thermal tolerance breadth ( $\sigma$ ) and fecundity ( $\rho$ ) from uniform distributions (Table 1).

181 In the first set of simulations, we evaluated which types of species and environments  
182 were associated with species persistence during climate change without management action. To



183 initialize the population size and range given the species' biotic parameter values ( $\gamma$ ,  $\sigma$ , and  $\rho$ )  
184 and the environmental parameter values ( $H$  and  $S$ ), we placed 4 individuals on each subpatch and  
185 simulated the model for 200 years with no average temperature change,  $\tau = 0^\circ\text{C}$  per year. Then  
186 we simulated climate change by adjusting the temperature change to  $\tau = 0.02^\circ\text{C}$  per year  
187 reflecting intermediate emissions climate scenario ( $2^\circ\text{C}$  over 100 years) and  $\tau = 0.04^\circ\text{C}$  per year  
188 reflecting a high emissions scenario ( $4^\circ\text{C}$  over 100 years) (Urban et al. 2012, IPCC 2014). We  
189 tracked whether or not the species persisted anywhere the landscape, and, following the  
190 methodology of a global sensitivity analysis (Cariboni et al. 2007), we ran a random forest  
191 classification (randomForest 4.6-14 package, R Version 4.03) with persistence/extinction as the  
192 dependent variable and  $\gamma$ ,  $\sigma$ ,  $r$ ,  $S$ , and  $H$  as the dependent variables.

193 In the second set of simulations, we evaluated which types of species would benefit from  
194 conservation management actions of increasing the local heterogeneity or decreasing the  
195 environmental stochasticity. We used the same set parameters generated above, but we modified  
196 the initial local heterogeneity to a set value  $H_1 = 1$  and initialized the population again over 200  
197 years with no average temperature change. Then we simulated how two management scenarios  
198 affected the final population after 100 years of increasing temperatures under both the  $2^\circ\text{C}$  and  
199  $4^\circ\text{C}$  scenarios. When unmanaged, we left the local heterogeneity at  $H_{2,a} = H_1 = 1$ , and when  
200 restoring heterogeneity, we changed the local heterogeneity to  $H_{2,b} = 2$ . We performed a similar  
201 set of simulations keeping heterogeneity constant but reducing stochasticity, such that the initial  
202 stochasticity was  $S_1 = 0.5$ , and the two scenarios were  $S_{2,a} = 0.5$  (unmanaged) and  $S_{2,b} = 0.25$   
203 (managed). In these simulations, we considered species to have benefited from restoration if the  
204 final population under management was greater than 105% of the value for the simulations  
205 without management. We compared population size rather than persistence to help us better

206 detect potential negative effects of management and gain a more nuanced understanding of  
207 potential benefits.

208

## 209 **Results**

210 Out of all species we simulated, 61.2% persisted without management intervention under  
211 4°C of temperature increase over 100 years, and 91.3% persisted under 2°C of temperature  
212 increase. Under both climate change scenarios, simulated species were less likely to persist or  
213 had a lower population size if they had shorter mean dispersal distance  $\gamma$ , narrower thermal  
214 tolerance  $\sigma$ , or lower fecundity  $\rho$ , and when they were in environments with higher interannual  
215 variation in stochasticity  $S$  or lower local heterogeneity  $H$  (Fig. 2, S1, S2; random forest out-of-  
216 bag error: 6.87% under 4°C, 6.47% under 2°C). In general, species with multiple biological  
217 limitations (e.g., species with both short dispersal and narrow thermal tolerance) were less likely  
218 to persist through climate change (Fig. 3, S3).

