

1 **Comparing management strategies for conserving communities of climate-threatened species with a**
2 **stochastic metacommunity model**

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6

7 **Abstract**

8 Many species are shifting their ranges to keep pace with climate change, but habitat fragmentation and
9 limited dispersal could impede these range shifts. In the case of climate-vulnerable foundation species
10 such as tropical reef corals and temperate forest trees, such limitations might put entire communities at
11 risk of extinction. Restoring connectivity through corridors, stepping-stones, or enhanced quality of
12 existing patches could prevent the extinction of several species, but dispersal-limited species might not
13 benefit if other species block their dispersal. Alternatively, managers might relocate vulnerable species
14 between habitats through assisted migration, but this is generally a species-by-species approach. To
15 evaluate the relative efficacy of these strategies, we simulated the climate-tracking of species in
16 randomized competitive metacommunities with alternative management interventions. We found that
17 corridors and assisted migration were the most effective strategies at reducing extinction. Assisted
18 migration was especially effective at reducing the extinction likelihood for short-dispersing species, but
19 it often required moving several species repeatedly. Assisted migration was more effective at reducing
20 extinction in environments with higher stochasticity, and corridors were more effective at reducing
21 extinction in environments with lower stochasticity. We discuss the application of these approaches to
22 an array of systems ranging from tropical corals to temperate forests.

23

24

25 **Introduction**

26 The projected rate of climate change threatens many species, especially dispersal-limited
27 species (Urban 2015). Habitat fragmentation intensifies this risk by causing the additional impediment of
28 needing to disperse over poor-quality habitat (Krosby et al. 2010). Moreover, when competing species
29 track climate change at differential speeds, faster dispersing species can block slower dispersing species
30 from tracking climate change (Urban et al. 2012). Such impediments can have ecosystem-wide
31 consequences when dispersal-limited species serve as foundation species, such as in forests (Honnay et
32 al. 2002) and tropical coral reefs (Munday et al. 2009). Though many coral reef species can disperse far
33 in their larval stage, differential dispersal ability and fragmentation could mean that some species are
34 unable to keep pace with climate change (Gaines et al. 2007; Munday et al. 2009). Similarly, competition
35 and the differential effects of climate change on tree species means that poleward species might
36 prevent equatorward species from tracking climate change, especially over fragmented landscapes
37 (Scheller & Mladenoff 2008).

38 One potential method of conserving dispersal-limited species is through assisted migration, or
39 the relocation of populations outside of the species' historical range to areas that will be more suitable
40 in response to climate change (McLachlan et al. 2007; Hoegh-Guldberg et al. 2008). Despite a long
41 history of conservation translocations within a species' historical range (Seddon et al. 2007), relocating a
42 species to a new area with novel species interactions could pose additional challenges. With little
43 precedent and high uncertainty, relocated populations could become invasive or spread diseases and
44 parasites (Mueller & Hellmann 2008; Ricciardi & Simberloff 2009). Even translocations within a species'
45 range are often unsuccessful without the additional complications of novel competitors, climate change,
46 and fragmentation (Fischer & Lindenmayer 2000; Bubac et al. 2019). To limit relocation failure, decision-
47 making frameworks for assisted migration generally seek to understand the uncertainty around the
48 optimal time and place to move a vulnerable species (McDonald-Madden et al. 2011). However, assisted

49 migration might have limited success when relocating species with narrow climate tolerance into
50 environments with high climate variability over time or low climate variability over space. Additionally,
51 assisted migration is often a single-species approach (Lawler & Olden 2011) that addresses the
52 symptoms of extinction risk instead of the root causes (e.g., habitat fragmentation; Fazy & Fischer
53 2009; Minter & Collins 2010). Despite potential risks and uncertainties, assisted migration is already
54 underway for several species at risk of extinction (Liu et al. 2012; Seddon et al. 2015; Wang et al. 2019)
55 and some variations of assisted migration are being tested in coral reefs (van Oppen et al. 2014; Kuffner
56 et al. 2020) and trees (Sáenz-Romero et al. 2021).

57 Alternatively, habitat restoration in and between fragmented habitats could assist the natural
58 dispersal of species that would otherwise be unable to track climate change (Lawler & Olden 2011).
59 Building habitat corridors (Beier & Noss 1998; Haddad et al. 2015) or stepping-stones reserves
60 (McDowell et al. 1991; Treml et al. 2008) might help increase connectivity and decrease extinction risk
61 from climate change (Robillard et al. 2015), and additional protection of existing reserves might bolster
62 source populations to increase overall persistence (Heller and Zavaleta 2009). Unlike the single-species
63 focus of assisted migration, increasing habitat protection or connectivity is a community-level approach
64 that could directly benefit multiple species that might otherwise be unable to disperse between
65 fragmented patches (Lawler & Olden 2011). However, increasing connectivity and habitat protection do
66 not specifically target species disproportionately affected by climate change, where biological limitations
67 in dispersal ability and negative effects of community interactions could prevent climate tracking
68 (Gilman et al. 2010; Urban et al. 2012). Among the restoration options, those that increase connectivity
69 inherently increase available habitat area, which could be critical for declining populations at risk of
70 extinction from climate change (Hodgson et al. 2009). While increasing connectivity typically has a
71 smaller effect on population outcomes than increasing protection or patch size, or reducing overall
72 habitat loss, in conservation generally (Harrison & Bruna 1999; Fahrig 2001; Falcy & Estades 2007),

73 increasing connectivity might have a greater impact when considering range shift dynamics under
74 climate change (Nuñez et al. 2013). Like assisted migration, the effectiveness of connectivity and
75 restoration-based approaches at conserving species can depend on spatio-temporal variability, as
76 stochasticity in connectivity can reduce species' persistence (Watson et al. 2012) while heterogeneity in
77 microclimates can increase persistence through climate change (Suggitt et al 2018). As an example of a
78 connectivity-based approach, protecting a marine reserve network focused on connectivity between
79 locations with different levels of temperature stress is one proposed approach to buffer coral reef
80 response to climate change (Mumby et al. 2011; Walsworth et al. 2019). For forest trees, connectivity
81 and restoration would involve creating large-scale networks of land-sharing or land-sparing between
82 disconnected forests (Fischer et al. 2014) or working with local landowners to encourage practices that
83 reduce barriers and promote species persistence (Krosby et al. 2010).

