

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). Paleoecological 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 paleoecological 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 (γ), thermal tolerance breadth (σ), and
105 fecundity (ρ). 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 τ , with a stochastic component with autocorrelation κ , 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 λ with the highest values around the thermal optimum ζ and a sharp decrease
136 above ζ . Given thermal tolerance breadth σ and fecundity ρ , 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 γ 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 (γ) from a log-uniform distribution
180 and the thermal tolerance breadth (σ) and fecundity (ρ) 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 (γ , σ , and ρ)
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°C over 100 years) and $\tau = 0.04^\circ\text{C}$ per year
188 reflecting a high emissions scenario (4°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 γ , σ , 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°C and
199 4°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 γ , narrower thermal
214 tolerance σ , or lower fecundity ρ , 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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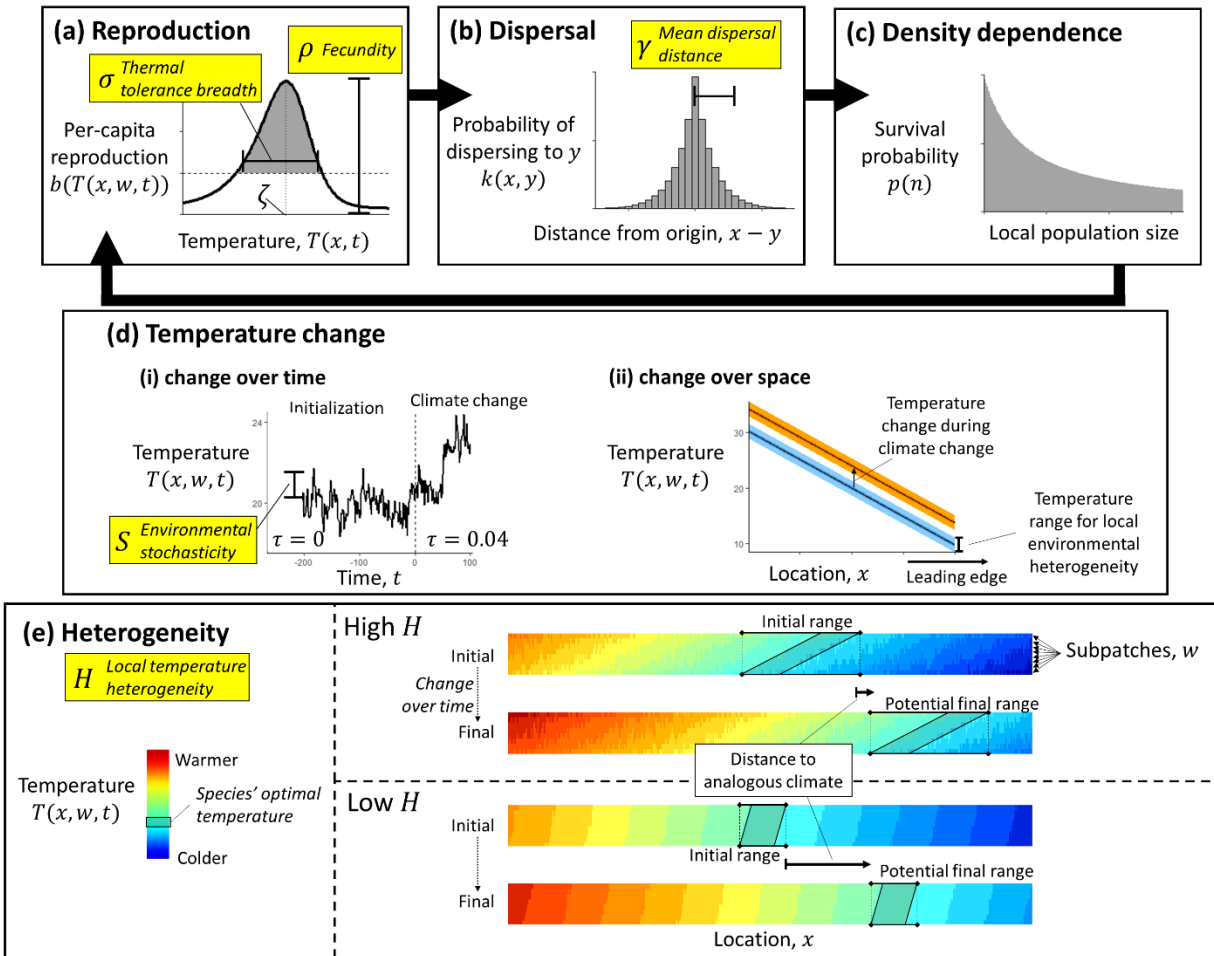
516 **Tables**

