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► **To cite this version:**

Felix Pellerin, Julien Cote, Elvire Bestion, Robin Aguilée. Matching habitat choice promotes species persistence under climate change. *Oikos*, 2019, 128 (2), pp.221-234. 10.1111/oik.05309. hal-02121046

HAL Id: hal-02121046

<https://hal.science/hal-02121046>

Submitted on 26 Nov 2020

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1 Matching habitat choice promotes species persistence under climate change

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3 ***Accepted in Oikos – Pellerin F, Cote J., Bestion E. & R. Aguilée. 2019. Oikos. 128(2):***
4 ***221-234. DOI : 10.1111/oik.05309***

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18

19

20 **Abstract:**

21 Species may survive under contemporary climate change by either shifting their range or
22 adapting locally to the warmer conditions. Theoretical and empirical studies recently
23 underlined that dispersal, the central mechanism behind these responses, may depend on
24 the match between an individuals' phenotype and local environment. Such matching habitat
25 choice is expected to induce an adaptive gene flow, but it now remains to be studied whether
26 this local process could promote species' responses to climate change. Here, we investigate
27 this by developing an individual-based model including either random dispersal or
28 temperature-dependent matching habitat choice. We monitored population composition and
29 distribution through space and time under climate change. Relative to random dispersal,
30 matching habitat choice induced an adaptive gene flow that lessened spatial range loss
31 during climate warming by improving populations' viability within the range (i.e. limiting range
32 fragmentation) and by facilitating colonization of new habitats at the cold margin. The model
33 even predicted in some cases range contraction under random dispersal but range
34 expansion under optimal matching habitat choice. These benefits of matching habitat choice
35 for population persistence mostly resulted from adaptive immigration decision and were
36 greater for populations with larger dispersal distance and higher emigration probability. We
37 also found that environmental stochasticity resulted in suboptimal matching habitat choice,
38 decreasing the benefits of this dispersal mode under climate change. However population
39 persistence was still better under suboptimal matching habitat choice than under random
40 dispersal. Our results highlight the urgent need to implement more realistic mechanisms of
41 dispersal such as matching habitat choice into models predicting the impacts of ongoing
42 climate change on biodiversity.

43 **Keywords:** species range shift, adaptation, dispersal, gene flow, individual-based model

44

45 **Introduction:**

46 Contemporary climate change threatens biodiversity worldwide by impacting species
47 persistence and distribution (Parmesan 2006, Selwood et al. 2015, Urban 2015). Species
48 may persist under climate change through two main non-exclusive responses: by tracking
49 suitable climatic conditions across space (geographical range shift, e.g. Hill et al. 2011, Chen
50 et al. 2011) or by adapting to the new local climatic conditions without shifting their
51 geographic range (populations' phenotypic shift, e.g. Boutin and Lane 2014, Merilä and
52 Hendry 2014). Both responses are strongly influenced by dispersal (i.e. movement from the
53 natal site to the first breeding site, or between successive breeding locations (Howard
54 1960)). Dispersal allows the colonization of new habitats made available by climate change
55 and induces a gene flow affecting population's phenotypic composition. Assuming that
56 individuals disperse with a constant probability and settle into randomly chosen habitats,
57 gene flow is predicted to swamp local adaptation by bringing non-adapted alleles into
58 populations (Lenormand 2002), which could compromise persistence under climate change
59 (Pease et al. 1989, Polechová et al. 2009).

60 However, dispersal is increasingly recognized to be a non-random process (Bowler
61 and Benton 2005, Edelaar et al. 2008, Clobert et al. 2009, Edelaar and Bolnick 2012, Travis
62 et al. 2012, Lowe and McPeck 2014). The different stages of this process (i.e. departure,
63 transience and settlement) are influenced by individual phenotype, local context and often
64 their match (i.e. matching habitat choice). Variation in the phenotype of individuals may imply
65 variation of fitness in specific environments which should select for inter-individual
66 differences in emigration and immigration decisions according to their fit to local
67 environmental conditions (Edelaar et al. 2008). Individuals are expected to move from
68 habitats where they expect a low fitness and to settle in habitats where they expect a higher
69 fitness, making dispersal an adaptive process.

70 Matching habitat choice has been demonstrated in various species (e.g. insects
71 (Karpestam et al. 2012), fishes (Bolnick et al. 2009), birds (Dreiss et al. 2012, Camacho et al.
72 2016, Benkman 2017), reptiles (Cote and Clobert 2007a, Cote et al. 2008)), for different
73 phenotypic traits matching different environmental conditions. For example, in three-spine
74 sticklebacks (*Gasterosteus aculeatus*), a mark-transplant-recapture experiment showed that
75 dispersers' preferences for lake and stream habitats depended on lake-like and stream-like
76 morphological attributes (Bolnick et al. 2009). Under stable environmental conditions,
77 matching habitat choice is predicted to promote adaptive gene flow compared to fitness
78 independent dispersal (Holt 1987, Jaenike and Holt 1991, Ruxton and Rohani 1999,
79 Armsworth and Roughgarden 2005a, 2008, Bolnick and Otto 2013, Scheiner 2016). Such
80 adaptive gene flow acts as one of the main factors favoring population adaptation and
81 differentiation on small spatio-temporal scales (Edelaar and Bolnick 2012, Bolnick and Otto
82 2013, Scheiner 2016, Edelaar et al. 2017). Despite the influence of matching habitat choice
83 on local eco-evolutionary dynamics, there remains scope for exploring whether this individual
84 behavioral process acting at a small spatial scale can influence species' responses to
85 environmental conditions at larger spatial scales.

86 Under variable environmental conditions, matching habitat choice and ensuing
87 adaptive gene flow may locally promote an efficient shift in mean populations' phenotypes
88 and therefore may influence species' responses to changing conditions such as ongoing
89 climate change. For example, in ectotherm species, physiology directly depends on external
90 temperature and individuals are characterized by a thermal phenotype (i.e. thermal optimum
91 and tolerance) that links their physiology and performance to temperature (Huey and
92 Stevenson 1979). This thermal phenotype can vary within species and populations (Artacho
93 et al. 2013, Goulet et al. 2017). Thereby, individual thermal optimum may shape individuals'
94 movements across a landscape through the filter of phenotypic adaptations to varying
95 temperature (Bestion et al. 2015). As climate warming is expected to increase local
96 mismatch between individual thermal optimum and local temperature, matching habitat

97 choice may make movements towards more suitable climatic conditions easier and promote
98 an efficient shift of species geographic distribution (Edelaar and Bolnick 2012). However to
99 our knowledge, this verbal prediction remains untested and the underlying mechanisms by
100 which matching habitat choice may influence species' responses to climate change are still
101 poorly understood.

102 Here we investigate the influence of matching habitat choice on species' responses to
103 climate change and more precisely how very local mechanisms, here non-random individual
104 movements, could influence species' global response to environmental change. We used an
105 individual-based model to tackle this question to allow precise integration of such a complex
106 process into the model. Thus, we developed a mechanistic individual-based model
107 representing a virtual species, inspired by the biology of ectotherm species, distributed along
108 a thermal gradient. We modeled two dispersal modes: random dispersal and matching
109 habitat choice. We simulated different rates of climate change and followed populations'
110 genetic composition through space and time. After quantifying the adaptiveness of gene flow
111 under both dispersal modes, we evaluated the influence of adaptive dispersal on extinction
112 risk at the edges of and within the spatial range, on the proportion of the geographical range
113 within which the species goes extinct during climate change and on the time to species
114 extinction.