219 On average, restoring heterogeneity along the temperature gradient (by doubling  $H$ )  
220 improved a species' likelihood of persisting through 4°C of temperature increase over 100 years  
221 more often than it decreased a species' likelihood of persisting (Fig. 3, Fig. 4a,c,e). Restoring  
222 heterogeneity also generally increased a species' population size relative to no action. However,  
223 when the temperature increased by only 2°C over 100 years, restoring local heterogeneity was  
224 more likely to decrease a species' population size, and the species that were more likely to  
225 benefit were those that were already likely to persist (Fig. S4, S5). In simulations with 4°C of  
226 temperature increase, species with shorter average dispersal particularly benefited from increased  
227 heterogeneity (Fig. 3). Though many of the species with the shortest dispersal ranges went  
228 extinct regardless of management, increasing the local heterogeneity was more likely to prevent

229 extinction and increase the final population size and rarely decreased population size or caused  
230 extinction (Fig. 4a). Species with longer dispersal ranges were less likely to go extinct without  
231 management, and increasing heterogeneity was less likely to benefit and more likely to decrease  
232 the population size or cause the extinction of these species. Species with narrow thermal  
233 tolerance or low fecundity were also unlikely to persist without heterogeneity restoration, but  
234 these species did not benefit as strongly and were more likely to experience negative effects from  
235 increased heterogeneity when compared with species with shorter dispersal ranges (Fig. 4c,e).

236         Decreasing the environmental stochasticity along the temperature gradient (by halving  
237 the value of  $S$ ) typically increased the persistence likelihood and population size (relative to no  
238 action) of species throughout our simulations under both the 2°C and 4°C increase scenarios  
239 (Fig. 4b,d,f, S5). Decreasing the stochasticity did not strongly benefit species with very short  
240 dispersal, narrow thermal tolerance, or low fecundity, as many of these species were likely to go  
241 extinct regardless of management action. Species with longer dispersal, narrower thermal  
242 tolerance, and higher fecundity were more likely to benefit from decreased stochasticity.

243         Comparing both restoration strategies in the 4°C increase scenario, we found that  
244 restoring heterogeneity was particularly beneficial to species with low dispersal (below the 25%  
245 quantile) but with high values in one or both of the other two traits (above the 75% quantile)  
246 (Fig. 3). For these combinations, restoring heterogeneity either prevented the species from going  
247 extinct or increased the final managed population size (at least 105% the population size of the  
248 unmanaged population) in a high proportion of simulations. However, species with high  
249 dispersal and low fecundity were unlikely to benefit from increased heterogeneity but were  
250 somewhat likely to benefit from decreased stochasticity. Species with low values in all three  
251 traits went extinct in every simulation, regardless of management.

252

## 253 **Discussion**

254 Overall, we found that simulated species were more likely to persist through climate  
255 change when they lived in temperature gradients with higher habitat heterogeneity and lower  
256 environmental stochasticity. This arises because species in heterogeneous environments do not  
257 need to disperse as far to reach analogues during climate change, and species are more likely to  
258 persist with more consistent year-to-year changes of lower environmental stochasticity. We also  
259 find that many species with strong biological limitations (e.g. short distance, narrow thermal  
260 tolerance, or low fecundity) might benefit from conservation management strategies that increase  
261 local climate heterogeneity or reduce interannual variation in climatic conditions. Although some  
262 of the species we modeled were negatively affected by these restoration efforts, the majority of  
263 species experienced long-term benefits from restoring heterogeneity or decreasing stochasticity,  
264 especially in our more extreme climate change simulations. These results build on previous  
265 findings that climate and habitat heterogeneity can maintain biodiversity in the absence of  
266 climate change (Stein et al. 2014, Gámez-Virués et al. 2015), suggesting that heterogeneity can  
267 also create refugia-like conditions to buffer against climate change.

268

### 269 *Approaches to restoring refugia*

270 Restoring climate refugia by restoring local climate heterogeneity might be achieved by  
271 modifying physical landscapes and ecological communities to resemble a pre-agricultural or pre-  
272 industrial state (Palmer et al. 2010; Morelli et al. 2016). In human-modified forest landscapes  
273 that have been converted to agriculture, this means not only maintaining several high-quality  
274 patches with diverse plant communities, but also scattering trees between the dense areas

