

2 **Fitness declines toward range limits and local adaptation to**
3 **climate affect dispersal evolution during climate-induced range**
4 **shifts**

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Abstract

14 Dispersal ability will largely determine whether species track their climatic niches during
climate change, a process especially important for populations at contracting (low-
16 latitude/low-elevation) range limits that otherwise risk extinction. We investigate whether
dispersal evolution at contracting range limits is facilitated by two processes that
18 potentially enable edge populations to experience and adjust to the effects of climate
deterioration before they cause extinction: a) climate-induced fitness declines toward
20 range limits, and b) local adaptation to a shifting climate gradient. We simulate a species
distributed continuously along a temperature gradient using a spatially explicit, individual-
22 based model. We compare range-wide dispersal evolution during climate stability vs.
directional climate change, with uniform fitness vs. fitness that declines toward range
24 limits (RLs), and for a single climate genotype vs. multiple genotypes locally adapted to
temperature. Dispersal decreased toward stable RLs when range-wide fitness was
26 uniform, but increased when fitness declined toward RLs, due to highly dispersive
genotypes maintaining sink populations at RLs, increased kin selection in smaller
28 populations, and an emergent fitness asymmetry that favoured dispersal in low-quality
habitat. However, this initial dispersal advantage at low-fitness RLs did not facilitate
30 climate tracking, as it was outweighed by an increased probability of extinction. Locally-
adapted genotypes benefited from staying close to their climate optima; this selected
32 against dispersal under stable climates but for increased dispersal throughout shifting
ranges, compared to cases without local adaptation. Dispersal increased at expanding RLs
34 in most scenarios, but only increased at the range centre and contracting RLs given local
adaptation to climate.

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Keywords: dispersal evolution, range shift, climate change, local adaptation, individual-
38 based simulation model, range contraction, fitness gradient, sink populations

40 **Introduction**

Modern-day climate change is already prompting widespread range shifts, through
42 expansions of polar and high-elevation range limits and contractions of equatorial and low-
elevation limits (Parmesan, 2006, Thomas *et al.*, 2006, Jump *et al.*, 2009). In a world of
44 shifting ranges, dispersal will become an increasingly critical trait, largely determining
whether many species can track their climatic niche (e.g. Anderson *et al.*, 2009, Schloss *et*
46 *al.*, 2012). Range shifts are often viewed as a species-level process, but it is equally
important to consider their effects at the population level. Dispersal ability may vary
48 among populations (Cwynar & MacDonald, 1987, Cody & Overton, 1996) and across
species' ranges (Hargreaves & Eckert, 2014). Loss of low-dispersal populations during
50 range shifts would decrease overall genetic diversity (Anderson *et al.*, 2008). This could be
especially significant at contracting limits, as low-latitude and low-elevation populations
52 may be better adapted to warmer temperatures, and may harbour a disproportionate
amount of species' overall genetic diversity if they served as refugia during ice-age range
54 contractions (Hampe & Petit, 2005). Loss of trailing edge populations could thus hinder
species' persistence in a warmer and increasingly variable world.

56 Dispersal is a complicated characteristic, but can evolve rapidly in response to
environmental change (Parmesan, 2006, Cheptou *et al.*, 2008, Phillips *et al.*, 2010).

58 Dispersal is often expected to be selected against at stable range edges, where dispersers

risk reduced or zero fitness by ‘falling off’ the range (MacArthur, 1972, Gros *et al.*, 2006),
60 but to evolve upwards at expanding range edges due to three processes. First, more
dispersive individuals are the most likely to reach the expanding front, a process of spatial
62 sorting that will be amplified over successive generations of expansion (Shine *et al.*, 2011).
Second, if fitness is negatively density-dependent, dispersers that colonize newly-available
64 habitat beyond the range edge gain a fitness advantage by escaping intra-specific
competition (Travis *et al.*, 2009). Third, successive founder events increase relatedness at
66 the leading edge. As density increases, this can increase kin selection for dispersal
(Kubisch *et al.*, 2013b), in which dispersal confers an advantage to related individuals by
68 reducing kin competition (Hamilton & May, 1977). Indeed, empirical studies of expanding
range limits have found increased dispersal at the expanding edge vs. range centre
70 (Thomas *et al.*, 2001, Phillips *et al.*, 2006, Monty & Mahy, 2010).