84 Given the potential trade-offs to each approach, we compare the relative efficacy of these
85 alternative management strategies to support species responses to climate change. To understand how
86 these strategies compare under a variety of conditions in terms of spatio-temporal climate variability,
87 we built a metacommunity model that simulates climate tracking of several randomized species
88 competing in a fragmented environment over a temperature gradient through a cycle of reproduction,
89 dispersal, and competition. Using this model, we compared a variety of management strategies to
90 conserve species' persistence and diversity: assisted migration, building habitat corridors, creating
91 stepping-stone reserves, and reinforcing areas that currently had high habitat quality.

92

93 **Methods**

94 To compare the potential for various conservation strategies to reduce extinction in
95 environments under different spatio-temporal conditions, we modeled metacommunity dynamics of

96 species competing on a one-dimensional linear temperature gradient subjected to climate change.
97 Building on the models by Backus & Baskett (2021) and Urban et al. (2012), all species in this
98 metacommunity compete for the same resources on the same trophic level; we focus on competition as
99 the central interspecific interaction because of its role in range limits (Connell 1972, Sexton et al. 2009)
100 and range shifts. Each species i has a discrete population size $n_i(x, y, t)$ that changes with time t and
101 space on both the large x and local scale y . All populations cycle through reproduction, dispersal, and
102 competition, each with demographic stochasticity. Each species has a unique thermal optimum ζ_i ,
103 dispersal distance γ_i , thermal tolerance breadth σ_i , and reproductive strength ρ_i . The carrying capacity
104 $K(x, y)$ varies over space to represent high- and low-quality habitat. After simulating metacommunity
105 dynamics with climate change, we compared extinction rates under each approach. Then we focused on
106 comparing corridors to assisted migration for different levels of environmental stochasticity and local
107 heterogeneity, and finally we analyzed the species characteristics associated with protection by each
108 approach.

109

110 *Climate variability and change*

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

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

118

119 Temperature increases linearly over time with environmental stochasticity, S , representing the
 120 magnitude of interannual variation in temperature across the environment. At the beginning of each
 121 time step, all patches simultaneously increase in temperature by an average value of τ , with a stochastic
 122 component with autocorrelation κ , and standard deviation S around white noise $\omega(t)$: $\epsilon(t + 1) =$
 123 $\kappa\epsilon(t) + \omega(t)\sqrt{1 + \kappa^2}$, with the square root term to remove the effect of autocorrelation on the
 124 variance (Wichmann et al. 2005). Altogether, the temperature in patch x changes over time is

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

125

126 *Metacommunity dynamics*

127 Each simulated species i has a population size of $n_i(x, y, t)$ individuals in patch
 128 x , subpatch y at discrete time t . All individuals reproduce simultaneously at the beginning of each time
 129 step with a reproductive output $b_i(T(x, y, t))$ as a function of time- and location-dependent
 130 temperature (Fig. 1a). Temperature-dependence is skew-normal, given skewness constant λ with the
 131 highest values around the species' thermal optimum ζ_i and a sharp decrease above ζ_i (Norberg 2004).
 132 Then given, thermal tolerance breadth σ_i and fecundity ρ_i , the reproductive output is

$$b_i(T(x, y, t)) = \exp\left(\rho_i \left\{ \exp\left[-\left(\frac{T(x, y, t) - \zeta_i}{\sigma_i}\right)^2\right] \cdot \left[1 + \operatorname{erf}\left(\lambda \frac{T(x, y, t) - \zeta_i}{\sigma_i}\right)\right] - 1\right\}\right) \quad (3)$$

133 (Urban et al. 2012). To incorporate demographic stochasticity, the number of propagules produced by
 134 individuals in patch x , subpatch y is a Poisson random variable with mean equal to the reproductive
 135 output, $n_i^*(x, y, t) \sim \text{Poisson}\left(n_i(x, y, t) b_i(T(x, y, t))\right)$ (Melbourne & Hastings 2008).

136 Next, each propagule disperses from its origin (Fig. 1b). Though reproduction occurs within the
137 subpatch level, dispersal occurs at a larger spatial scale (between patches). Therefore, the model pools
138 together all propagules in a patch prior to dispersal, such that the total number of propagules in patch x
139 at time t is $N_i^*(x, t) = \sum_{y=1}^W n_i^*(x, y, t)$. We adapt the Laplace dispersal kernel to a discrete-space
140 analog, defining γ_i as the mean absolute distance (in patches) that individuals move from their origin

141 and let kernel parameter $q_i = \frac{\gamma_{i+1} - \sqrt{\gamma_i^2 + 1}}{\gamma_i}$. Thus, the probability of a propagule from patch x moving to
142 patch z is

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

143 (Backus & Baskett 2021). All propagules disperse from patch x throughout all patches with a
144 multinomial random vector. After arriving at patch z , propagules randomly distribute among the W
145 subpatches of patch z . The resulting number of dispersed propagules in patch z , subpatch y , at time t is
146 $n_i^{**}(z, y, t)$.

147 Lastly, dispersed propagules compete for limited space and resources within each subpatch,
148 given a location-dependent carrying capacity $K(x, y)$ in each subpatch that remains constant over time
149 (except when modified through management action) (Fig. 1c). The value of $K(x, y)$ varies over space
150 depending on the degree of habitat fragmentation. Density-dependent survival in this model is a
151 variation on lottery competition (Sale 1978; Chesson & Warner 1981) with temperature dependence,
152 with a higher chance of survival around a species thermal optimum ζ_i (Eq. 3). Altogether, each individual
153 of species i has an equal probability of surviving,

$$p_i(x, y, t) = \left(1 + \frac{\sum_{j=1}^S b_j(x, y, t) n_j^{**}(x, y, t)}{b_i(x, y, t) K(x, y)} \right)^{-1}. \quad (5)$$

154

155 The total number of individuals that survive in patch x , subpatch y , after competition is a binomial
156 random variable $n_i(x, y, t + 1) \sim \text{Binomial}(n_i^{**}(x, y, t), p(n_i^{**}(x, y, t)))$ (Melbourne & Hastings 2008).

157

158 *Management interventions*

159 We simulated six types of management strategies. Four of these strategies involved increasing
160 the habitat quality in particular locations. To keep these strategies ecologically comparable, we
161 increased the total carrying capacity by an amount defined as the “total area restored”, E . We let
162 $K_u(x, y)$ be the unmanaged carrying capacity of patch x , subpatch y , and $K_m(x, y)$ be the carrying
163 capacity after management. Then the total area restored is $E = \sum_{x=1}^L \sum_{y=1}^W (K_m(x, y) - K_u(x, y))$.