275 (Fischer et al. 2010; Arroyo-Rodríguez et al. 2020). Approaches to integrate natural habitat into  
276 human-dominated landscapes, such as wildlife-friendly farming practices (Green et al. 2005) and  
277 their incentivization through agri-environmental schemes (Donald & Evans 2006), provide an  
278 opportunity to restore lost heterogeneity (Fischer et al. 2008) that might then improve species  
279 persistence through climate change. For example, many dispersal-limited climate-threatened  
280 herpetofauna in Romania could lose all livable climate space by the 2050s (Popescu et al. 2013).  
281 However, because of recent political change in eastern Europe, many areas that were previously  
282 deforested for agriculture have become abandoned and fragmented (Bălteanu & Popovici 2010).  
283 Others have already suggested restoring these abandoned areas into traditional farming  
284 landscapes with heterogeneous vegetation to benefit the people and biodiversity in the region  
285 (Fischer et al. 2012), and our theoretical results suggest this could also help buffer dispersal-  
286 limited species persist through rapid climate change.

287 Restoring climate refugia by reducing environmental stochasticity might be difficult to  
288 manage on a large scale, but it might be possible in a few situations. Canopy cover can affect  
289 temperature extremes, acting as climate refugia on forest floors and riparian environments  
290 (Davies 2010; De Frenne et al. 2013; Reiter et al. 2020). Clear-cut areas experience a greater  
291 range in temperatures than deciduous or mixed forests (Barbier et al. 2008). Forestry practices  
292 that promote diverse stands of deciduous or mixed trees could minimize the magnitude of  
293 temperature extremes and minimize stochasticity, which our theoretical results suggest could  
294 increase the persistence of long-distance-dispersing, low-fecundity species under climate change.

295

296 *Species traits associated with benefits from refugia restoration*

297 Species with limited dispersal ability are expected to be among the most at risk of

298 extinction from climate change because they are unlikely to disperse far enough to reach  
299 analogous climates to their historic ranges given projected rates of climate change (Pearson  
300 2006; Urban 2015). Accordingly, we found that the shortest-distance dispersing species were  
301 most likely to go extinct when unmanaged during our climate change simulations, and these  
302 species disproportionately benefited from simulated heterogeneity restoration. However,  
303 heterogeneity restoration only benefited dispersal-limited species if they also had either broad  
304 thermal tolerance or high fecundity, while species that were limited by all three demographic  
305 traits went extinct regardless of management intervention. Given these expectations, example  
306 candidates of species likely to benefit from restoring habitat heterogeneity might include plant  
307 species that would be classified as ruderal or stress tolerant (Grime 1977), such as early-to-mid  
308 successional plants (Meier et al. 2012) or alpine shrubs adapted to unique soil types (Damschen  
309 et al. 2012). Similarly, many reptiles and amphibians have limited dispersal ability and narrow  
310 climate tolerance, but relatively high fecundity (Araújo et al. 2006), suggesting that they might  
311 especially benefit from heterogeneity restoration.

312         As compared to restoration of spatial heterogeneity restoration, reducing the  
313 environmental stochasticity was more likely to benefit species with longer average dispersal and  
314 lower fecundity in our simulations. However, many of the species that disproportionately  
315 benefitted from stochasticity reduction were likely to persist through climate change even  
316 without restoration. Moreover, long-distance-dispersing, low-fecundity species might be rare  
317 given the typical positive correlation between dispersal distance and fecundity in taxon such as  
318 plants (Beckman et al. 2017). Because dispersal allows individuals to reach higher quality  
319 environments under temporally unpredictable conditions, it can drive the evolution of dispersal  
320 under high environmental stochasticity (Levin et al 1984; McPeck & Holt 1992), and species

321 with greater dispersal ability could be less common in historically low-stochasticity  
322 environments. Species with high dispersal and low fecundity could be large longer-lived animal  
323 species with high investment in offspring care, including many mammals and birds, though  
324 longer life histories also provide a buffer against environmental stochasticity (Halley et al. 2018).  
325 Even birds with higher dispersal ability have become uncoupled with their optimal climate in the  
326 past few decades (Viana & Chase 2022), but this could be driven by transient populations in  
327 heterogenous environments (Coyle et al. 2013).