115 **Methods:**

116 All parameters used in the model are summarized in Table 1.

117 Environment:

118 Individuals were distributed on a two dimensional landscape (i.e. grid map) constituting 1700
119 lines (latitudes) and 15 columns (longitudes) built as a tube to avoid edge effects. A thermal
120 gradient representing mean annual temperatures with 0.01°C increment per space unit
121 occurred along the latitudinal axis. Before climate change, temperature ranged from 19°C to

122 36°C, preventing any individual from surviving at the edges of the latitudinal axis according to
123 their initial genotypic/phenotypic values (Table 1) and therefore avoiding edge effects on the
124 latitudinal axis. Temperature along the longitudinal axis was constant (no environmental
125 stochasticity, though see robustness section). We assumed that all map cells could sustain a
126 population with constant carrying capacity K through space and time (i.e. continuous
127 landscape with no unsuitable habitats). We simulated two levels of climate change (1°C or
128 2°C of warming over 100 years) by uniformly increasing temperature at each location through
129 time.

130 Population dynamics and genetics:

131 We modeled a sexual species with two life stages (juveniles and adults). Each individual was
132 characterized by a thermal phenotype represented as a Gaussian function of survival
133 dependency to temperature with constant variance among individuals and mean
134 corresponding to individual thermal optimum:

$$S(T) = e^{-\frac{(T-T_{opt})^2}{2\sigma^2}} \quad (1)$$

135 with $S(T)$ being the survival probability, T the local temperature, σ^2 the gaussian variance and
136 T_{opt} the thermal optimum. This optimum was genetically determined by 25 additive
137 independent diploid loci with values taken from real numbers (i.e. genotypic values
138 corresponding to phenotypic ones; the thermal optimum of each individual was thus obtained
139 by averaging all allele values of its genotype). As a complex continuous trait, we considered
140 that the thermal optimum was genetically determined by many independent loci with
141 infinitesimal effects on the phenotypic trait. We arbitrarily chose to fix this number at 25. We
142 assume no environmental effect (i.e. no phenotypic plasticity). In each population at each
143 time step (one time step corresponds to one year), individuals could disperse, then
144 reproduce (adults only) and survive or die (Supplementary material Appendix A: Figure A1).

145 Reproduction was independent of temperature. Each adult female produced a
146 number of offspring taken from a Poisson distribution, with a mean fecundity of 2.
147 Reproducing males were randomly chosen from the same patch. For each transmitted allele,
148 mutation occurred with a probability of 10^{-5} (Table 1). The new allele was taken from a
149 Gaussian distribution centered on the mean parental allele value and of arbitrary variance
150 1.11. With such variance, 95% of new alleles were in a ± 1 interval around the parental
151 value. The sex of offspring was randomly chosen, resulting in a population sex-ratio of 1:1 at
152 birth.

153 At the end of each time step, individuals died or survived. If juveniles survived they
154 became adults and the adult stage lasted until individuals died. Survival probability depended
155 on the match between thermal phenotype and external temperature in juveniles and adults
156 (i.e. Gaussian function of temperature (equation (1)); Supplementary material Appendix A:
157 Figure A1). For each phenotype, the Gaussian function was scaled such that within the
158 temperature range of $\pm 2.4^{\circ}\text{C}$ around the optimal temperature (which corresponds to the
159 temperature range in which the non-scaled survival probability was always higher than 0.05),
160 the mean survival probability was equal to 0.12 for juveniles and 0.5 for adults (Table 1). As
161 observed in many species (e.g. Martin 1995 (birds), Pike et al. 2008 (reptiles), Gaillard and
162 Yoccoz 2003 (mammals)), we considered the survival probability to be lower in juveniles than
163 in adults. Survival was also density dependent: when current population size in a patch, N ,
164 exceeded carrying capacity K , each individual was killed with a probability $1 - N/K$, so that
165 the population size did not exceed on average the carrying capacity after the survival event.
166 The density-dependent survival event occurred after the phenotype-dependent survival
167 event.

168 We implemented two different dispersal modes, random dispersal and matching
169 habitat choice. In the case of matching habitat choice, the departure probability of each
170 individual depended on its expected lifetime reproductive success (LRS) (Le Galliard et al.
171 2008) and was exclusively driven by local thermal adaptation, that is the match between

172 individual thermal phenotype and local temperature (i.e. survival probability without density
 173 dependence called hereafter thermal survival probability; Supplementary material Appendix
 174 A: Figure A1). The lifetime reproductive success was calculated without density dependence
 175 for one year (i.e. the adult stage) for adults and for two years (i.e. the juveniles and the adult
 176 stage) for juveniles.

$$LRS_{adult} = Fecundity + thermal\ survival\ probability * Fecundity \quad (2)$$

$$LRS_{juvenile} = thermal\ survival\ probability * LRS_{adult}$$

177 with LRS_{adult} and $LRS_{juvenile}$ being the lifetime reproductive success of adults and juveniles
 178 respectively. As we did not know the number of years an individual could live, we assumed
 179 the same reproductive success over the years for adults. LRS_{adult} was therefore calculated for
 180 one year as calculating LRS over a longer period of time will not change its value. Emigration
 181 probability for each individual was calculated as $1 - LRS$ and scaled to mimic realistic
 182 dispersal probabilities observed in nature. We considered higher dispersal in juveniles than
 183 in adults, as observed in species where natal dispersal is dominant over breeding dispersal
 184 (e.g. Greenwood and Harvey 1982). Dispersal probability thus varied from 0.3 to 0.5 for
 185 juveniles and from 0.15 to 0.35 for adults (Table 1). The detailed formula was as follow:

$$\varepsilon = \varepsilon_{basal} + (\varepsilon_{max} - \varepsilon_{basal}) * \left(1 - \left(\frac{LRS}{LRS_{max}}\right)\right) \quad (3)$$

186 with ε the dispersal probability, ε_{basal} the lower dispersal bound (e.g. 0.3 in juveniles), ε_{max} the
 187 upper dispersal bound (e.g. 0.5 for juveniles), LRS the lifetime reproductive success
 188 (equation (2)) and LRS_{max} the maximum LRS obtained when individual thermal optimum
 189 perfectly matches local temperature. Dispersers could visit all habitats on the perimeter of a
 190 circle centered on the middle of the departure habitat and of radius exactly equal to the
 191 dispersal distance and settled in the habitat that maximized their lifetime reproductive
 192 success (Supplementary material Appendix A: Figure A2). We assumed that dispersers had
 193 access to every habitat on that perimeter, including those where only a corner was on the

194 circle's perimeter (i.e. as each habitat corresponded to a square on the map). Habitats at a
195 distance from the departure habitat lower than the dispersal distance cannot be chosen to
196 settle. Within a simulation, dispersal distance was fixed and all individuals thus dispersed at
197 the same distance from their departure habitat. When more than one habitat maximized their
198 lifetime reproductive success, dispersers settled randomly in one of these habitats
199 (Supplementary material Appendix A: Figure A2).