Most models of dispersal evolution at non-equilibrium range limits consider
72 biological invasions into unlimited and uniformly good habitat, rather than gradual
expansions (or contractions) following directional climate change (Hargreaves & Eckert,
74 2014). Although climate-induced range shifts share some important features with
invasions, namely spatial sorting, kin structuring, and competition escape that should
76 select for dispersal at the expanding front, range shifts may differ in several important
ways. First, new habitat will become available gradually; thus dispersers at the leading
78 edge still risk overshooting the range, potentially constraining the evolution of increased
dispersal. Second, fitness often declines towards range limits imposed by habitat (e.g.
80 climatic) constraints (Kawecki, 2008, Sexton *et al.*, 2009). This means that at the leading
edge, new habitat would initially be of lower quality than habitat at the existing range limit,

82 which might further constrain evolution of increased dispersal. Further, fitness declines
can influence dispersal evolution at stable range limits (Dytham, 2009), and pre-existing
84 dispersal patterns might affect the speed or success of future range shifts (Phillips, 2012).
Finally, when fitness declines are driven by climate, directional climate change will result in
86 a gradual habitat deterioration at the contracting edge, providing a lead-time during which
populations experience the effects of climate change and might adapt before the climate
88 becomes entirely unsuitable. Although fitness declines toward range limits are common in
nature (Abeli *et al.*, 2013) and theoretically important for dispersal evolution at stable
90 limits (Dytham, 2009), their effect on changing range limits has not been explored.

In contrast to the considerable attention given to stable and expanding range limits,
92 there has been almost no theoretical or empirical study of evolution at contracting limits
(Hampe & Petit, 2005, Hargreaves & Eckert, 2014). If contractions happen via local
94 extinctions that increase the spatial isolation of habitat patches, dispersal may be selected
against as dispersers from isolated edge populations run an increased risk of landing in
96 unsuitable habitat (Simmons & Thomas, 2004). Selection against dispersal could create an
ecological trap by preventing warm-edge populations from tracking their climate niche,
98 causing their eventual extinction. However, given local adaptation to temperature, climate
warming might select for increased dispersal throughout the range, as dispersive
100 individuals from warmer regions outcompete non-dispersive individuals no longer adapted
to local temperature conditions (Hargreaves & Eckert, 2014).

102 Here we develop a model to explore dispersal evolution at both expanding and
contracting range limits during climate-change induced range shifts. We consider a species
104 with random dispersal and a single dispersal and reproductive event during its lifetime,

akin to an annual plant with wind- or gravity-dispersed seeds. The species is distributed
106 across a continuous environmental gradient (e.g. temperature changing with latitude or
elevation), and the landscape is uniformly permeable to dispersers (no dispersal barriers).
108 Reproductive success declines with increasing density, conferring a fitness advantage to
individuals that colonize newly available habitat. We first consider two scenarios where all
110 individuals have the same temperature tolerance: 1) a 'table top' fitness distribution, where
fitness is uniform across the range and drops immediately to zero beyond (Fig. 1a); 2) a
112 'trapezoid' to 'triangle' fitness distribution, with a plateau or peak of high fitness in the
range centre and a linear fitness decline towards range edges (i.e. marginal-quality edge
114 habitat; Fig. 1b,c). These scenarios can be thought of as representing a species with a
clearly defined thermal tolerance (which imposes range limits), whose phenotypic
116 plasticity compensates completely (scenario 1) or partially (scenario 2) for the
temperature gradient within this tolerance. We then consider a third scenario: a species
118 made up of many genotypes locally-adapted to temperature, whose fitness declines linearly
away from their temperature optima (Fig. 1d). We explore the effects of declining habitat
120 quality toward range edges and local adaptation to climate on dispersal evolution across
the range, under both stable and changing climates. We also explore the contributions of
122 individual vs. kin selection to dispersal evolution. Our model is as simple as possible to
maximize tractability and generality; we end by discussing the potential effects of relaxing
124 constraints and the broad implications for range shifts under climate change.

126 **Materials and Methods**

Model landscape and growth dynamics

128 We based our model on that of Phillips (2012), considering an annual species with discrete
generations and asexual (clonal) reproduction. We modelled the species' range as a grid of
130 square patches arranged in $nrow$ rows by $ncol$ columns, where columns represented the
axis of environmental variation. For simplicity we envision a temperature gradient, but the
132 model applies to any gradient that could experience directional change (e.g. precipitation).
The first and last columns represent the limits of the species' environmental tolerance and
134 therefore its range limits, beyond which survival was impossible (patches beyond the
range were not modelled explicitly). The first and last rows were made adjacent to one
136 another, preventing edge effects in the direction perpendicular to climate change. Thus, all
patches except those at range limits shared a border with four other patches (above, below,
138 left, and right), to which they were potentially connected by dispersal. Each patch had the
carrying capacity K . Initially, $K*nrow*ncol$ individuals were assigned randomly to the
140 $nrow*ncol$ patches, so that on average patches started at carrying capacity.