328         Restoration to increase spatial heterogeneity or buffer environmental stochasticity did not  
329 alleviate extinction risk for species within the bottom quartiles for all three of dispersal, climate  
330 tolerance, and fecundity in our simulations. For such species, alternative management  
331 approaches to mitigating climate-driven extinction (Heller & Zavaleta 2009; Backus et al. 2022)  
332 might more effectively reduce extinction risk. For example, assisted migration, the intentional  
333 movement of the species to a location that is projected to be more suitable under projected  
334 climate change (McLachlan et al. 2007; Schwartz et al. 2012), could allow a species to reach a  
335 suitable future climate despite dispersal and fecundity limitations, although moving a species  
336 into a new location could bring the risks of invasion (Mueller & Hellmann 2008; Hewitt et al.  
337 2011). Another risk of assisted migration is that these species might fail to establish in their  
338 recipient communities after relocation because of species interactions, especially for species with  
339 low thermal tolerance in a stochastic environment, causing a loss to the source population  
340 (Peterson & Bode 2021; Backus & Baskett 2021). For such species, one potential management  
341 strategy to promote thermal tolerance is assisted gene flow, the introduction of climate-tolerant  
342 traits or other beneficial traits from other populations into climate-threatened populations, such  
343 as through the relocation of locally adapted individuals within a species' range (Aitken &

344 Whitlock 2013). Furthermore, for species with sufficient dispersal to track climate change but  
345 are limited by habitat fragmentation, management to increase connectivity between high-quality  
346 patches, such as the establishment of corridors, might prove more effective (Heller & Zavaleta  
347 2009; Lawler & Olden 2011).

348

### 349 *Model assumptions and future directions*

350 Our model provides a first step towards quantifying the expected efficacy of restoring  
351 climate refugia, a widely considered conservation tool among several types of ecosystems  
352 (Davies 2010; Chollett & Mumby 2013; Morelli et al. 2016). Further theoretical research might  
353 expand on many of the simplifying assumptions we made in this model. In particular, our model  
354 considers single populations in isolation of an ecological community, but a species' ability to  
355 shift its range with climate change generally depends on species interactions (Urban et al. 2012).  
356 These interactions could be crucial, as competing species could slow climate tracking by  
357 preventing species from dispersing poleward, especially if there is differential dispersal ability  
358 between interacting species (Urban et al. 2012). If longer-distance dispersing species colonize  
359 newly restored environments before shorter-distance dispersing species, competition could  
360 dampen the benefits of heterogeneity restoration. Also, our model assumed a constant carrying  
361 capacity, reflecting equal habitat quality throughout our simulated landscape. Patchy  
362 environments could mean that short-dispersing species would be unable to disperse over larger  
363 scale temperature gradients (e.g., latitudinally), which could increase the benefit of restoring  
364 local climate heterogeneity. As managers continue to consider climate refugia as a conservation  
365 tool for climate change, further ecological models adapted to specific species and ecosystems can  
366 reveal potential costs and benefits of management actions that affect climate heterogeneity and



367 environmental stochasticity in practice.