200 In case of random dispersal, individuals dispersed with a constant probability (0.3 for
201 juveniles and 0.15 for adults; Table 1). As the effective dispersal rate in the case of matching
202 habitat choice was not constant over space and time, we set the random dispersal probability
203 to be equal to the lower dispersal probability ϵ_{basal} from the matching habitat choice scenario.
204 We also ran simulations with random dispersal probability set to the upper dispersal
205 probability ϵ_{max} from the matching habitat choice mode, allowing us to compare random
206 dispersal with matching habitat choice scenarios for comparable dispersal probability (see
207 robustness section). Dispersers visited all habitats on the perimeter of a circle centered on
208 the middle of the departure habitat and of radius equal to the dispersal distance and settled
209 in a randomly chosen habitat among these visited habitats (Supplementary material
210 Appendix A: Figure A2). Again, all individuals thus dispersed at the same distance from their
211 departure habitat. It allowed us to compare results obtained under matching habitat choice
212 to the random dispersal mode without having differences in the effective dispersal distances
213 between dispersal modes. The results we obtained by comparing simulations under both
214 dispersal modes were thus only due to the direct effect of habitat choice in emigration and
215 immigration decisions. The dispersal distance was fixed within simulations; we ran
216 simulations with five dispersal distances (2, 3, 4, 5, 6 units on the landscape per dispersal
217 event corresponding to a change of 0.02, 0.03, 0.04, 0.05 and 0.06°C on the thermal
218 gradient).

219 To disentangle the influence of emigration from immigration in the matching habitat
220 choice mode, we ran simulations with adaptive emigration only (dispersal probability

221 depending on the match between phenotype and habitat of origin but random settlement
222 decision) and adaptive immigration only (fixed dispersal probability but settlement decision
223 depending on the match between phenotype and habitat visited).

224 Simulations:

225 At the beginning of simulations, we built a landscape and implemented a population of size
226 corresponding to the carrying capacity at each location of that landscape (i.e. the entire
227 landscape was inhabited at carrying capacity, fixed at 100 individuals at every location of the
228 map). For each individual, the allele values of the 25 loci determining the thermal optimum
229 were taken from a uniform distribution between 29 and 33°C (Table 1). The initial sex-ratio
230 was 1:1 and the proportions of juveniles and adults were 0.5 each. The system evolved
231 under stable climate for 600 years. As mutations brought new alleles into the populations, the
232 range was not stabilized and the species would invade the landscape after a sufficient time
233 under stable climate. We choose 600 years of stable climate before simulated climate
234 change because it matched the minimum time needed for all phenotypes expressed from the
235 initial distribution of genotypes (i.e. uniform distribution between 29°C and 33°C) to be
236 distributed on the landscape among all parameter values we tested. In the parameter set that
237 led to the widest range size, the individuals were distributed between latitude 100 and
238 latitude 900 corresponding to a range of temperature from 27 to 35°C on the grid. We also
239 ran simulations with 800 years of stable climate and did not observe any difference in the
240 results we obtained from those obtained with 600 years of stable climate (Supplementary
241 material Appendix I: Figure I1-I4). Then we simulated climate change for 600 years with two
242 levels of climate change (1°C and 2°C of warming over 100 years) by uniformly increasing
243 temperature at each location through time.

244 The model was coded in C++ using the GNU Scientific Library for random numbers
245 generation (Galassi et al. 2009) and outputs were analyzed using R3.3.1 (R Development
246 Core Team 2010).

247 We show the results for 20 sets of parameters values (2 dispersal modes * 2 levels of
248 climate change * 5 dispersal distances), each one replicated 50 times. Simulations with
249 adaptive emigration only and adaptive immigration only were replicated 20 times. Extra
250 simulations for the robustness of results against various parameters of the model were
251 replicated 20 times. The number of replication was sufficient to obtain very low standard error
252 in our results as running simulations with 40 replicates gave the same results.

253 Outputs:

254 At the end of each time step, we calculated the mean thermal survival probability (i.e. the
255 mean survival probability of all individuals without density dependence) through time for
256 residents, immigrants and emigrants of each population across the range. We then
257 calculated gene flow adaptation as the difference between immigrants' relative adaptation
258 (i.e. difference between the mean thermal survival probability of immigrants and the mean
259 thermal survival probability of residents of each population) and emigrants' relative
260 adaptation (i.e. difference between the mean thermal survival probability of emigrants and
261 the mean thermal survival probability of residents of each population).

262 The proportion of range loss was computed as $1-N_t/N_0$ with N_t the number of non-
263 empty latitudes (i.e. one individual at least was present at the given latitude) at time t and N_0
264 the number of non-empty latitudes at time 0 (i.e. just before the start of the climate change).
265 The extinction time was computed as the number of years of climate change needed for all
266 populations to go extinct. When extinction did not occur during the simulation time (600
267 years), extinction time was arbitrarily recorded as 600 years. Range contraction was
268 computed as $1-R_t/R_0$ with R_t being the range size (difference between extreme occupied
269 latitudes) at time t . Range fragmentation was computed as $(R_t - N_t)/R_t$. Finally, the local
270 mean thermal fitness load was computed at each location and time as one minus the mean
271 thermal survival probability of residents.

272 Robustness:

273 To test for the robustness of our results regarding the influence of major demographic
274 parameters known to impact species' responses to climate change, we ran additional
275 simulations for different parameter values of mean survival probability, fecundity, carrying
276 capacity and dispersal probability. We varied the basal dispersal probability ϵ_{basal} from 0.2 to
277 0.4 for juveniles and from 0.05 to 0.25 for adults. For simplicity, the range of variation of the
278 emigration probability for matching habitat choice was fixed at 0.2 in all simulations. We
279 added extra simulations of random dispersal with emigration probability of 0.5 and 0.6 for
280 juveniles and 0.35 and 0.45 for adults, corresponding to the maximal emigration probability at
281 which individuals could disperse in the matching habitat choice simulations. This allowed us
282 to compare results obtained under matching habitat choice and random dispersal with similar
283 dispersal rate. The different values for each parameter are provided in Table 1.

284 We also tested the influence of spatio-temporal environmental stochasticity on our
285 results. Environmental stochasticity could influence species' responses to climate change
286 because it should reduce the adaptiveness of the immigration decision in matching habitat
287 choice mode (a right choice at time t could be wrong at time $t+1$). At each time step (i.e. one
288 year), the temperature of each cell of the map was calculated as the current mean
289 temperature of the latitude + γ , with γ being a temperature randomly taken from a uniform
290 distribution centered on 0 and of variance determined by the level of environmental
291 stochasticity. The higher the environmental stochasticity is, the farther the temperature of a
292 habitat can be from the mean temperature of the latitude. An individual that chooses a
293 habitat that fits its phenotype at time t could therefore be maladapted the year after as the
294 temperature changes stochastically. We ran simulations with environmental stochasticity
295 corresponding to the temperature difference between 2 latitudes (0.01°C), 10 latitudes
296 (0.1°C) and 100 latitudes (1°C). Parameters values are summarized in Table 1.