Individuals could produce R_{max} offspring per generation in the absence of
142 competition, but their realized number of offspring was affected by both the density of the
patch they inhabited and stochasticity. Realized offspring numbers were drawn from a
144 Poisson distribution with mean λ . Reproduction was negatively density dependent. As in
other models of dispersal evolution (Travis *et al.*, 2009, Phillips, 2012), the offspring left by
146 an individual in a patch with population N was calculated using an individual-based version
of the Hassell-Comins discrete-time population growth model (Hassell & Comins, 1976):

148

$$\lambda = R_{\max} / \left(1 + \frac{N}{K} (R_{\max} - 1)\right) \quad [1]$$

150

where λ is the average number of offspring per individual. Thus, patches at carrying capacity tended to produce enough offspring to replace themselves ($\lambda = 1$), while patches below and above carrying capacity tended to grow ($\lambda > 1$) and shrink ($\lambda < 1$), respectively.

154

In the initial generation, each individual was assigned a dispersal probability D , drawn randomly from a uniform distribution between 0 and 1. Offspring inherited their parent's D ; to generate variability for the model to act on, D was subject to mutations, arising with probability μ_D per offspring. When mutations occurred, the offspring's D was drawn from a normal distribution with a mean equal to its parent's D and standard deviation of σ_D (mutant D -values < 0 or > 1 were discarded and re-drawn). We ran models varying both mutation parameters from 0.001 – 0.1, but this affected only the time to reach a stable range-wide distribution of D (see Fig. S1.1 in Appendix S1 for example runs).

162

Immediately after reproducing, the parental generation died and offspring either remained in their natal patch (probability $1 - D$) or dispersed (probability D). Dispersal direction was determined randomly among the four cardinal directions, with equal probability. Dispersers faced a dispersal cost, $cost$, the probability of dying during dispersal, and those at range edges also risked dispersing beyond the range where fitness was 0. After dispersal the population was censused and the cycle started anew.

168 **Range-wide fitness scenarios**

To explore the effects of deteriorating conditions towards range limits and local adaptation to the environmental gradient, we considered three scenarios:

170

1) *Single climate genotype, uniform fitness across the range*

172 Fitness was uniform across the environmental gradient but fell immediately to zero beyond
 the range, resulting in a ‘table top’ fitness distribution (Fig. 1a). This distribution provides
 174 a baseline for comparison with scenarios 2 and 3 below. It is also consistent with classic
 theory on dispersal evolution toward stable range limits (MacArthur, 1972) and the
 176 starting point of other models (e.g. Dytham, 2009), facilitating comparison to previous
 work.

178 2) *Single climate genotype, declining fitness towards range limits*

To explore the effect of declining habitat quality toward range limits we specified a number
 180 of columns at each range limit (*margin*) across which fitness declined linearly to zero (Fig.
 1b-d). For columns within the area of marginal habitat ($col \leq margin$ or $col \geq (ncol-$
 182 $margin+1)$), the fitness decline was modelled by multiplying the expected number of
 offspring (eq. [1]) by an environment-relative fitness parameter w based on the
 184 individual’s position along the gradient (col):

$$186 \quad w = \frac{col}{margin + 1} \quad \text{or} \quad w = \frac{ncol - col + 1}{margin + 1}$$

188 for the left (trailing) and right (leading) margins, respectively, such that

$$190 \quad \lambda = wR_{\max} / \left(1 + \frac{N}{K} (R_{\max} - 1)\right) \quad [2]$$

192 (Phillips, 2012). Note that the realized carrying capacity will be less than K in these
 marginal regions. Elsewhere (i.e. $margin < col < ncol-margin+1$), $w = 1$. We explored
 194 different values of $margin$, creating fitness distributions ranging from table top ($margin =$
 0) to triangular ($margin = (ncol-1)/2$), with a variety of trapezoid-shaped distributions in
 196 between (Fig. 1).