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373

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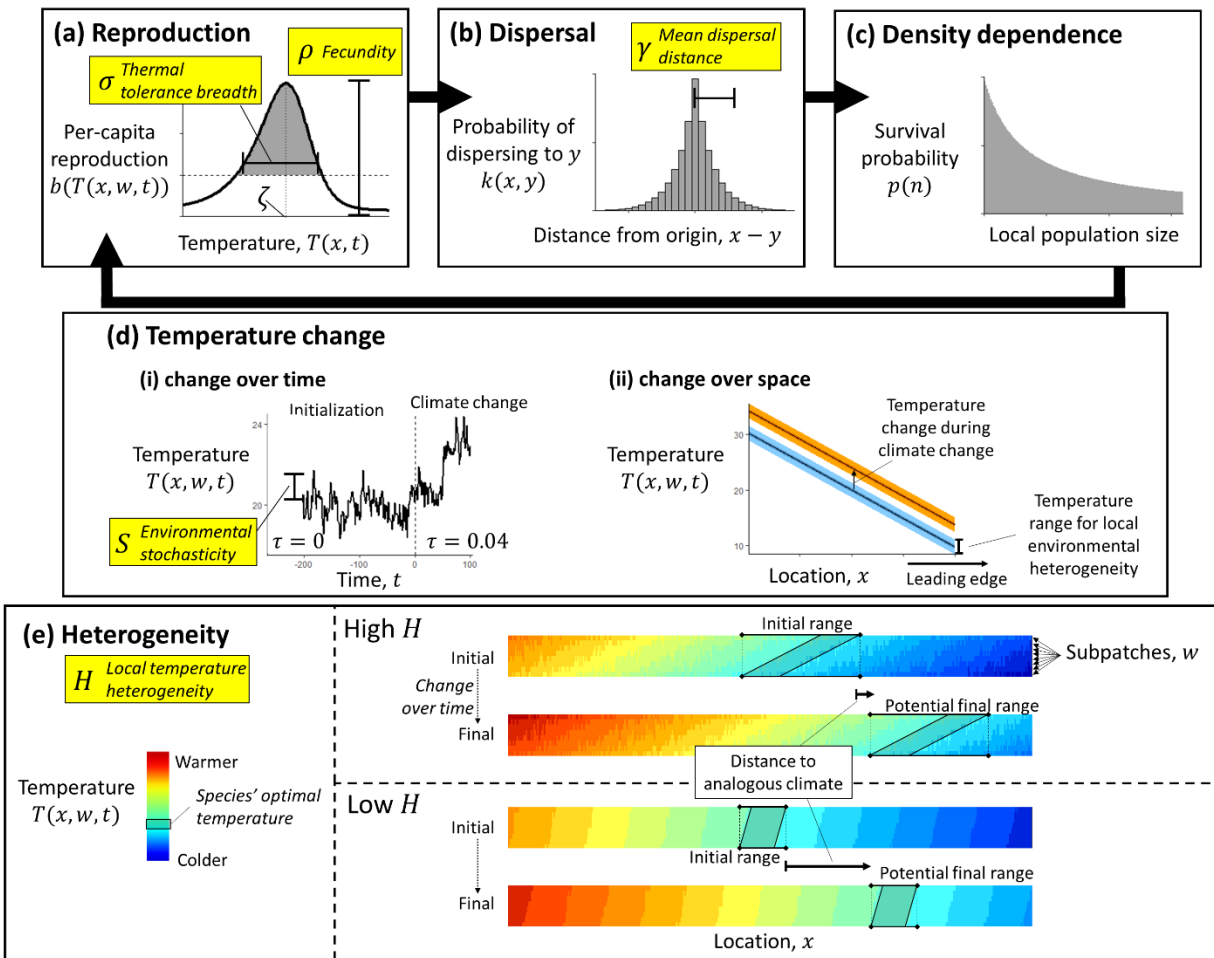
516 **Tables**

517 **Table 1:** Parameter definitions and values used throughout simulations.