164 With the “restore all” strategy, we increased the carrying capacity in all subpatches evenly by
165 $\frac{E}{LW}$. With the “corridor establishment” strategy, we increased the carrying capacity in all locations that
166 were below a threshold carrying capacity and raised the minimum carrying capacity for all subpatches to
167 that threshold. We numerically adjusted this threshold until the total area was E . With the “stepping-
168 stone” strategy, we first identified all locations below a threshold. For each region with multiple patches
169 below this threshold, we raised the carrying capacity for all subpatches in the middle 50% quantile of
170 the gap but left the outer 25% quantiles at initial values. We adjusted this threshold until the total area
171 restored was E . With the “reinforce” strategy, we increased the carrying capacity of all subpatches
172 above a threshold, adjusting until the total area was E .

173 Following Backus & Baskett (2021), we simulated assisted migration by relocating species when
174 the total metapopulation of a species falls below a threshold of η individuals (Fig. 1f). After the
175 population of a species i fell below η , we relocated a fraction of the population ϕ to a location with a
176 temperature approximately equivalent the species thermal optimum ζ_i in the future. To find this, we

177 identified all locations with temperatures $\bar{T}(x, t) \leq \zeta_i + 0.2$. To avoid relocating a species into an area
178 with low habitat quality, we only relocated the population into locations that fit the above specifications
179 with $K(x, y) > 5$. We spread individuals between all subpatches within 5 patches (2 on either side of
180 the target location). After relocating a population, we did not relocate that species again for $\alpha = 5$ years
181 to avoid relocating a population recovering from a previous relocation. Following optimal parameter
182 values from Backus & Baskett (2021), we relocated ϕ of the total population and only μ survived
183 relocation (Table 1). To limit assisted migration (to be somewhat comparable to habitat quality
184 modification strategies), we only simulated relocations until we reached a maximum limit of F .

185

186 *Numerical implementation*

187 For our simulations, we used parameter values from Table 1. We used $L = 512$ patches and
188 with $W = 8$ subpatches (a total of 2^{12} discrete locations). The initial mean temperature across the
189 temperature gradient varied linearly from the poleward edge to the equatorward edge. Annual
190 temporal autocorrelation was κ , based on the measured combined global land-surface air and sea-
191 surface water temperature anomalies from 1880 to 1979 (GISTEMP Team 2019; Lenssen et al. 2019).

192 On average, the carrying capacity was a temperature-independent constant $K(x, y) = 8.25$ per
193 subpatch so each patch could carry a total of 66 individuals at carrying capacity. In our simulations, we
194 focus on two theoretical arrangements of high- and low-quality areas to represent different types of
195 fragmentation: one with few wide gaps in habitat quality and one with several narrow (Fig. 1e). In each,
196 the outer edges ($x \leq 64$ and $x \geq 465$) are at a constant intermediate carrying capacity $K(x, y) = 8.25$,
197 while the center ($65 \leq x < 464$) varies sinusoidally such that

$$K(x, y) = \frac{1}{4} + 8 \left(1 + \sin \left(\frac{(x - 64)\pi}{G} \right) \right). \quad (6)$$

198 In environments with few wide gaps, $G = 50$, such that there are four full sine waves in the central
199 region (spanning roughly 18.5°C of temperature change over space). In environments with several
200 narrow gaps, $G = 12.5$, with 16 full sine waves in the central region.

201 In each set of simulations, we first generated the environment by randomly selecting the
202 standard deviation of local heterogeneity H and environmental stochasticity S (Table 1). Next, we
203 generated 64 species, selecting unique random values for each species' thermal optima ζ_i , thermal
204 tolerance breadth σ_i , and dispersal distance γ_i . We numerically derived the reproductive strength ρ_i ,
205 such that each species had the same overall reproductive potential $B = 10$ when integrating over
206 temperature, emulating a jack-of-all-trades–master-of-none trade-off (Levins 1968). To generate the
207 initial distribution and population size for all species in the community, we placed 4 individuals from all
208 species in all subpatches and ran the model for 500 time steps with no change in average yearly
209 temperature ($\tau = 0^\circ\text{C}/\text{year}$). At the end of this initialization phase, we used the final population sizes for
210 each species in all subpatches as the initial conditions for climate change simulations.

211 Next, we simulated climate change on these initialized communities by adjusting the average
212 yearly temperature change to $\tau = 0.04^\circ\text{C}/\text{year}$, roughly based on a “business-as-usual” projected
213 scenario (Urban et al. 2012, IPCC 2021). This scenario provides the greatest number of extinctions with
214 which to compare the relative efficacy of the different management strategies, where we expect that
215 relative efficacy (the focus of our analysis) to remain consistent across different climate scenarios. For
216 each community, we simulated the model for both 30 or 100 time steps after applying one of several
217 management scenarios and degrees of management effort. In particular, starting at the beginning of the
218 climate change (shift from $\tau = 0^\circ\text{C}/\text{year}$ to $\tau = 0.04^\circ\text{C}/\text{year}$), we simulated “restore all”, “corridor
219 establishment”, “stepping-stone”, and “reinforce” management strategies with total area restored
220 values between $E = \frac{1}{8}LW$ and $E = 8LW$ (with 16 total variations; Table 1). Similarly, we simulated two

221 threshold values for assisted migration ($\eta = 50$ or $\eta = 75$ individuals) with a maximum number of
222 relocations between $F = 1$ and $F = 64$ (with 16 total variations; Table 1). For comparison, we also
223 simulated community dynamics with no management effort ($E = 0$ and $F = 0$).

224 To evaluate how spatio-temporal heterogeneity affected management outcomes, we compared
225 the number of extinctions prevented for corridor establishment and assisted migration ($\eta = 75$) under
226 different levels of environmental stochasticity and local heterogeneity. To use comparable scenarios
227 between these strategies, we chose values for E and F such that both strategies had a similar number of
228 extinctions on average ($E = 4WL$ for corridors and $F = 8$ for assisted migration). To evaluate which
229 species benefited under the different management strategies, we found the extinction probability for
230 each management action for species in each community that faced a variety of climate limitations: the
231 species with the shortest average dispersal distance, the species with the narrowest thermal tolerance,
232 the species with strongest competition in the poleward and equatorward direction (smallest difference
233 in ζ_i values), and a random species for comparison.