297 We also considered density dependence in matching habitat choice to test for the
298 influence of the other factors involved in dispersal decisions. We thus included the density-
299 dependent survival term in the lifetime reproductive success of both juveniles and adults:

LRS_{adult} with density

= Fecundity + thermal survival probability

* density dependent survival probability * Fecundity

(4)

$LRS_{juvenile}$ with density

= thermal survival probability

* density dependent survival probability * LRS_{adult}

300 Finally, we ran simulations with low mutation rate (10^{-7} per locus; Table 1) to study
301 the influence of mutations on the velocity of range shift.

302 **Results:**

303 We observed that matching habitat choice induced an adaptive gene flow under climate
304 change (Figure 1A, Supplementary material Appendix 2: Figure B1A, B2A) while gene flow
305 was never adaptive in the random dispersal mode. Such adaptive gene flow resulted in a
306 higher thermal survival probability (i.e. survival probability without density dependence) of all
307 individuals in the case of matching habitat choice than in the case of random dispersal
308 (Figure 1B, Supplementary material Appendix 2: Figure B1B, B2B). In the matching habitat
309 choice mode, we observed that thermal survival probability was generally higher for
310 immigrants than for residents and emigrants excepted at time 0 where thermal survival
311 probability was maximal for all individuals (Figure 1B and Supplementary material Appendix
312 B: Figure B1B, B2B). In some cases, we also observed that residents' thermal survival
313 probability was higher than emigrants' thermal survival probability (for example: Figure 1A;
314 Dispersal distance: 2 space units; Time: 200 years). In the matching habitat choice mode,
315 immigrants were therefore better adapted than residents and emigrants were therefore less
316 adapted than residents, resulting in an adaptive gene flow. Conversely, we did not observe

317 any difference in thermal survival probability between residents, immigrants and residents
318 from the random dispersal modes (Figure 1B and Supplementary material Appendix B:
319 Figure B1B, B2B), preventing gene flow from being adaptive.

320 The adaptive gene flow due to matching habitat choice decreased the probability that
321 populations go extinct under both climate change scenarios tested and, when extinction
322 occurred, matching habitat choice delayed it (Figure 2C, D). The spatial range loss was
323 always lower with matching habitat choice than when individuals moved randomly (Figure
324 2A, B). The difference in spatial range loss between dispersal modes could be large for some
325 sets of parameters. For example, while climate warming led to an extensive loss of 50 % of
326 the species range under a certain set of parameters of the random dispersal mode, in the
327 matching habitat choice mode the same set of parameters led to an expansion of the spatial
328 range (e.g. Figure 2A, dispersal distance: 3 space units). The spatial range loss was above
329 25% for most of the parameter values in the random dispersal mode (9 out of 10 sets of
330 parameters), while it only surpassed 25% in three out of 10 sets of parameters in the
331 matching habitat choice mode (Figure 2A, B). Furthermore, matching habitat choice almost
332 always allowed species persistence for longer periods of time than random dispersal with a
333 time to extinction up to four times longer in the adaptive than in the random dispersal mode
334 (Figure 2C, D). In the random dispersal mode, species went extinct during simulation time for
335 three out of five dispersal distances under 1°C of warming over 100 years, while extinction
336 was not observed during simulation time under matching habitat choice (Figure 2C). For
337 faster climate change, matching habitat choice always extended time to extinction compared
338 to random dispersal (Figure 2D).

339 Matching habitat choice decreased spatial range loss owing to fewer local extinctions
340 both at the edges of the spatial range and within the spatial range compared to random
341 dispersal. The spatial range was less contracted in the matching habitat choice mode (Figure
342 3A, B), because the colonizing front was moving faster (Figure 4 and Supplementary material
343 Appendix C: Figure C1). This faster colonizing front, closer to the speed of climate change,

344 was explained by individuals moving more in the direction of their shifting climatic niche when
345 dispersal was adaptive (Figure 4 and Supplementary material Appendix C: Figure C1). It
346 promoted species' range shift and reduced population extinction at the edges of the
347 distribution. However for the lowest dispersal distance, the speed of the colonizing front was
348 slower than the speed of the climate, meaning that the range was not shifting as fast as the
349 climatic niche in the case of matching habitat choice, leading to important range size
350 reduction. For higher dispersal distances, the speed of the colonizing front was as fast as or
351 even faster than the speed of climate evolution in the case of matching habitat choice (Figure
352 4C,E). This was never the case in the random dispersal mode. The speed of the colonizing
353 front could be faster than the speed of climate in case of matching habitat choice because of
354 mutations. Mutations allowed new phenotypes to appear and these phenotypes, when
355 dispersal distance was sufficient, could colonize new habitats at the cold margin of the range.
356 Matching habitat choice promoted such colonization and we thus observed a faster
357 colonizing front than the speed of the climate only in the case of matching habitat choice
358 mode. When mutation rate was low, the speed of the colonizing front never overtook the
359 speed of the climate (Supplementary material Appendix C: Figure C2).

360 For all parameter values, matching habitat choice also reduced local population
361 extinctions within the spatial range (Figure 3D,E) compared to random dispersal mode.
362 Under random dispersal mode, extinctions within the range often occurred right behind the
363 colonizing front (Supplementary material Appendix D: Figure D1B). Local maladaptation was
364 indeed high at this location (Supplementary material Appendix D: Figure D1C) because of
365 the non-adaptive gene flow preventing any change in the mean populations' phenotype in
366 response to climate change (Supplementary material Appendix D: Figure D1D). Under
367 matching habitat choice, adaptive gene flow prevented strong maladaptation behind the
368 colonizing front, reducing fragmentation of the range (Supplementary material Appendix D:
369 Figure D1).

370 The influence of matching habitat choice on species' response to climate change
371 could be explained by adaptive emigration, adaptive immigration or the combination of both.
372 When we modeled adaptive immigration with no adaptive emigration, most results were
373 similar to the scenario where both emigration and immigration were adaptive. Indeed, the
374 spatial range was better maintained (Supplementary material Appendix E: Figure E1A,B),
375 less contracted (Supplementary material Appendix E: Figure E2A,B) and – to a lesser extent
376 – less fragmented (Supplementary material Appendix E: Figure E2C,D) and the extinction
377 time was longer (Supplementary material Appendix E: Figure E1C,D) than under random
378 dispersal for most parameter values. On the contrary, the results with adaptive emigration
379 and no adaptive immigration were similar to those obtained under random dispersal
380 (Supplementary material Appendix E: Figures E1, E2).