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

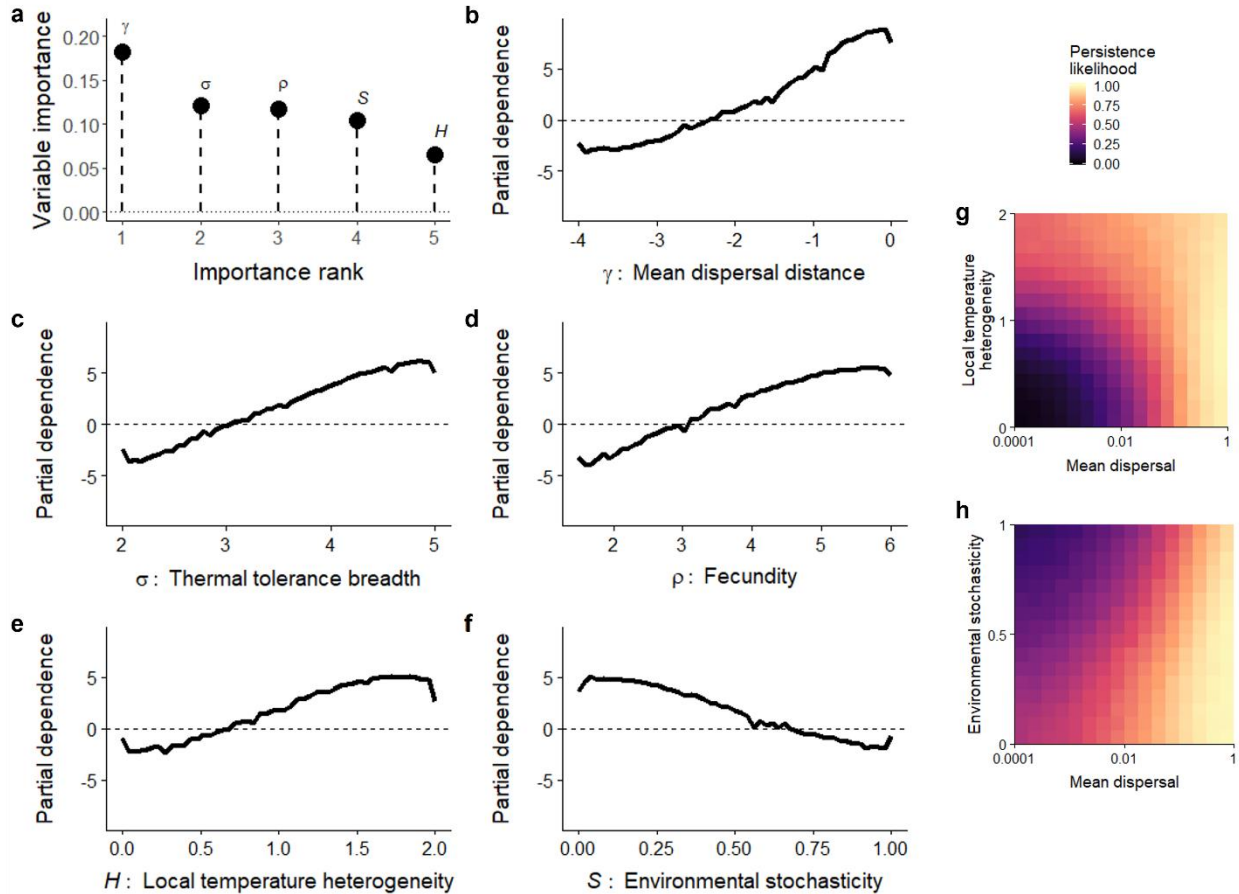
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Parameter	Symbol	Values	Units
Species' mean dispersal distance	γ	Log-uniform; 10^{-4} to 1	patches
Species' thermal tolerance breadth	σ	Uniform; 2 to 5	°C
Species' fecundity	ρ	Uniform; 1.5 to 6	-
Local temperature heterogeneity	H	Uniform; 0 to 2	°C
Environmental stochasticity	S	Uniform; 0 to 1	°C
Species' thermal optimum	ζ	20	°C
Skewness constant	λ	-2.7	-
Total patches	L	512	patches
Subpatches per patch	W	8	subpatches
Subpatch carrying capacity	K	8	individuals
Mean annual temperature change	τ	0 or 0.04	°C/year
Annual temporal autocorrelation	κ	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 ζ , thermal tolerance breadth σ , and
 526 fecundity ρ . (b) Individuals disperse across patches with a mean dispersal distance γ . 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