3) Multiple locally-adapted climate genotypes

198 The effect of local adaptation on dispersal evolution was explored using a variation of
 scenario 2 in which the species was made up of many genotypes, each adapted to a specific
 200 temperature along the gradient (Fig. 1d). Whereas individuals in the previous scenarios
 inherited only their D value, individuals in this scenario also inherited a value H , defining
 202 their temperature optimum. H -genotypes had triangular fitness distributions; maximum
 fitness was experienced in column H , from which fitness declined linearly across a number
 204 of columns defined by $g.margin$ (Fig. 1d). All H -genotypes had the same temperature
 tolerance breadth (the triangles' base): $2(g.margin)+1$. To achieve the fitness distribution
 206 shown in Fig. 1d, where no genotype's tolerance is truncated by the species' overall
 tolerance, we constrained $g.margin$ to be $\leq margin$ and modelled H from $g.margin+1$ to
 208 $ncol-g.margin$ (Fig. 1d). Accordingly, if $g.margin < margin$ there were genotypes locally
 adapted to marginal temperatures (Fig. 1d). For genotypes adapted to regions of optimal
 210 fitness (i.e. $margin < H < ncol-margin+1$), fitness declines away from H were modelled by
 multiplying the expected number of offspring in eq. [1] for an individual in column col by
 212 the genotype-relative fitness parameter h ,

$$214 \quad h = \max \left[\frac{(g.margin + 1) - |H - col|}{(g.margin + 1)}, 0 \right] \quad [3]$$

216 For genotypes adapted to regions of marginal fitness, h was multiplied by a factor, m , so
 that maximum genotype fitness (fitness at the genotype's optimum) decreased linearly
 218 throughout the range margin, as in Fig. 1d:

$$220 \quad m = \begin{cases} \frac{H}{margin + 1} & \text{for } H \leq margin \\ 1 & \text{for } margin < H < ncol - margin + 1 \\ \frac{ncol - H + 1}{margin + 1} & \text{for } H \geq ncol - margin + 1 \end{cases}$$

222

The resulting equation for the expected number of offspring for a given genotype was

$$224 \quad \lambda_g = mhR_{\max} / \left(1 + \frac{N}{K} (R_{\max} - 1) \right) \quad [4]$$

226 In the first time step, individuals were assigned the H value of the column they occupied,
 unless they occupied the outermost range edges to which no genotypes were adapted ($col <$
 228 $g.margin + 1$, or $col > ncol - g.margin$). In this case they were assigned the H of the nearest
 locally-adapted column, $g.margin + 1$ or $ncol - g.margin$, respectively.

230 Our model is designed to explore the effect of prior local adaptation on dispersal
 evolution, but not the relative importance of evolution in dispersal vs. environmental
 232 tolerance, as insufficient data on heritability and quantitative variation in these traits exist

to meaningfully bound such a model. H was therefore subject to mutation with probability
234 μ_H , which was kept $< \mu_D$ (see Discussion). Mutated H values were drawn from a normal
distribution with a mean of the parental H and standard deviation σ_H relative to $ncol$ (i.e. σ_H
236 $= 0.01$ is 1% of $ncol$), and rounded to the nearest integer. To prevent endless range
expansion, H -values beyond the species' original tolerance were discarded and redrawn. In
238 other words, we assume the species currently lacks sufficient genetic variation to adapt to
climates beyond those in its current range (see Discussion).

240 To explore the effect of local adaptation, we ran models with the same species-level
fitness distribution with and without local adaptation. Climate change caused rapid
242 extinction if $g.margin$ was 0 (i.e. genotypes only survived at one location), so we
approximated a table-top fitness distribution using $g.margin = margin = 1$.

244 **Climate change**

Models were run for 1500 generations; 500 generations of stable climate to allow dispersal
246 and density to equilibrate, followed by 1000 generations of directional climate change,
simulated by uni-directionally shifting suitable habitat by a mean of $avshift$ columns per
248 generation (longer runs did not alter the range-wide D pattern; D simply fluctuated around
a long-term average in each column). The realized climate shift in a particular generation
250 was drawn randomly from a Poisson distribution with a mean of $avshift$. Climate shifts
created an area of uncolonized but suitable habitat at the leading edge of the species'
252 current distribution, and an equal-sized unsuitable area at the trailing edge where
individuals 'fell off' and perished. The range-wide fitness distribution remained the same,
254 so when fitness declined toward range limits climate change improved conditions at the
leading edge, and worsened conditions at the contracting edge.