234

235 **Results**

236 Habitat corridors, stepping-stone reserves, and restoring all locations reduced the number of
237 species that went extinct during climate change, and each of these strategies reduced extinctions
238 further when restoring a larger total area (Fig. 2a,c). However, the reinforcing strategy had a negligible
239 effect on extinctions. Both corridors and stepping-stones benefitted with relatively little area restored
240 with diminishing returns with higher area restored, while restoring all locations reduced extinctions
241 nearly linearly with increased area restored. On average, corridors reduced the number of extinctions
242 more than all other restoration-based strategies with equivalent area restored. Stepping-stones reduced

243 extinctions similarly to equivalent corridors with little area restored, but corridors were more effective
244 than stepping-stones with higher area restored, especially in environments with fewer, larger gaps.

245 Assisted migration reduced extinctions on average, even with very few relocation events (Fig.
246 2b,d). However, increasing the maximum number of relocations above 16-24 did not reduce the average
247 number of extinctions further. At this point, assisted migration prevented more extinctions on average
248 than corridors at the highest area restored value we simulated. Both population thresholds for assisted
249 migration that we simulated ($\eta = 50$ and $\eta = 75$) had similar extinction rates with equivalent relocation
250 maximums.

251 Corridors were most effective at preventing extinctions in environments with low environmental
252 stochasticity and moderate local heterogeneity (Fig. 3a,c), while assisted migration was most effective in
253 environments with high heterogeneity and moderate stochasticity (Fig. 3b,d). Neither management
254 strategy was effective at reducing the number of extinctions in environments with low heterogeneity
255 and high stochasticity.

256 Randomly chosen species in simulated communities had a lower extinction probability under
257 both corridor and assisted migration strategies, but the shortest dispersing species in a community
258 disproportionately benefited more than random species (Fig. 4). Without management action, the
259 shortest dispersing species had greater than 50% of going extinct throughout all variations of our
260 simulations. Both management strategies reduced these extinction probabilities by more than 14% at
261 similar effort levels ($E = 4WL$ and $F = 8$). Reduction in extinction probability was greater for shortest
262 dispersers than for random species in all scenarios. Other species likely to face extinction during climate
263 change (narrowest thermal tolerance and the smallest difference in thermal optima with neighboring
264 species on either pole- or equator-ward edges) were also less likely to face extinction with either
265 management strategy, but only assisted migration reduced the extinction of these species

266 disproportionately more than random species. Distinguishing the efficacy of assisted migration and
267 corridors for different species and environmental conditions required longer-run (100 time step)
268 simulations, as shorter-run (30-time step) simulations did not have enough extinctions to determine the
269 impact of management interventions on extinction likelihood (2.0%-3.5% of species going extinct in 30
270 time steps *versus* 18.4%-31.6% of species going extinct in 100 time steps; Figs. S1-S2).

271

272 **Discussion**

273 Most of the simulated management strategies reduced extinction probability under climate
274 change in our simulated communities, and they reduced extinction rapidly with an initial investment in
275 conservation effort. Without climate change, corridors, even when low quality, can facilitate species'
276 movement and long-term persistence in a metacommunity (Haddad & Tewksbury 2005; Williams et al.
277 2005). Adding to this, our model suggests that even relatively low-quality corridors between higher-
278 quality areas could reduce extinction during climate change. Because restoring connectivity also
279 increases total habitat area, the effects of increased connectivity and increased area are often
280 confounded (Hodgson et al. 2009). Though many previous studies suggest that habitat reinforcement is
281 often better at protecting species than connectivity restoration (Harrison & Bruna; Fahrig 2001; Falcy &
282 Estades 2007), our results suggest that corridors are likely to be better at increasing the persistence of
283 range shifting species in the presence of climate change than other methods of connectivity and
284 protection that restore the same amount of area.

285 Similar to corridors, assisted migration reduced extinctions on average, even with relatively few
286 relocation events in our model. Because many species in the simulated communities face little
287 extinction risk from climate change, focusing relocation on a small number of vulnerable species was
288 able to have a disproportionate effect on community-wide extinctions. If only a small number of species

289 are at risk or conservation benefits can be realized by focusing on few species (Simberloff 1998; Enquist
290 et al. 2020), but the few species at risk of extinction could require a high investment in management
291 effort on their own. In practice, many conservation translocations are unsuccessful (Fischer &
292 Lindenmayer 2000; Bubac et al. 2019), so managers might need to relocate a single species several times
293 to increase the overall chance of establishment in the recipient location (Backus and Baskett 2021). Even
294 after successfully establishing a new population, species with weak dispersal ability might continue to
295 lag behind shifting climates and face extinction later. As climate change continues, these conservation-
296 reliant species (*sensu* Scott et al. 2005) may depend on repeated direct management actions without
297 increased connectivity (Lawler & Olden 2011).

298 Because we found relatively few extinctions in our nearer term simulations (30 time steps; Figs.
299 S1-S2), the difference in the efficacy of management approaches was negligible, and we required long-
300 run simulations (100 time step) to show the efficacy of corridors and assisted migration. This potential
301 time lag to observable impact presents a challenge for monitoring to verify anticipated outcomes or
302 adjusting management as needed in an adaptive management approach (Rist et al 2013). However,
303 nearer-term impacts of management action might be evident in cases where optimal climates have
304 already shifted away from species' historical ranges, as has occurred for many species (Chen et al. 2011;
305 Poloczanska et al. 2013), and our results suggest that near-term biodiversity conservation management
306 can have long-term benefits for species persistence.

307

308 *Types of species benefitting from each management strategy*

309 Adding to the extinction risks caused by fragmentation, many species are at risk of extinction
310 from climate change because of a variety of biological limitations (Pearson 2006; Gilman et al. 2011;
311 Urban et al. 2012; Urban 2015). We found that both corridors and assisted migration were effective at

312 reducing the extinction of species with short dispersal in our model. These species benefited from
313 increased connectivity regardless of the size of low-quality gaps. A previous simulation study showed
314 that longer-dispersing competitors were likely to block shorter-dispersing species from tracking climate
315 change in competitive communities with variable dispersal ability (Urban et al. 2012). Without
316 connectivity, short-dispersing species that might disperse over patchy landscapes, but low population
317 sizes, low propagule pressure, and strong competition means that these new populations are unlikely to
318 establish (Lockwood et al. 2005; Plein et al. 2016). For corals, the species that are likely to have shorter
319 average dispersal range, and likely to benefit from either corridor-like connectivity or assisted migration,
320 are brooding species that release larvae directly from polyps rather than those that broadcast gametes
321 into the water column (Ayre & Hughes 2000). Dispersal distance of trees is generally thought to be a
322 function of seed size, tree height, and mode of dispersal (Bullock et al. 2016), where shorter trees that
323 disperse seeds by wind or ballistics are more likely to have shorter dispersal than taller trees that
324 dispersed seeds by birds.