518

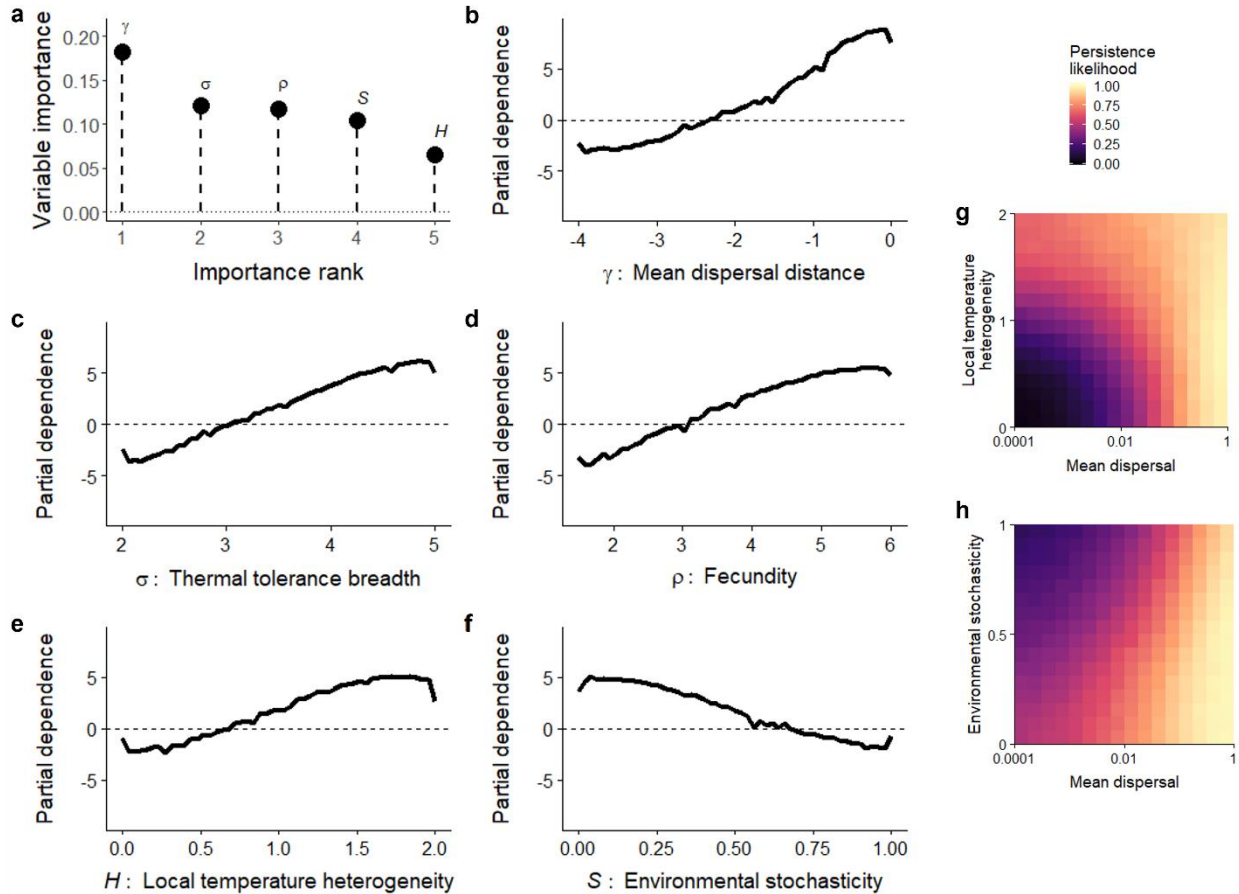
Parameter	Symbol	Values	Units
Species' mean dispersal distance	$\gamma$	Log-uniform; $10^{-4}$ to 1	patches
Species' thermal tolerance breadth	$\sigma$	Uniform; 2 to 5	°C
Species' fecundity	$\rho$	Uniform; 1.5 to 6	-
Local temperature heterogeneity	$H$	Uniform; 0 to 2	°C
Environmental stochasticity	$S$	Uniform; 0 to 1	°C
Species' thermal optimum	$\zeta$	20	°C
Skewness constant	$\lambda$	-2.7	-
Total patches	$L$	512	patches
Subpatches per patch	$W$	8	subpatches
Subpatch carrying capacity	$K$	8	individuals
Mean annual temperature change	$\tau$	0 or 0.04	°C/year
Annual temporal autocorrelation	$\kappa$	0.767	-

519 **Figures**



520  
 521 **Figure 1:** During each time step of the model, the population cycles through (a) reproduction, (b)  
 522 dispersal, and (c) density dependence, then (d) the mean temperature changes, determining the  
 523 environmental conditions for the next time step. We explore a range of values for parameters highlighted  
 524 in yellow. (a) Per capita reproductive output  $b_i(T(x, w, t))$  is skew-normal, dependent on temperature  
 525  $T(x, w, t)$ . This function depends on species' thermal optimum  $\zeta$ , thermal tolerance breadth  $\sigma$ , and  
 526 fecundity  $\rho$ . (b) Individuals disperse across patches with a mean dispersal distance  $\gamma$ . After arriving in the  
 527 destination patch, they redistribute among local subpatches. (c) Individuals compete over limited space,  
 528 where each subpatch has a carrying capacity  $K$ . In each subpatch, individual survival probability  $p(n)$   
 529 decreases as local population size increases. (d.i) Temperature changes over time depending on  
 530 environmental stochasticity parameter  $S$ . After an initialization phase with no temperature change  
 531 ( $\tau=0.04$ ), the model shifts to the climate change phase ( $\tau = 0.04$ ). (d.ii) Mean temperature decreases  
 532 linearly over space from the equatorward to the poleward side, and each location  $x$  has a range of  
 533 temperatures from local heterogeneity between subpatches. During climate change, the average  
 534 temperature increases by 4°C (or by 2°C) over 100 years. (e) Each patch in space contains  $W$  subpatches.  
 535 The standard deviation of the temperature among subpatches within a patch depends on the local  
 536 temperature heterogeneity  $H$ . Between the beginning and end of climate change, analogous temperatures  
 537 are closer with higher rather than lower local temperature heterogeneity.  
 538