256 **Model exploration and summarization**

Our intent was to explore the effects of declining fitness toward range edges and pre-
 258 existing local adaptation on range-wide dispersal evolution. All parameters were explored
 in initial runs (see Appendix S1), but those with little effect on final D patterns (K , r , μ_D , σ_D)
 260 are kept constant in the results presented in the main text. Table 1 gives typical parameter
 values; when possible we retain those used in Phillips (2012) to maximize comparability.
 262 Smaller realized population sizes in poor-quality habitat edge could select for dispersal
 indirectly via kin selection (Hamilton & May, 1977). To explore how D was influenced by
 264 individual selection alone, we used the method of Poethke et al. (2007) to eliminate patch-
 level kin structure; models were run as described above except that immediately before
 266 dispersal individuals were randomly redistributed among rows within columns (i.e.
 environments), while maintaining the size of each patch.

268 To summarize results, for each column of each model run we calculated mean D
 across the $nrow$ rows (Fig. 2 shows typical realizations) and the change in mean D
 270 following climate change: $\Delta D = (\text{mean } D \text{ after climate change, generation 1500}) - (\text{mean } D$
 in last generation of stable climate, generation 500).

272

Results

274 Several model components affected evolved dispersal probability (D) consistently across
 fitness scenarios. The highest D s from the initial distribution of 0 to 1 were lost by the end
 276 of the stable-climate phase, due to dispersal *cost* and risk of dispersing beyond the range.
 Higher dispersal *cost* decreased D throughout the range and diminished differences
 278 between edge and centre (Fig. 3). Faster rates of *avshift* prompted evolution of higher D

(Fig. 2). For some parameter combinations, D values that evolved at the leading edge
 280 persisted as the range shifted and previously leading-edge locations became more central.
 This ‘smearing’ effect increased as *avshift* increased, or as dispersal mutation (μ_D or σ_D),
 282 *cost*, or range size (*ncol*) decreased (Fig. 3, Appendix S1). As *ncol* increased extinctions also
 took longer (not shown; *ncol* had little effect across stable ranges). Smaller population
 284 sizes, i.e. lower K or in poor-quality habitat defined by *margin* > 0, selected for increased D
 via increased kin selection (Appendix S1). However, the overall effects of fitness declines,
 286 local adaptation, and climate change on range-wide patterns in D were qualitatively
 consistent whether models allowed for both kin and individual selection (e.g. Fig 3),
 288 increased kin selection ($K = 10$; Fig. S1.3), or individual selection only (Fig. S1.4).

Single climate genotype, uniform fitness across the range

290 *Stable range, margin = 0*

D evolved to be lowest at range edges, due to the risk of dispersing to zero-fitness areas
 292 beyond the range (Fig. 3a).

Shifting range, margin = 0

294 Directional range shifts selected for increased D at the leading range edge (Fig. 2, 3a vs. b,
 4a). This was due partially to spatial sorting for dispersal, as the expanding front left
 296 behind non-dispersers, and partially due to new mutations, as maximum D always
 increased during range shifts. As long as dispersal bore a cost, D was greatest at the leading
 298 edge (Fig. 3b). When *cost* = 0, D in the range centre was so high before climate change that
 even though D increased at the expanding edge (Fig. 4a), it remained highest in the centre
 300 (Fig. 3). When *cost* = 0, D values evolved at the leading edge persisted as the range shifted,

such that climate change decreased D just behind the leading edge (Fig. 4a). Thus at the
 302 expanding edge *cost* scenarios seem to converge upon D values that enabled individuals to
 keep up with climate change without overshooting the range.

304 Climate change rarely affected dispersal at the range centre and contracting edge
 (Fig. 3a vs. b), and the nature of the effect depended on *cost*. At the trailing edge non-
 306 dispersers were overtaken by the shifting climate window; at low *cost* (0 - 0.1) this
 increased D , but at *cost* > 0.1 D was so low before climate change that this had no effect
 308 (Fig. 4a). In the range centre, climate change increased D slightly if *cost* = 0 but otherwise
 had no effect (Fig. 4a). However, if the range was small or climate change fast, high D from
 310 the expanding edge spread back, increasing D throughout the range (Fig. 2; *avshift* = 0.8).

The species tracked its climate niche successfully for all but the highest values of
 312 *cost* (> ~0.95 if *avshift* = 0.1) and *avshift* (Fig. 5). Beyond these values the unoccupied area
 at the leading edge increased until the species was overtaken by the shifting climate and
 314 went extinct.