381 Dispersal distance had a strong influence on observed patterns. The higher the
382 dispersal distance was, the higher the thermal survival probabilities of residents, of
383 immigrants and of emigrants were, particularly in the matching habitat choice mode (Figure
384 1B, Supplementary material Appendix B: Figure B1B, B2B). While dispersal was always
385 adaptive under matching habitat choice (Figure 1A, Supplementary material Appendix B:
386 Figure B1A, B2A), dispersal distance had to be sufficiently high to maintain a high survival
387 probability through time for all individuals (Figure 1B, Supplementary material Appendix B:
388 Figure B1B, B2B). As dispersal distance positively influenced thermal survival probability, it
389 also positively influenced range loss limitation, time of persistence, limitation of range
390 contraction and range fragmentation (except under random dispersal for a warming of
391 2°C/100 years; see below) and colonization success in the two dispersal modes (Figure 2, 3,
392 4). However, its effect was much larger in the matching habitat choice mode than in the
393 random dispersal mode. For example, an increase of 1 unit in dispersal distance induced a
394 12% reduction in range loss under random dispersal whereas the same increase allowed a
395 shift from a range loss of 45% to a range expansion of 20% under matching habitat choice
396 (Figure 2A; dispersal distance of 2 and 3 units). Dispersal distance also promote species

397 range shift under climate change by increasing the speed of the colonizing front in both
398 random dispersal and matching habitat choice (Figure 4). However, despite the positive
399 influence of dispersal distance, matching habitat choice promoted species' responses to
400 climate change compared to random dispersal even for low dispersal distances (i.e. 2 space
401 units).

402 The only situation where dispersal distance did not positively influence species'
403 response to climate change was for range contraction under random dispersal and a
404 warming of 2°C/100 years (Figure 3D). In this case, fragmentation was higher for
405 intermediate dispersal distance than for low and high dispersal distances. At low dispersal
406 distance, the range was nearly extinct after 100 years of warming (range loss equal to 1 in
407 case of random dispersal with a dispersal distance of 2 space unit; Figure 2B), preventing
408 fragmentation from being high (if the range is small, extinction within the range should be
409 rare). When dispersal distance increased, the part of the range that remained after 100 years
410 of warming also increased (Figure 2B) allowing fragmentation to rise (Figure 3D).

411 In addition to dispersal distance, we explored the influence of the major demographic
412 parameters of the model that are survival probability, fecundity, carrying capacity and
413 emigration probability, on species' responses to climate change. We found that our
414 conclusions held for the different parameter values we tested for. In all cases, matching
415 habitat choice reduced range loss during climate change compared to random dispersal
416 (Figure 5). For the majority of parameter values, matching habitat choice also extended
417 extinction time, reduced range contraction and range fragmentation (Supplementary material
418 Appendix F: Figure F1-F3). The higher the survival probability, fecundity, carrying capacity or
419 emigration probability was, the lower the range loss during climate change was for both
420 species performing matching habitat choice and random dispersal. Range loss during climate
421 change however depended much more on survival probability and fecundity than on carrying
422 capacity which had a very low impact (Figure 5). Interestingly, emigration probability had a
423 greater impact on species performing matching habitat choice than on those dispersing

424 randomly. For example, a 0.4 increase in juveniles emigration probability reduced range loss
425 of 0.25 during climate change with random dispersal whereas a 0.1 increase in juveniles
426 emigration probability reduced range loss of 0.6 with matching habitat choice (Figure 5,
427 warming = 1°C/100 years).

428 We also tested for the influence of other factors involved in dispersal decisions such
429 as conspecific density. We found that matching habitat choice depending on temperature
430 and local density improved the persistence of populations (i.e. lower extinction rate
431 (Supplementary material Appendix G: Figure G1A,B) and extended time to extinction
432 (Supplementary material Appendix G: Figure G1C,D)) compared to random dispersal, by
433 reducing range contraction (Supplementary material Appendix G: Figure G2A,B) and range
434 fragmentation (Supplementary material Appendix G: Figure G2C,D). Differences between
435 results with and without the dependency of matching habitat choice on local density were
436 well below the range of differences observed between matching habitat choice and random
437 dispersal modes (Figure 2 and 3 versus Supplementary material Appendix G: Figure G1 and
438 G2).

439 Finally, our conclusions also held for the different levels of spatio-temporal
440 environmental stochasticity we tested for, while stochasticity led to less adaptive dispersal
441 decisions. For all parameters values, spatial range loss for matching habitat choice during
442 climate change was lower than, or at least equal to random dispersal (Figure 6). For the
443 majority of parameter values, matching habitat choice also extended extinction time, reduced
444 range contraction and range fragmentation (Supplementary material Appendix H: Figure H1-
445 H3). In both dispersal modes, spatial range loss was positively correlated to environmental
446 stochasticity. However, in most cases, environmental stochasticity had a stronger impact on
447 range loss for the matching habitat choice mode than for the random dispersal mode (Figure
448 6A). Indeed, for the different dispersal distances tested, range loss under climate change in
449 case of random dispersal was not impacted by low to moderate environmental stochasticity
450 while range loss was impacted under matching habitat choice, confirming the negative

451 influence of environmental stochasticity on the optimality of matching habitat choice. Under
452 very high environmental stochasticity, range loss strongly increased for both dispersal
453 modes. For this high environmental stochasticity, species went extinct in both random
454 dispersal and matching habitat choice for low dispersal distance and a warming of 2°C/100
455 years (Figure 6B) such that the benefit of matching habitat choice on species range loss
456 compared to random dispersal was lost.

457 **Discussion:**

458 In this study, we demonstrated that matching habitat choice induces an adaptive gene flow
459 enhancing individuals' mean survival probability, reducing population extinction risk and
460 improving species persistence under climate change compared to random dispersal. We
461 investigated the influence of matching habitat choice on population dynamics and adaptation,
462 revealing the specific mechanisms by which this local-scale dispersal strategy increases
463 population persistence under climate change at a larger scale. Matching habitat choice (i)
464 promotes colonization and therefore species' range expansion and (ii) reduces population
465 extinction within the range and therefore range fragmentation.

466 Predictions for the probability of extinction and for the time to extinction under random
467 dispersal and matching habitat choice greatly differed in magnitude. We even found
468 qualitatively different predictions in some cases, where the model predicted range
469 contraction under random dispersal while it predicted range expansion under matching
470 habitat choice, especially for large dispersal distances (Figure 2, 3). The predicted
471 differences for the time to extinction can be so large that the species was predicted to go
472 extinct in 200 years in the random dispersal mode while no extinction was recorded for 600
473 years of continuing climate change in the matching habitat choice mode. Therefore, for
474 species performing matching habitat choice efficiently, this dispersal mode has to be
475 considered when predicting populations' range shift and extinction risk.

476

477 In our model, the benefits of matching habitat choice on species' responses to climate
478 change depend much more on adaptive immigration than emigration decisions
479 (Supplementary material Appendix E: Figure E1, E2). Emigration decisions depend on
480 individuals gathering information on local thermal conditions and assessing their phenotypic
481 match to these conditions while immigration decisions entail a comparison of thermal
482 conditions throughout the environment. Individuals would therefore have to visit numerous
483 candidate habitats to choose the most suited one (Delgado et al. 2014). Species with low
484 prospecting and dispersal abilities should thus be more at risk facing climate change as they
485 might not be able to visit enough patches to choose habitats adaptively (Edelaar et al. 2008).
486 However, accumulating studies evidenced fine-tuned processes underlying informed
487 dispersal and many species may gather information on surrounding habitats before
488 emigration (Cote and Clobert 2007b, Jacob et al. 2015a). These additional processes may
489 reinforce the effects of adaptive immigration decisions by allowing species to orient their
490 movements towards habitats with suitable thermal conditions.