325 In comparison, species narrow thermal tolerance and strong competition benefited more from
326 assisted migration than restoration-based approaches. In corals, based on a trait-dependent clustering
327 analysis of life history strategies, those with narrow thermal tolerance (i.e., outside of the “generalist”
328 and “stress-tolerant” categories) and likely to experience strong competition (i.e., outside of the
329 “competitive” category) fall into a category of “weedy” life histories, which are associated with small
330 colony sizes and reproduction via brooding (where brooding increases reproductive success at low
331 population sizes compared to mass spawning; Darling et al. 2012). Tree species with narrow geographic
332 ranges may have narrow climate tolerance (though see Early & Sax 2014), whereas early successional
333 species may face higher competition (Grime 1987).

334 Note that restoration and assisted migration are not dichotomous and can be integrated
335 together in a larger management plan (Lawler & Olden 2011). Most tree species have low dispersal

336 relative to climate change (Corlett & Westcott 2013), and most corals have narrow climate tolerance
337 relative to climate change (Hughes et al. 2017), so these species could be threatened by climate change
338 for multiple reasons. In these cases, increasing connectivity would benefit most species in the
339 community and assisted migration would benefit those that disproportionately lag behind climate
340 change.

341

342 *Environmental characteristics for different management strategies*

343 In our simulations, the optimal management strategy depended on the characteristics of the
344 environment. For example, species in environments with low stochasticity might especially benefit from
345 corridor establishment over assisted migration. Because corridors are relatively small or low quality
346 compared to the higher quality areas they connect, the population sizes in those corridors would be
347 relatively small and susceptible to extinction (Lande 1993). Lower environmental stochasticity could
348 allow a species to track climate change gradually, alongside several species competing to keep pace with
349 climate change and move through the same limited area of a corridor. In coral reefs, one might identify
350 regions of lower stochasticity through maps of past and projected degree heating weeks, a cumulative
351 stress metric that predicts coral bleaching, which can then serve to inform the designation of reserve
352 networks (Mumby et al 2011). In forests, one might preserve larger patches with smaller perimeter-to-
353 area ratio, as edges between forest and fragments experience higher environmental stochasticity and
354 frequency of rare weather events (Laurance 2004; Laurance et al. 2011).

355 In contrast, we found assisted migration to be particularly effective at reducing extinction in
356 environments with moderate-to-high stochasticity. Because small populations are more likely to face
357 extinction in environments with high environmental stochasticity (Lande 1993), both donor and
358 recipient populations could face high extinction probability during assisted migration in stochastic

359 environments. However, the benefits of moving a species near its optimal climate likely outweigh the
360 risks of establishment failure on average, especially when planning multiple relocation events and
361 relocating a fraction of a single population each time (Backus & Baskett 2021). Therefore, assisted
362 migration might become an increasingly relevant management tool with increasing environmental
363 variation and extreme events with climate change, such as marine heat waves in coral reefs (Fordyce et
364 al 2019) and extreme droughts or fires affecting forests (Keeley & Syphard 2016; Williams et al. 2019). In
365 our model, assisted migration was also more effective at reducing extinction in environments with
366 higher local heterogeneity. Heterogeneous environments can act as climate refugia (Dobrowski 2011,
367 Morelli et al. 2016), reducing the velocity of climate change or the negative effects of interannual
368 variation. Because a highly heterogeneous recipient location is more likely to have a suitable
369 microclimate for the relocated population to establish, relocating a population into a refugia-like
370 environments could limit the risk of moving the population into the wrong place at the wrong time. For
371 coral reefs, such local-scale heterogeneity and refugia might arise from fore-reef/back-reef structure,
372 depth gradients, and physical structures that drive variability in local upwelling or tidal currents (Smith
373 et al 2017). For forests, high local-scale heterogeneity is often found in areas with steep elevational
374 gradients with similarly steep climate gradients (Morelli et al. 2016).

375

376 *Model assumptions*

377 Even though a small amount of restoration or few relocations had large conservation benefits in
378 our simulations, the actual economic and logistical costs of these strategies can be expensive. The total
379 area restored metric does not fully reflect the economic costs of these approaches. To simplify
380 comparison, we assumed that one unit of area restored (increasing the carrying capacity of the
381 community by one individual) is equivalent for all species, regardless of how that area restored is

382 distributed around the simulated environment. Realistically, conservation efforts and cost would vary
383 across species and location (Naidoo et al. 2006; Magris et al. 2015). A corridor that spreads conservation
384 spending across a wider range of low-quality areas would not be equivalent to a stepping-stone
385 approach that uses the same spending in a smaller, condensed region. Also, considering inherent
386 variation in land and water value or quality (Newburn et al. 2005), it would be difficult to improve the
387 habitat quality of some locations, such as urban coastal waters, beyond a certain point. If the cost of
388 protecting unbroken habitat corridors is prohibitive, “land sharing” approaches that allow conservation
389 and human use to co-occur could enable connectivity (Green et al. 2005; Fischer et al. 2014).

390 Our model also simplifies some important ecological and evolutionary dynamics that might
391 complicate comparisons between restoration and assisted migration-based approaches. In particular,
392 our simple competition-based model does not include trophic interactions or disease dynamics.
393 Incorporating these interactions could allow for relocated species to become invasive or spread disease,
394 both of which are potential risks of assisted migration (Ricciardi & Simberloff 2009; Hewitt et al. 2011).
395 We also ignore evolutionary dynamics in this model. Evolutionary dynamics could increase the
396 effectiveness of connectivity-based approaches, as natural dispersal would favor increased gene flow of
397 climate-tolerant genes as species naturally track climate change through corridors (Sgrò et al. 2011).

398 Lastly, we compared the extinction probability of species in our model, but other conservation
399 goals might include maintaining ecosystem function or maintaining biomass for harvesting, among other
400 goals. These alternative goals could favor different management strategies, as the benefits of each
401 strategy are weighed by stakeholders depending on their willingness to engage in assisted migration
402 with its high perceived risk or restoration-based approaches which could involve stakeholders giving up
403 their land or harvesting rights. Further analysis of alternative management strategies to buffer against
404 extinction from climate change and other conservation goals would benefit from a structure-decision

405 making approach that considers the full array of risks, benefits, and uncertainties related to the array of
406 potential stakeholder goals.