Single climate genotype, declining fitness towards range limits

316 *Stable range, margin > 0*

Introducing a fitness decline towards range limits reversed the range-wide dispersal
 318 pattern, such that D evolved to be highest at range edges (Fig. 3). The region of elevated D
 corresponded roughly to the region of deteriorating habitat quality (*margin*; Fig. 3a). As
 320 *margin* increased so did the unoccupied areas at range edges where fitness was too low to
 sustain populations (note the decreasing range-widths from top to bottom panels, Fig. 3a).

322 We tested whether increased D in marginal habitat resulted from spatial sorting in
 demographic sink populations (Hargreaves & Eckert, 2014) and/or *in situ* selection. We

324 identified sink populations by changing dispersal distance from 1 to 0 cells. Preventing
dispersal decreased the occupied area (Fig. 6; the size of sink habitat did not change for
326 *cost* 0 or 0.5 so we present *cost* = 0.05 only). This confirmed that the outermost
populations were demographic sinks, sustained by dispersers from interior populations,
328 spatially sorting for higher *D*. However, *D* was also elevated in non-sink populations close
to range limits (Fig. 6), so we tested for selection for *D* in marginal habitat at three
330 distances from the edge (see Appendix S2). We tracked the reproductive success of an
individual in a population defined by a typical model run under two scenarios: 1) all the
332 individual's offspring remain in the natal patch, vs. 2) all offspring disperse to adjacent
patches, half to a better patch and half to a worse patch. Offspring dispersal increased
334 fitness for individuals near the range limit, but not for those in marginal habitat closer to
the range centre (Fig. S2). Thus extremely poor conditions selected for dispersal even
336 though only $\frac{1}{2}$ (scenario above) or $\frac{1}{4}$ (in model simulations) of randomly dispersing
offspring land in a patch better than the natal patch.

338 *Shifting range, margin > 0*

Marginal edge habitat strongly affected dispersal evolution during range shifts. *D* increased
340 at the expanding edge, as seen in uniform habitat, but decreased at contracting edges (Fig.
4b) although it remained higher than in the range centre (Fig. 3a vs. b). Climate change
342 increased the unoccupied area at the leading edge, i.e. species did not fully track their
climatic range when habitat quality deteriorated towards range edges (Fig. 2). Further,
344 despite higher mean *D*, increasing the proportion of marginal habitat reduced the speed of
climate shift needed to cause extinction (Fig. 5).

346 **Local adaptation to climate**

Stable range

348 Local adaptation favoured *H*-genotypes that stayed close to their climate optima. Under
stable conditions this penalized dispersal (Fig. 3a vs. c). This was especially true as
350 genotype tolerance decreased (Fig. 3; *g.margin* = 1 vs. 25), and in the range centre under
low-*cost* scenarios, where *D* experienced little selection in single-genotype models (Fig. 3).

352 *Shifting range*

During climate change selection favored genotypes that tracked their climate optima. *D*
354 increased across the range (Fig. 2), whereas in single-genotype models central and trailing-
edge *D* only increased when *cost* ≈ 0 (Fig. 4a vs. c, b vs. d). Local adaptation thus increased
356 both spatial sorting for dispersal (non-dispersers get left behind) and selection for
dispersal (non-dispersers eventually have zero fitness) throughout the range. When
358 *g.margin* > 1 and *cost* > 0, *D* was still greatest at the leading edge, due to the additional
advantage of colonizing vacant habitat (Fig. 3d).

360

Discussion

362 We investigated the effects of fitness deterioration towards range limits, local adaptation to
climate, and directional climate change on dispersal evolution across a species' range. Our
364 model expands upon the few existing models of dispersal-evolution during range shifts
across environmental gradients (Phillips, 2012, Kubisch *et al.*, 2013a), by modelling the
366 contracting as well as expanding range limit, and by considering the effects of fitness
gradients toward range edges. Dispersal evolution, especially at contracting limits, was

368 profoundly affected by fitness declines toward range limits, which increased dispersal, and
by local adaptation to climate, which suppressed dispersal during climate stability but
370 generally increased dispersal throughout the range during climate change.