491 The benefits of performing matching habitat choice compared to random dispersal
492 may therefore depend on species ability to disperse and to gather accurate information on
493 thermal conditions. Our results indeed show that dispersal distance and emigration
494 probability positively influenced the benefit of adaptive gene flow - resulting from matching
495 habitat choice - on population persistence, range fragmentation and range shift as a minimal
496 dispersal distance is required to maintain a high survival probability through time. The
497 minimal dispersal distance corresponded here to a distance from two to three times the
498 distance at which the climatic niche was moving from low to high latitudes (e.g. minimal
499 dispersal distance from 2 space units for a warming of 1°C/100 years). In the conditions of
500 our model, 2 space units corresponded to 0.02°C variations along the gradient. In the real
501 world, a typical annual temperature decrease with latitude is -0.75°C per degree latitude (Van
502 De Water et al. 1994). Given that one degree latitude corresponds approximately to 110km
503 around 45° latitude, dispersal distances of 2 space units in our model correspond to

504 distances of 2.93 km for temperate areas. Such distance might be achievable by many
505 species as the mean maximum dispersal distance for species dispersing actively was found
506 to be 9.12 km (Jenkins et al. 2007). We found that above this minimal dispersal distance,
507 species could track climate change without suffering range size reduction. Overall, species
508 with lower dispersal abilities should therefore be more at risk from climate change because
509 they might not be able to track suitable climatic conditions and to choose habitats adaptively
510 (Pearson 2006, Schloss et al. 2012).

511 We think our model could be applied to a large variety of species with good
512 movement skills. However, as outlined above, our model is restricted to species able to
513 perceive variation in thermal conditions and perform matching habitat choices accordingly.
514 Matching habitat choice might therefore be easier to perform on an altitudinal than on a
515 latitudinal axis because of the steeper thermal gradients. In mountain areas, temperature can
516 strongly vary at local spatial scales, allowing species with low dispersal ability and/or low
517 thermal sensitivity to detect and choose habitats with suitable microclimates. However, in
518 lowland areas, species may also be able to perform matching habitat choice as implemented
519 in our model. Climate change may induce important variations during a restricted period of
520 the year (e.g. summer) while changes in mean annual temperature would appear small as in
521 our model. These punctual variations might be enough to influence species dispersal,
522 especially for ectotherms in which small variations near the upper physiological thermal limits
523 induce important fitness changes (Huey et al. 2012). The pertinence of matching habitat
524 choice should nonetheless be ascertained on a case-by-case basis.

525 Our conclusions may further depend on the optimality of dispersal decisions.
526 Suboptimal emigration and immigration decisions can result from low prospecting skills and
527 from variability in climatic conditions and environmental conditions induced by habitat
528 fragmentation or environmental stochasticity. Indeed, in our model, environmental
529 stochasticity led to suboptimal immigration decisions due to temporal low predictability of the
530 climate and to increased range loss in the matching habitat choice mode. Induced

531 suboptimal decisions however still increased species persistence under climate change in
532 comparison to random dispersal. This is in accordance with the observations of Edelaar and
533 Bolnick (2012) on population adaptation and differentiation under stable climate for random,
534 suboptimal and optimal immigration decisions. Similarly to environmental stochasticity,
535 landscape fragmentation magnifies dispersal costs and should therefore hamper the
536 exploration of surrounding habitats reducing the optimality of dispersal decisions (Jacob et al.
537 2015b, Cote et al. 2017). Landscape fragmentation might therefore decrease the observed
538 benefits of matching habitat choice and might underpin the expected synergetic effects of
539 climate change and fragmentation on population persistence and spatial range shift
540 dynamics (Brook et al. 2008). This hypothesis remains to be tested. Finally, habitat choice
541 may also become suboptimal in the presence of other major dispersal drivers. For example,
542 intraspecific competition may influence individuals' fitness differently than local thermal
543 conditions (Paterson and Blouin-Demers 2017). Matching habitat choice may therefore
544 depend on adaptation to both local climates and local density. In our model, the responses to
545 climate warming were similar when matching habitat choice depended on both thermal
546 adaptation and local density and when matching habitat choice depended on thermal
547 adaptation only (Supplementary material Appendix G:Figure G1, G2). On top of those
548 discussed above, we expect our conclusions to hold qualitatively for other sources of
549 variation in the optimality of habitat choice.

550 Some other assumptions of our model may be critical to our results. Among these
551 assumptions, selection occurred on survival only. Survival, but not reproductive success,
552 depended on local temperature and density. It implies that non-adapted individuals could
553 reproduce and transmit their genes to the next generation before dying. It should therefore
554 slow down the adaptive process and increase the impact of non-adapted gene flow on
555 population adaptation under random dispersal. If selection was occurring on both
556 reproduction and survival, selection would be stronger and adaptation faster, reducing the
557 transmission of maladapted genes to the next generation and thus the impact of maladapted

558 individuals. As a consequence, it should limit the influence of maladaptive gene flow under
559 random dispersal that is involved in range limitation under stable climate (Kirkpatrick and
560 Barton 1997, Lenormand 2002, Bridle and Vines 2007) and may reduce the observed
561 differences in population extinction and species' range shift between random dispersal and
562 matching habitat choice. However, our conclusions should qualitatively hold as matching
563 habitat choice promotes dispersal and gene flow in the direction of the moving climatic niche
564 compared to random dispersal. Colonization of new habitats should therefore remain higher
565 under matching habitat choice than under random dispersal.

566 Matching habitat choice positively influenced species' responses to climate change by
567 limiting the mismatches between individuals' phenotypes and local environments (Figure 1A).
568 Phenotypic plasticity may also limit such mismatches. Phenotypic plasticity has been
569 demonstrated to influence species' responses to climate change by limiting range size
570 reduction (Valladares et al. 2014). Recent models allowing evolution of both matching habitat
571 choice and phenotypic plasticity demonstrated that under temporally stable climate (i.e. no
572 change in the mean temperature in the landscape but environmental stochasticity
573 integrated), phenotypic plasticity evolved more frequently than matching habitat choice
574 (Scheiner 2016, Edelaar et al. 2017). However under climate change, phenotypic plasticity
575 might delay evolutionary response in the long term, whereas matching habitat choice
576 promotes it by inducing an adaptive gene flow (Valladares et al. 2014). Under such
577 conditions, the benefit of phenotypic plasticity could be lower than those of matching habitat
578 choice, promoting the evolution of the latter. On the other hand, phenotypic plasticity could
579 limit the mismatch between phenotypes and climate until the limits of plasticity are reached. If
580 plasticity evolved, it could allow further coping with environmental change without any
581 evolutionary change of the traits under selection. Depending on the cost of plasticity and
582 matching habitat choice, both mechanisms could thus evolve to facilitate species' responses
583 to climate change. Future models could tackle this question by allowing the evolution of both

584 phenotypic plasticity and matching habitat choice under a continuous period of climate
585 change.