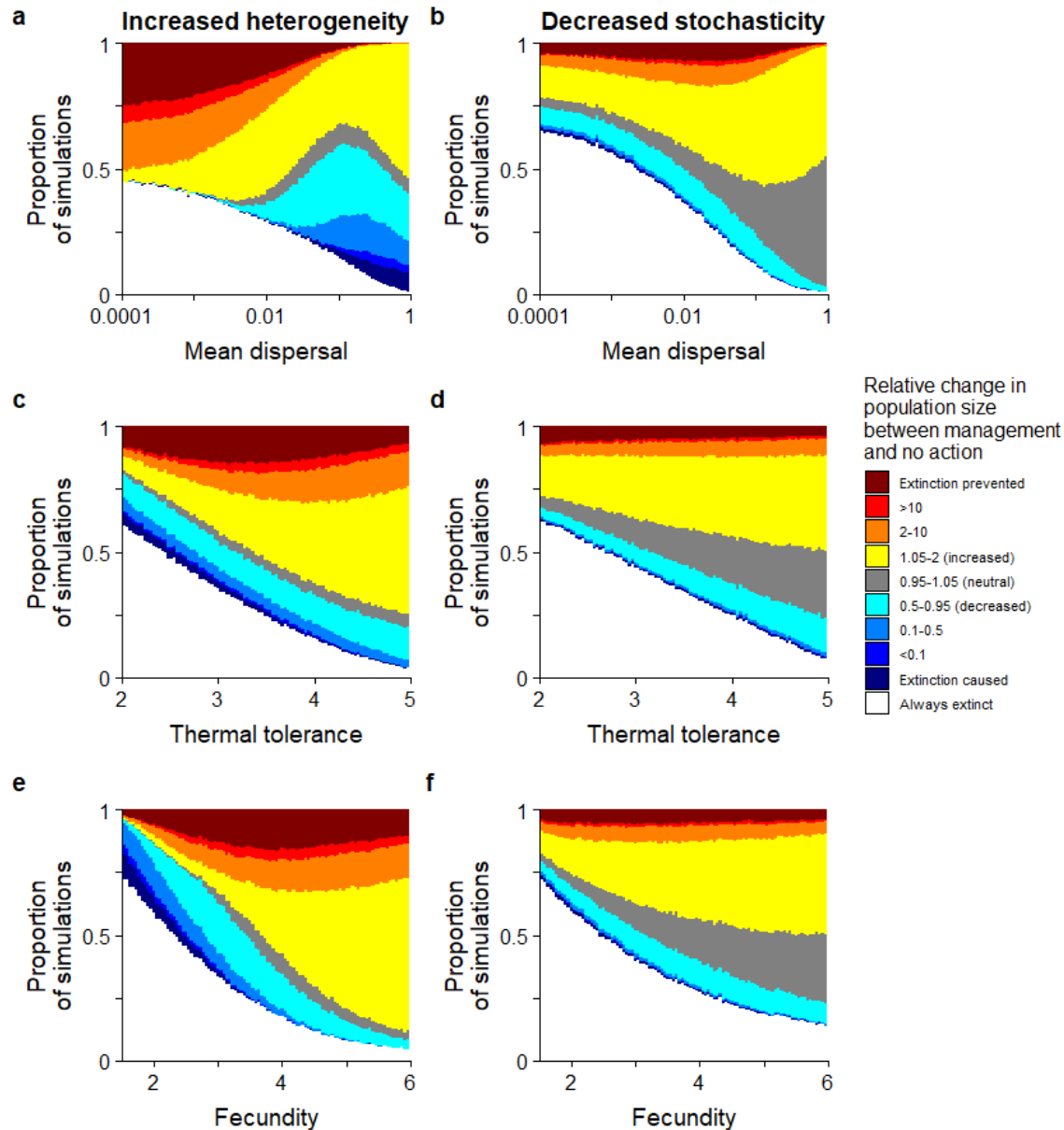
539  
 540 **Figure 2:** Importance of biotic and abiotic parameters from random forest classifications for randomized  
 541 species persistence through climate change by 4°C over 100 years. (a) Relative unscaled permutation  
 542 importance of dispersal distance ( $\gamma$ ), thermal tolerance breadth ( $\sigma$ ), fecundity ( $\rho$ ), local climate  
 543 heterogeneity ( $H$ ), and environmental stochasticity ( $S$ ). (b-f) Partial dependence of biotic and abiotic  
 544 parameters. Vertical axis is the log-odds of species' persistence through the simulation (higher values  
 545 indicate a greater persistence likelihood). (g-h) Persistence likelihood grouped by mean dispersal ability  $\gamma$   
 546 (horizontal axis) and either local temperature heterogeneity  $H$  (vertical axis in g) or environmental  
 547 stochasticity  $S$  (vertical axis in h).  
 548