Deteriorating habitat quality is the primary theoretical explanation for range limits
372 (Sexton *et al.*, 2009) and underlies many in nature (Abeli *et al.*, 2013, Hargreaves *et al.*,
2014). Our model predicts dispersal will decline toward stable range limits when habitat
374 quality is uniform, as found previously (Gros *et al.*, 2006, Dytham, 2009), but increase
toward stable limits when habitat quality declines. Although higher dispersal at range
376 limits is often considered a signature of increased population turnover (e.g. Darling *et al.*,
2008), our result is consistent with previous, perhaps underappreciated, models of fitness
378 gradients imposed by birth rates (as in our model) and carrying capacity (Dytham, 2009,
Kubisch *et al.*, 2010, Kubisch *et al.*, 2011). In our model, increased dispersal towards poor-
380 quality, stable range margins was driven by three mechanisms. First, spatial sorting
increased dispersal in demographic sink habitats, as populations were maintained by
382 continual immigration of dispersers. Second, smaller realized population sizes resulted in
increased kin selection for dispersal to reduce competition among relatives (Fig. S1.4).
384 Finally, low fitness along a gradient caused a fitness asymmetry. Even though equal
numbers of offspring dispersed up and down the fitness gradient, dispersal was selected
386 for wherever fitness was so low that eventual extinction in the natal patch was likely. In
other words, getting any offspring into a better environment was a substantial fitness gain,
388 whereas sacrificing offspring to a worse environment was a negligible loss.

Higher dispersal at stable range limits could provide a 'head start' during range
390 shifts, but when it arises from sink dynamics may be counteracted by reduced offspring

quality or quantity (Angert *et al.*, 2011). Increasing the extent of sub-optimal habitat
392 increased dispersiveness in our model, but nevertheless reduced the speed of climate
change that caused extinction (Fig. 5), presumably due to reduced reproductive rates and
394 population sizes at range edges. Non-directional climate fluctuations during periods of
overall stability could also select for dispersal at range edges, as edge habitat is continually
396 lost and recolonized. Whether this occurs and might be more advantageous during range
shifts than selection from sink habitats deserves further exploration.

398 Many species' range limits are at least partially imposed by climate gradients that
will shift directionally under climate change (Parmesan, 2006, Klimeš & Doležal, 2010). We
400 use temperature gradients for illustration, as they contribute to many range limits (Sunday
et al., 2012), but other such gradients include precipitation (e.g. Burt & Holden, 2010) and
402 salinity (e.g. Suikkanen *et al.*, 2013). This is the first attempt to extend models of dispersal
evolution across fitness gradients to consider subsequent gradient shifts. At expanding
404 range edges, our prediction of increased dispersal is consistent with models of invasions
(e.g. Travis *et al.*, 2009, Kubisch *et al.*, 2010, Phillips, 2012). At contracting limits, climate
406 change degraded already poor-quality habitat, shifting populations further down the
fitness gradient. Although introducing poor quality edge-habitat selected for greater
408 dispersal (Fig. 3), further deterioration via climate change did not further increase
dispersal (Fig. 4); climate change simply overtook individuals at the contracting edge.

410 Local adaptation to climate affected dispersal throughout the range, selecting
against dispersal when climate was stable and for dispersal during range shifts. Local
412 adaptation to environmental gradients may be widespread in sessile organisms (Hereford,
2009), and has been found at range-wide scales (Griffith & Watson, 2005, Colautti &

414 Barrett, 2013). A previous model without dispersal evolution suggested local adaptation to
a shifting gradient could impede range shifts if cool-adapted individuals block the
416 expansion of warm-adapted genotypes (Atkins & Travis, 2010). Our model suggests that
local adaptation may have additional effects via its influence on dispersal. If local
418 adaptation selects against dispersal in stable environments, populations may start at a
dispersal disadvantage, especially if dispersal evolves slowly compared to the rate of
420 climate change, or if some dispersal variation is lost during periods of stability, akin to its
loss after long-distance colonization of islands (Cody & Overton, 1996). However, if
422 dispersal evolves freely, local adaptation may promote increasing dispersal throughout
shifting ranges. This could help maintain genetic diversity by reducing founder effects,
424 since central and trailing populations would also found new populations rather than being
left behind (Phillips *et al.*, 2010). Eventually, however, higher dispersal might overwhelm
426 local adaptation as genotypes mix and, in sexual species, interbreed.

Indeed, sexual reproduction can have profound and varied consequences for
428 dispersal evolution and local adaptation, depending on species' mating ecology. For
example, population genetic models show that strong inbreeding depression can select for
430 increased dispersal, but that the inbreeding-avoidance benefit of dispersal is eroded by
local adaptation and subsequent outbreeding depression (mating between distantly related
432 individuals that disrupts beneficial gene associations) (Auld & Rubio de Casas, 2012). At
rapidly expanding range limits, sex can impede evolution of increased dispersal if
434 outcrossers are unable to find mates, or enhance it via assortative mating of high-dispersal
individuals (see Hargreaves & Eckert, 2014 for a comprehensive review). In our model,

436 asexuality prevented the breakdown of local adaptation; in sexual species selection for
increased dispersal during range shifts could degrade local adaptation over time.