586 The influence of informed dispersal on local adaptation and population differentiation
587 has been theoretically well-studied (Holt 1987, Armsworth and Roughgarden 2005a, b, 2008,
588 Ravné et al. 2009, Bolnick and Otto 2013, Holt and Barfield 2015). Others have
589 investigated its evolution under various conditions (Travis et al. 1999, 2009, Hovestadt et al.
590 2010, Scheiner 2016, Edelaar et al. 2017) and its feedback effect on dispersal propensity,
591 range limits and range expansion (Enfjäll and Leimar 2009, Kubisch et al. 2010, 2011,
592 Bocedi et al. 2014, Poethke et al. 2016). Here we investigated the effect of a particular type
593 of informed dispersal, matching habitat choice, on species' responses to climate change.
594 Using a simple model with robust predictions, we showed that neglecting these mechanisms
595 may lead to inaccurate estimates of species extinction risk and spatial range shift. Similarly,
596 matching habitat choice should greatly affect predictions of population dynamics,
597 evolutionary adaptation, species interactions, and changes in community composition in
598 response to climate warming. While our model focused on the match between thermal
599 optimum and external temperature, conclusions should be similar for any other phenotypic
600 trait interacting with environmental variables affected by contemporary global change (e.g.
601 hygrometry and UV intensity). We therefore recommend future research to pay more
602 attention to matching habitat choice when studying populations' dynamics and spatial range
603 shift to improve model predictions and management policies.

604 **Data accessibility:**

605 Source code of the simulations will be deposited on Dryad upon acceptance.

606 **Competing interests:**

607 The authors declare no competing financial interests.

608 **Authors' contributions:**

609 EB and JCo designed the study. All authors developed the model. FP analyzed the results
610 and all authors discussed them. FP wrote the first draft of the manuscript and all authors
611 contributed substantially to revisions.

612 **Funding:**

613 F. P. was supported by a PhD fellowship from the French “Ministère de la Recherche et de la
614 Technologie”. JCo was supported by an ANR-12-JSV7-0004-01 and by the ERA-Net
615 BiodivERsA, with the national funder ONEMA, part of the 2012-2013 BiodivERsA call for
616 research proposals. EB was supported by a young researchers’ award from the Bettencourt-
617 Schueller foundation. This work was supported by the French Laboratory of Excellence
618 project “TULIP” (ANR-10-LABX-41). This work was performed using the cluster EDB-Calc
619 (which includes software developed by the Rocks(r) Cluster Group at the San Diego
620 Supercomputer Center, University of California) of the laboratory “Evolution et Diversité
621 Biologique”.

622 **Acknowledgements:**

623 We are grateful to S. Meylan, O. Ronce and E. Fronhofer for comments and suggestions on
624 the models and results. We thank Pim Edelaar, Justin Travis and reviewers for their useful
625 comments on the manuscript. We thank Aïsha Bruendl for editing the manuscript. We thank
626 P. Solbès for support on the EDB-Calc system.

627

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765

766 **Table caption:**

767 **Table 1:** Summary of the model parameters and their values in the main simulations and in
768 extra simulations performed for robustness analyses.

769 **Figures captions:**

770 **Figure 1: Adaptiveness of gene flows and thermal survival probability.** Adaptiveness of
771 the gene flow (**A**) and the thermal survival probability of emigrants, immigrants and residents
772 (**B**) through time for different dispersal distances in case of matching habitat choice (circles
773 and solid lines (**A**) and blue bars (**B**)) or random dispersal (triangles and dashed lines (**A**),
774 and green bars (**B**)). Results were obtained under a climate change scenario of 1°C of
775 warming over 100 years. **A**) Thermal adaptiveness of total gene flow through time for
776 different dispersal distances for the matching habitat choice (black) and random dispersal
777 (white) scenarios (see methods for details). **B**) Thermal survival probability of emigrants
778 (dark blue for matching habitat choice, dark green for random dispersal), immigrants
779 (medium blue for matching habitat choice, medium green for random dispersal) and
780 residents (light blue for matching habitat choice, light green for random dispersal) through
781 time for different dispersal distances in case of matching habitat choice (blue bars) and
782 random dispersal (green bars). Means (\pm SD) over 50 simulations are shown.

783 **Figure 2: Consequences of adaptive gene flow on species responses to climate**
784 **change.** Proportion of spatial range loss (**A,B**) and extinction time (**C,D**) depending on
785 dispersal distance in case of matching habitat choice (black bars) or random dispersal (white
786 bars) and for two climate change scenarios (scenario **A,C**: 1°C/100 years, scenario **B,D**:
787 2°C/100 years). Spatial range loss was measured after 200 years of warming for scenario **A**
788 and after 100 years of warming for scenario **B**. When the species persisted until the end of
789 simulations (600 years), the extinction time was indicated as 600 years. Means (\pm SD) over
790 50 simulations are shown.

791 **Figure 3: Spatial range contraction and fragmentation.** Proportion of spatial range
792 contraction (**A,B**) and spatial range fragmentation (**C,D**) depending on dispersal distance in
793 case of matching habitat choice (black bars) or random dispersal (white bars) and for two
794 climate change scenarios (scenario **A,C**: 1°C/100 years, scenario **B,D**: 2°C/100 years).
795 Spatial range contraction was measured after 200 years of warming for scenario **A** and after
796 100 years of warming for scenario **B**. Spatial range fragmentation was measured between 0
797 and 200 years of warming for scenario **C** and between 0 and 100 years of warming for
798 scenario **D**. Means (\pm SD) over 50 simulations are shown.

799 **Figure 4: Colonization dynamics.** Mean speed dynamics of colonizing front though time in
800 case of matching habitat choice (black solid line) or random dispersal (light gray solid line)
801 and for two climate change scenarios (scenario **A,C,E**: 1°C/100 years, scenario **B,D,F**:
802 2°C/100 years). To keep up with the pace of climate change, the front speed should be as
803 high as the dashed line. Three different dispersal distances were tested: 2 space units
804 (scenarios **A,B**), 3 space units (scenarios **C,D**) and 4 space units (scenarios **E,F**). Mean
805 curves over 50 simulations are shown.

806 **Figure 5: Influence of demographic parameters on spatial range loss during climate**
807 **change.** Proportion of spatial range loss depending on survival probability (**A,B**), fecundity
808 (**C,D**), carrying capacity (**E,F**) and emigration probability (**G,H**) in case of matching habitat
809 choice (open circle, solid line) or random dispersal (open triangle, dashed line) and for two
810 climate change scenarios (scenario **A,C,E,G**: 1°C/100 years, scenario **B,D,F,H**: 2°C/100
811 years). Spatial range loss was measured after 200 years of warming for scenario **A,C,E,G**
812 and after 100 years of warming for scenario **B,D,F,H**. In **A,B**) only juvenile survival probability
813 was represented but it was associated with adult survival probability (0.5 for juvenile survival
814 probability of 0.12 and 0.6 for juvenile survival probability of 0.25). In **G,H** the x axis
815 represented the basal juvenile emigration probability. It was associated with an adult
816 emigration probability (0.05 for the basal juvenile emigration probability of 0.2, 0.15 for the
817 basal juvenile emigration probability of 0.4, 0.25 for the basal juvenile emigration probability

818 of 0.4, 0.35 for the basal juvenile emigration probability of 0.5 and 0.45 for the basal juvenile
819 emigration probability of 0.6). In case of random dispersal emigration probabilities for
820 juveniles and adults was fixed whereas emigration probabilities could vary in case of
821 matching habitat choice (from 0.2 to 0.4 and 0.05 to 0.25 for juveniles and adults respectively
822 for the basal juvenile emigration probability of 0.2; from 0.3 to 0.5 and 0.15 to 0.35 for
823 juveniles and adults respectively for the basal juvenile emigration probability of 0.3; from 0.4
824 to 0.6 for juveniles and adults respectively for the basal juvenile emigration probability of 0.4).
825 Means (\pm SD) over 50 (parameter values of main simulations (Table A1)) or 20 (parameter
826 values of extra simulations (Table A1)) simulations are shown.