407

408 **Acknowledgments**

409 We thank L. Bay, C. Clements, R. Gates, S. Harrison, C. Logan, M. McClure, C. Muhlfeld, S. Sawyer, M.
410 Schwartz, R. Waples, and A. Whipple for their thoughtful conversations at the managed relocation
411 workshop at UC Davis that informed this manuscript.

412

413 **Data accessibility**

414 Simulation code, simulation results, and code to reproduce the plots in this paper are available at
415 <https://github.com/gabackus/comparingManagementStrategies>.

416

417 **Funding statement**

418 This work was supported by the National Science Foundation [grant #1655475].

419

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599 **Tables**

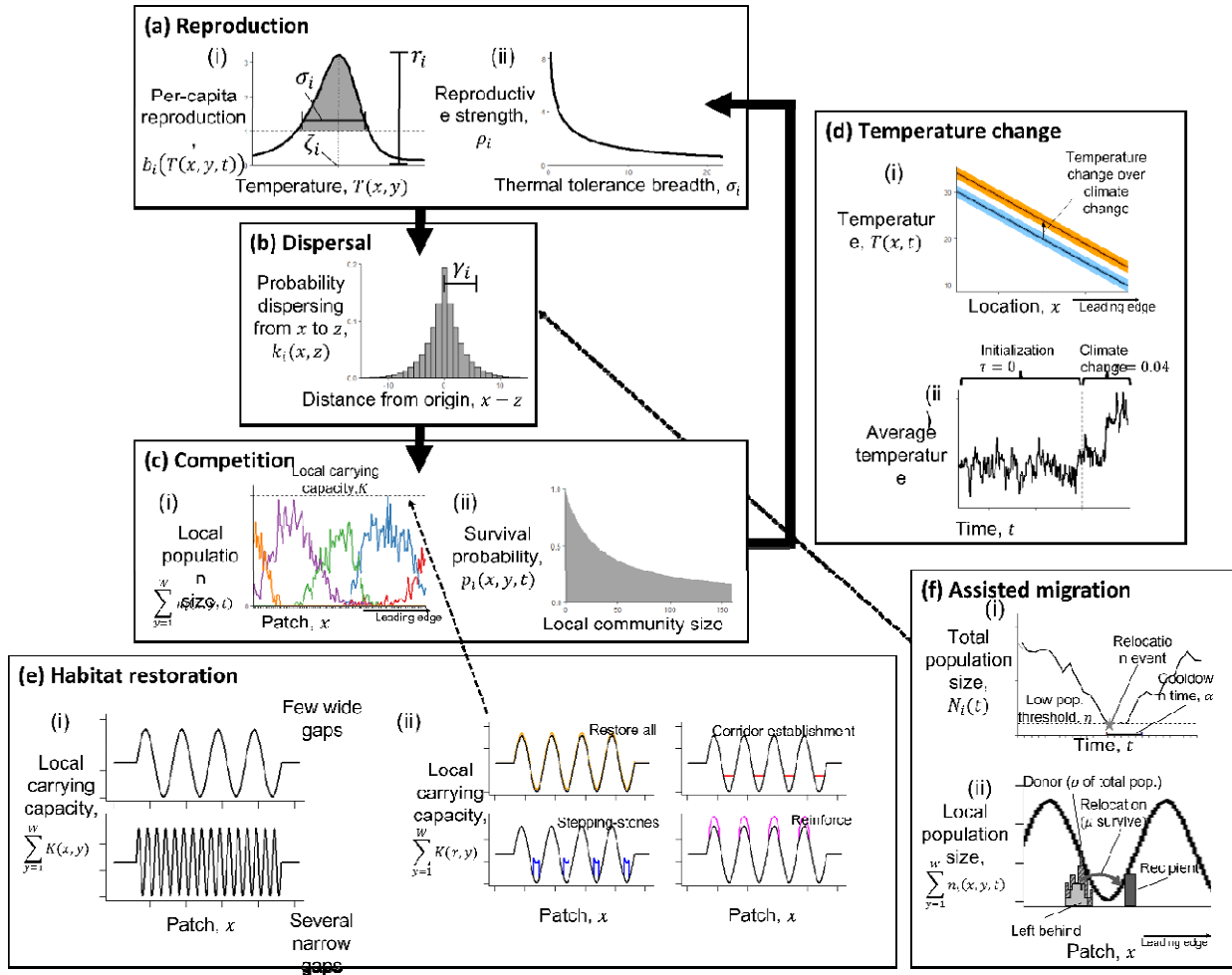
Table 1: Definitions of the symbols used in the model.

Parameter	Symbol	Values	Units
Total species in pre-initialized community	Ω	64	species
Dispersal distance of species i	γ_i	Lognormal; mean=2.5, st. dev.=2.5	patches
Thermal optimum of species i	ζ_i	Uniform; 9.78 to 30.22	°C
Thermal tolerance breadth of species i	σ_i	Lognormal; mean=5, st. dev.=5	°C
Reproductive strength of species i	ρ_i	Derived from σ_i	-
Skewness constant	λ	-2.7	-
Fraction of population relocated	ϕ	0.55	-
Assisted migration survival probability	μ	0.8	-
Low population threshold	η	50 or 75	individuals
Cooldown time between relocations	α	5	years
Total patches	L	512	patches
Subpatches per patch	W	8	
Subpatch carrying capacity	$K(x, y)$	Varies with space (average 8.25)	Individuals
St. dev. in local temperature heterogeneity	H	Uniform; 0 to 2	
St. dev. in interannual temporal stochasticity	S	Uniform; 0 to 1	
Mean annual temperature change	τ	0.04	°C/year
Annual temporal autocorrelation	κ	0.767	-
Annual temporal standard deviation	ψ	low=0.1639, high=0.6556	°C
Total area restored	E	$\frac{1}{8}LW$ to LW (by $\frac{1}{8}LW$), LW to $8LW$ (by LW)	individuals
Maximum relocations allowed	F	1 to 8 (by 1), 8 to 64 (by 8)	relocations