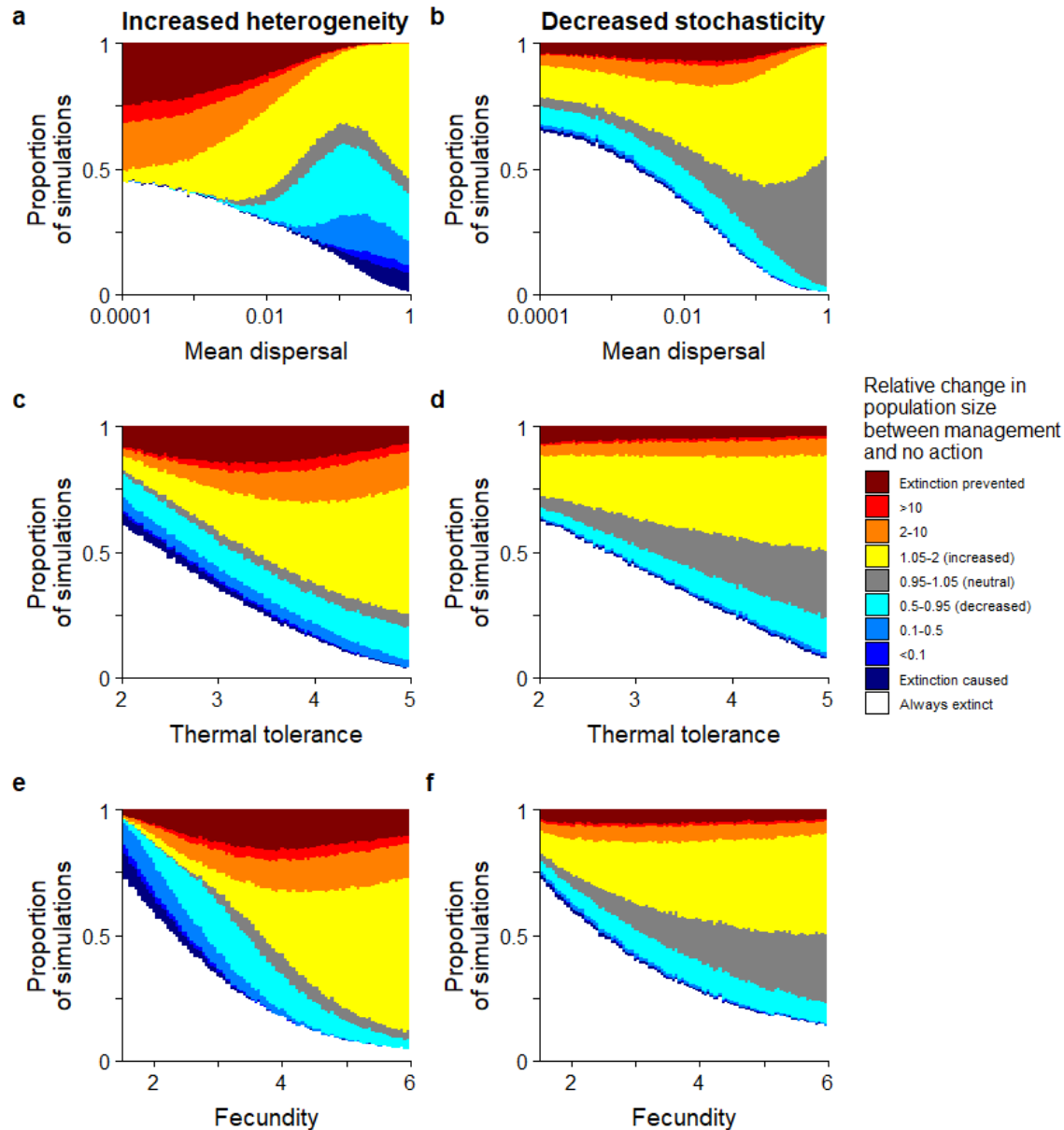


539
 540 **Figure 2:** Importance of biotic and abiotic parameters from random forest classifications for randomized
 541 species persistence through climate change by 4°C over 100 years. (a) Relative unscaled permutation
 542 importance of dispersal distance (γ), thermal tolerance breadth (σ), fecundity (ρ), 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 γ
 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 γ (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.