827 **Figure 6: Influence of environmental stochasticity on spatial range loss during climate**
828 **change.** Proportion of spatial range loss depending on environmental stochasticity in case of
829 matching habitat choice (circles and solid lines) or random dispersal (triangles and dashed
830 lines) for different dispersal distances (**A,B**: 3 space units; **C,D**: 4 space units; **E,F**: 5 space
831 units) and for two climate change scenarios (scenario **A,C,E**: 1°C/100 years, scenario **B,D,F**:
832 2°C/100 years). The level of environmental stochasticity determined how much the
833 temperature of habitats on a given latitude could vary around the current mean temperature
834 of this latitude (see methods section for details). Spatial range loss was measured after 200
835 years of warming for scenario **A,C,E** and after 100 years of warming for scenario **B,D,F**.
836 Means (\pm SD) over 50 (parameter values of main simulations (Table A1)) or 20 (parameter
837 values of extra simulations (Table A1)) simulations are shown.

838

839 **Table:**

Parameters	Main simulations	Extra simulations
Fecundity	2	1 and 3
Mean juvenile survival probability	0.12	0.25
Mean adult survival probability	0.5	0.6
Carrying capacity K	100	50 and 150
Juvenile emigration probability range for matching habitat choice (ϵ_{basal} and ϵ_{max} for	0.3 - 0.5	0.2 – 0.4 and 0.4 – 0.6

juveniles)		
Adult emigration probability range for matching habitat choice (ϵ_{basal} and ϵ_{max} for adults)	0.15 – 0.35	0.05 – 0.25 and 0.25 – 0.45
Juvenile emigration probability for random dispersal	0.3	0.2, 0.4, 0.5 and 0.6
Adult emigration probability for random dispersal	0.15	0.05, 0.25, 0.35 and 0.45
Dispersal distance	2, 3, 4, 5 and 6	3, 4 and 5
Mutation probability	10^{-5}	10^{-7}
Loci number	25	25
Initial allele range	29 – 33°C	29 – 33°C
Time of stable climate	600	800
Warming time	600	600
Level of climate change	1 and 2°C/100 years	1 and 2°C/100 years
Environmental stochasticity	0°C	0.01, 0.1, 1°C
Thermal gradient	0.01°C/latitude	0.01°C/latitude
Number of latitude on the map	1700	1700
Number of longitude on the map	15	15
Replicate	50	20

840

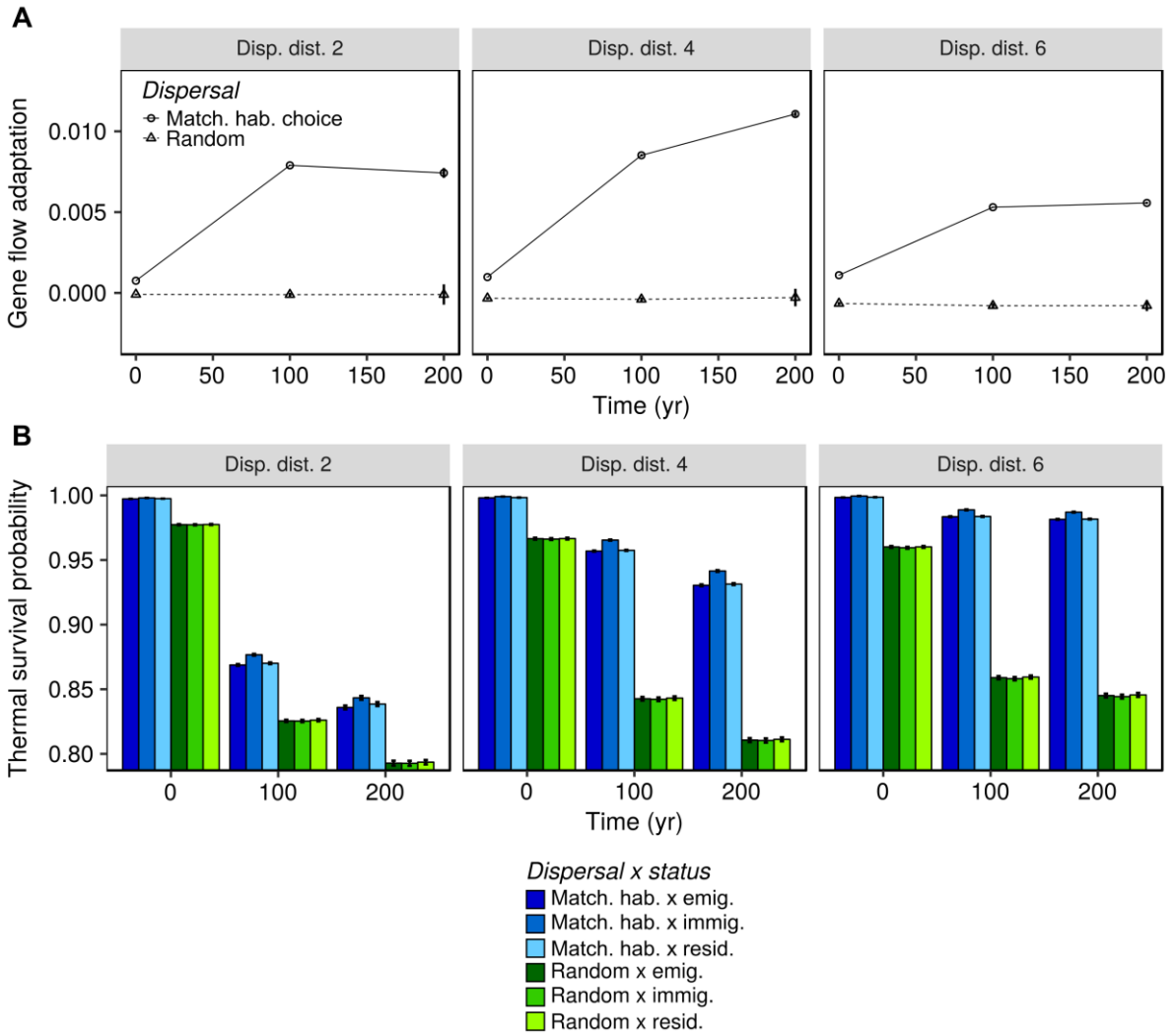
841 **Table 1: Summary of the model parameters and their values in the main simulations**

842 **and in extra simulations performed for robustness analyses.**

843

844 **Figures:**

845 **Figure 1**



846

847