600

601

602 **Figures**

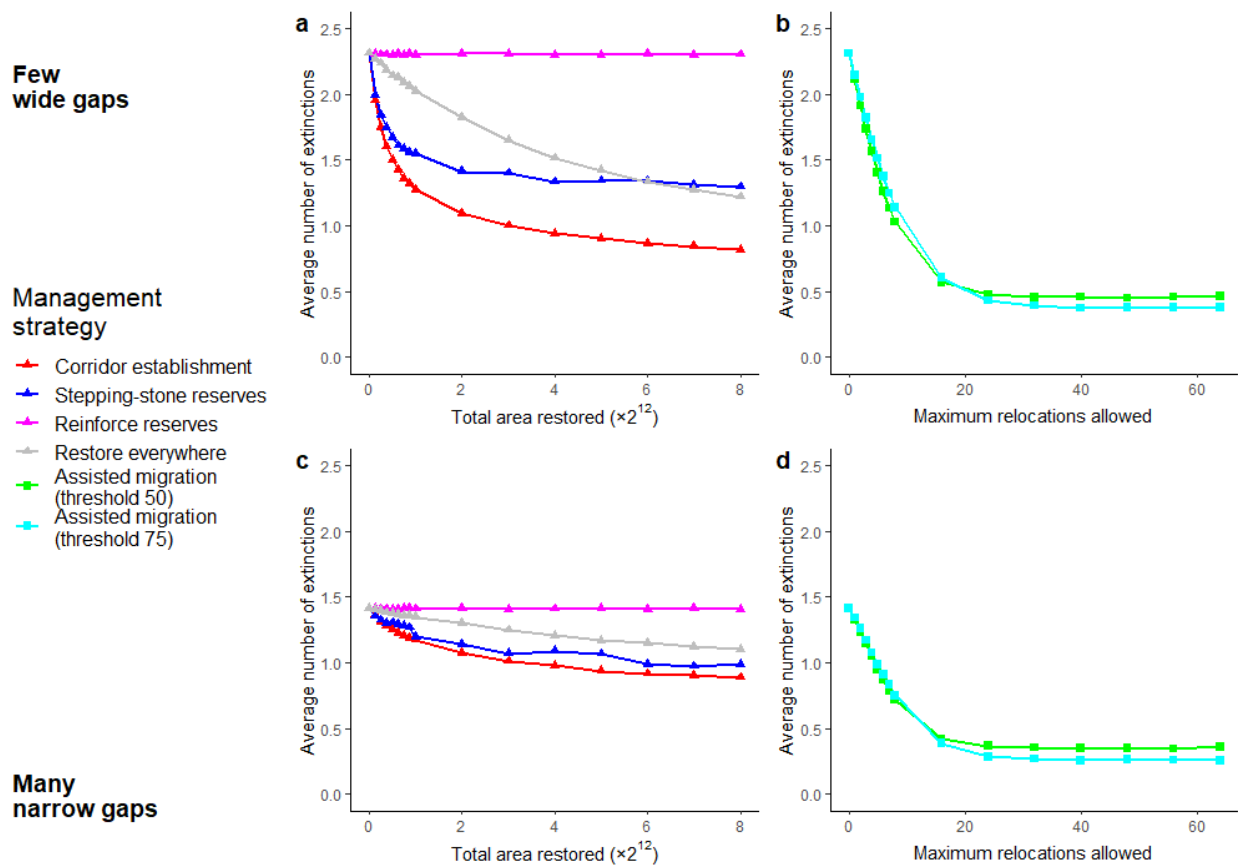


603

604 **Figure 1:** Figure 1: During each time step of the model, all extant species cycle through (a)
 605 reproduction, (b) dispersal, and (c) competition before (d) the temperature changes and the
 606 next time step continues. (a.i) Per capita reproductive output is skew-normal,
 607 dependent on temperature. This function is shaped by species' thermal optimum
 608 and thermal tolerance breadth. (a.ii) Reproductive strength scales the total reproductive
 609 output so that species with narrow (specialists) have higher reproduction and species with
 610 broad (generalists) have lower reproduction. (b) The dispersal kernel is a long-tailed "double
 611 geometric" distribution with a mean dispersal distance. (c.i) All species compete over limited
 612 space, where each patch has a carrying capacity. Here each line represents a different
 613 species. (c.ii) In each patch, individual survival probability decreases as the total
 614 community size increases. (d) Temperature changes stochastically over time. (d.i) Mean
 615 temperature decreases linearly with space. Over time, between (lower line) and
 616 (upper line), the temperature increases. (d.ii) Temperature variation over time depends on level
 617 of environmental stochasticity. The vertical dashed line designates when the model changes
 618 from the initialization phase (average temperature change ()) to the climate change and
 619 intervention phase (). Climate change only occurs after a relatively stable

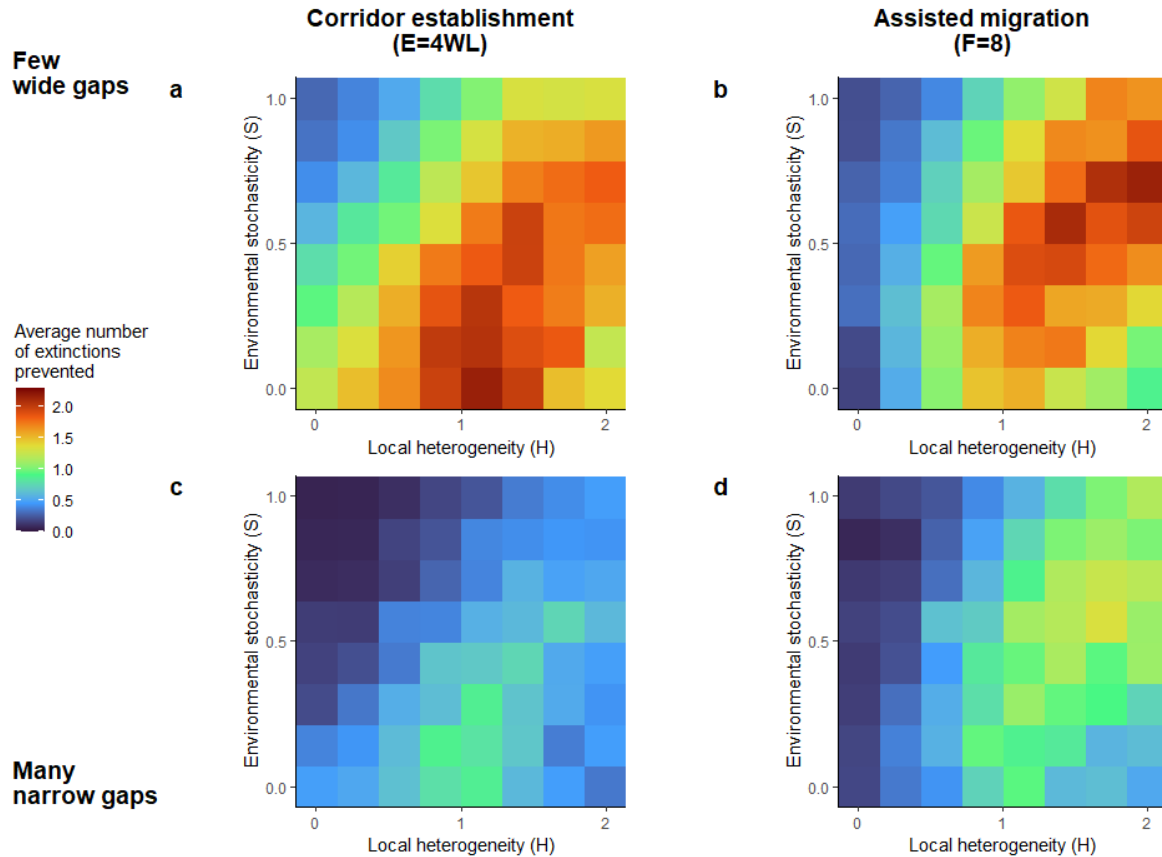
620 metacommunity has been assembled, after 100 time steps have passed with no extinctions.
 621 (e.i) Two types of fragmented environments compared: one with few large gaps and one with
 622 several narrow gap. (e.ii) Each of the four restoration management strategies (colored lines).
 623 Each involved increasing the integral of carrying capacity over space by an amount E more than
 624 the original carrying capacity (black lines). (f.i) Relocation occurs once the total population of a
 625 species falls below a threshold η . To avoid repetition while the species recovers, no relocations
 626 occur during a cool-down period following relocation α . (f.ii) A fraction ρ of the population is
 627 removed from its original distribution and moved to the closest new location where the
 628 average temperature $\bar{T}(x, t) \leq \zeta_i + 0.2$ and the carrying capacity $K(x, y) > 5$ (only a fraction
 629 μ survive). Remaining individuals disperse naturally.