				Proportion of species persisting after no action	Proportion of species in which the final managed population is higher (lower) than in simulations with no management		
					increasing heterogeneity	decreasing stochasticity	
Simulated species	High dispersal distance	High thermal tolerance breadth	High fecundity	0.9994	0.9996 (0.00)	0.34 (0.01)	
			Low fecundity	0.98	0.019 (0.96)	0.56 (0.14)	
		Low thermal tolerance breadth	High fecundity	0.97	0.65 (0.23)	0.60 (0.05)	
			Low fecundity	0.41	0.003 (0.46)	0.43 (0.05)	
	Low dispersal distance	High thermal tolerance breadth	High fecundity	0.73	0.99 (0.00)	0.49 (0.17)	
			Low fecundity	0.33	0.52 (0.04)	0.22 (0.16)	
		Low thermal tolerance breadth	High fecundity	0.34	0.63 (0.01)	0.28 (0.11)	
			Low fecundity	0.00	0.00 (0.00)	0.00 (0.00)	
	All species				0.61	0.51 (0.18)	0.40 (0.11)

549

550 **Figure 3:** Results from simulations when the average temperature increases by 4°C over 100 years,  
 551 categorizing species into highest or lowest quartiles of biotic parameters. Higher trait values (in the upper  
 552 quartile) are highlighted in blue, and lower trait values are highlighted in orange. The final two columns  
 553 represent the proportion of species that benefit from either increasing heterogeneity or decreasing  
 554 stochasticity (final population size of the species more than 105% relative to simulations without  
 555 management action) and the proportion that are negatively affected in parentheses (final population size  
 556 less than 95% relative to simulations without management action). Darker colors in the final three  
 557 columns represent higher values.





558  
 559 **Figure 4:** Relative effect of increasing local heterogeneity (a,c,e) or decreasing environmental  
 560 stochasticity (b,d,f) on a species' fate under a 4°C increase over 100 years compared to no action, under a  
 561 range of values for mean dispersal  $\gamma$  (a,b), thermal tolerance (c,d), and fecundity (e,f). The vertical axis  
 562 indicates frequencies of outcomes within bins that represent different species fates: white indicates  
 563 simulations where the species goes extinct during climate change regardless of management. Dark red  
 564 indicates simulations where a species goes extinct with no action but persists with management. Hues  
 565 from yellow to red indicate simulations where management increases a species' population size relative to  
 566 no action. Gray indicates simulations where a species persists, and management has little effect on the  
 567 final population size. Hues from cyan to blue indicate simulations where management decreases a  
 568 species' population size relative to no action. Dark blue indicates that management caused the species to  
 569 go extinct.