630



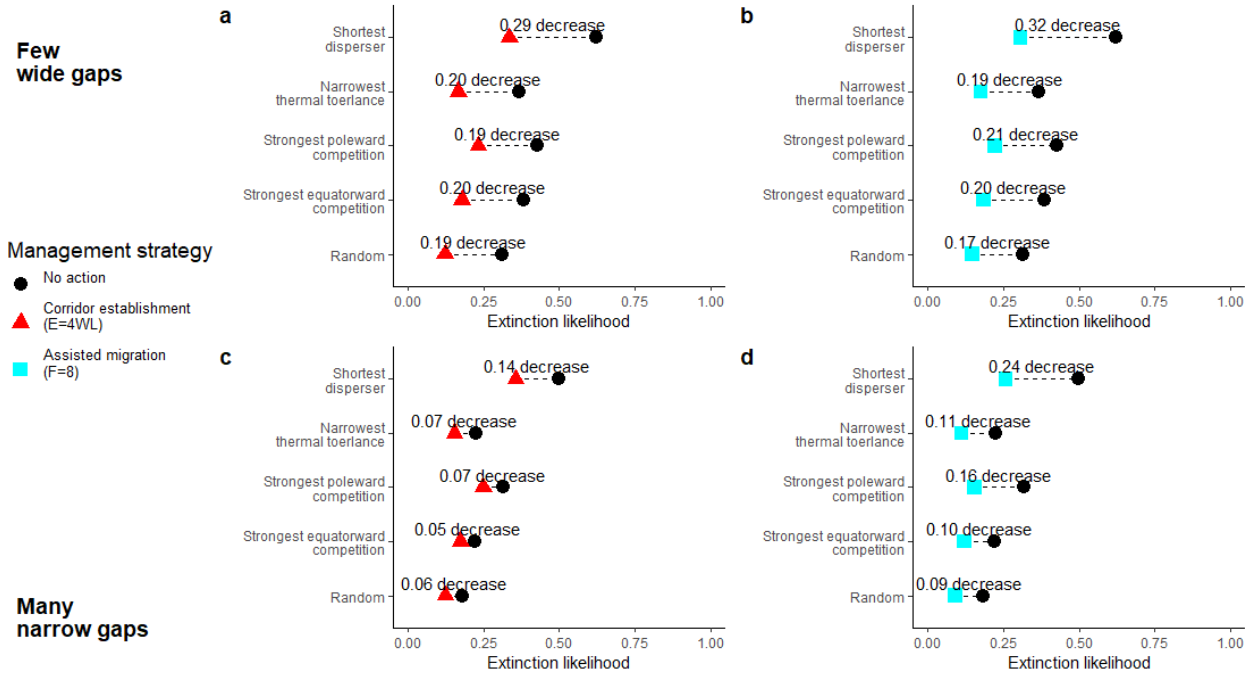
631

632 **Figure 2:** Average number of extinctions after 100 years (y-axis) in climate change simulations
 633 depending on management strategy (color/shape), amount of area restored for restoration-
 634 based modification (a,c) or maximum number of relocations allowed for assisted migration (b,d;
 635 x-axis), and environment structure (a-b: few wide gaps, c-d: many narrow gaps). Each point is
 636 the mean of 10000 simulations.



637

638 **Figure 3:** Average number of species prevented from extinction over 100 years (color) in
639 climate change simulations as it depends on local heterogeneity H (standard deviation of
640 temperatures per patch, x-axis) and environmental stochasticity S (standard deviation of
641 interannual variation in temperature, y-axis). Each box represents the mean of between 135
642 and 189 simulations within an 8x8 quantiles of the range of all simulations. Panels (a) and (c)
643 represent simulations with corridor establishment and panels (b) and (d) represent simulations
644 with assisted migration. The total area restored in corridor establishment ($E = 4WL$) and the
645 maximum number of relocations in assisted migration ($F = 8$) represent two cases where these
646 two strategies prevent a similar number of extinctions on average for the “few wide gaps”
647 environment, but not when comparing across equivalent levels of H and S . (a,b) represent
648 simulations of environments with few wide gaps and (c,d) represent simulations of
649 environments with several narrow gaps.



650

651 **Figure 4:** Likelihood that a species went extinct in 100 years (x-axis) in our climate change
 652 simulations depending on management strategy (color/shape, with corridors in panels a,c and
 653 assisted migration in panels b,d), which particular species it was in the community (y-axis) and
 654 environment type (a-b: few wide gaps, c-d: many narrow gaps). The particular species here are
 655 the species within the internal region of the environment ($65 \leq x < 464$) with the shortest
 656 dispersal distance γ_i , the species with the narrowest thermal tolerance σ_i , the species in the
 657 community with extant neighboring species community closest to that species thermal
 658 optimum ζ_i , and a randomly chosen species. Each point is the mean of 10000 simulations.