438 To impose range limits in our model and explore the effect of local adaptation on
dispersal rather than their relative importance in responding to environmental change, we
440 did not allow adaptation to conditions outside the species' original tolerance (i.e. no niche
expansion), nor rapid evolution in climate tolerance. Indeed, unless other constraints are
442 imposed, species with unrestricted local adaptation simply invade the entire simulated
landscape (Kubisch *et al.*, 2013a). Although these assumptions will not be universally true,
444 both are empirically justifiable. First, lack of genetic variation in a range-limiting trait is a
major hypothesis for the evolutionary maintenance of range limits ('genostasis'; Bradshaw,
446 1991). A scenario similar to that in our model could arise if a species expanded its range
via local adaptation of a range-limiting trait, until directional selection expended the trait's
448 genetic variation (Hoffmann & Blows, 1994). Examples of species with both climate-
constrained ranges and strong local adaptation to climate within the range (e.g. cocklebur
450 Griffith & Watson, 2005, Griffith & Watson, 2006, purple loosestrife, Colautti *et al.*, 2010,
Colautti & Barrett, 2013) demonstrate that such scenarios are biologically realistic,
452 although too few empirical tests exist to know how common they are. That climate change
often produces range contractions at warm edges further suggests that many species are
454 constrained in their ability to adapt to new climates (Thomas *et al.*, 2006, Bradshaw &
Holzapfel, 2008). In contrast, several studies have detected evolution of increased
456 dispersal ability at expanding range limits of plants (Cwynar & MacDonald, 1987, Monty &
Mahy, 2010) and animals (Niemela & Spence, 1999, Thomas *et al.*, 2001, Phillips *et al.*,
458 2006), suggesting that for some species at least, adaptation may proceed more quickly for

dispersal vs. climate tolerance. We also did not allow evolution in the breadth of climate
460 tolerance (*g.margin*). Both climate change and increasing dispersal might select for a more
generalist climate strategy, potentially breaking down local adaptation. If data on the
462 quantitative variation and heritability of dispersal and environmental tolerance could be
obtained, modelling their joint evolutionary response to climate change, including potential
464 feedbacks, would be a fascinating avenue for future work.

A primary goal of this research was to explore dispersal evolution at contracting
466 range limits, a topic rarely addressed to date. Without local adaptation to climate, range
contractions had little effect on dispersal, other than eliminating genotypes at the extreme
468 edge, bringing D slightly closer to central D values (Fig. 4). It would be interesting to
explore contractions across landscapes where habitat quantity (vs. quality) declines
470 toward range limits. Patchy habitat should select for dispersal if patches are ephemeral
and persistence reliant on repeated recolonization. However, if patches are stable, their
472 isolation might select against dispersal, as dispersers risk landing in unsuitable space
around isolated patches (Travis & Dytham, 1999). Environmental change that increases
474 temporal variability and extinction-recolonization dynamics might therefore select for
increased dispersal. In contrast, range contraction via permanent patch extinction (e.g.
476 habitat loss) could select against dispersal, creating an evolutionary trap for edge
populations. We also assumed that contracting range limits were limited by the same
478 gradient as leading limits, but this need not be so. For example, experimental evidence
suggests that species' low elevation and equatorial limits are more likely to be imposed by
480 inter-specific interactions than high elevation and polar limits (Hargreaves *et al.*, 2014).

This might mean that species have a buffer of climate tolerance that would delay
482 contractions, and resulting dispersal evolution, at warm limits (Sunday *et al.*, 2012).

Including habitat-quality gradients, local adaptation, and both leading and
484 contracting limits in models of range-wide dispersal evolution is an important step forward
in predicting how ranges might respond to climate change. Our model revealed substantial
486 effects of several often-ignored aspects of climate-induced range shifts, and makes three
empirically testable predictions about their signature on dispersal evolution: 1) dispersal
488 should be greater at the leading edge of shifting ranges than in the range centre or at the
trailing edge, 2) dispersal at the leading edge should be greater during range shifts than
490 before, and 3) given local adaptation to climate (or an environmental variable shifting with
climate, e.g. insects adapted to hosts whose ranges are shifting), dispersal should also
492 increase during range shifts at the range centre and contracting edge. The first pattern can
easily be tested by sampling populations across space (e.g. Simmons & Thomas, 2004), the
494 second and third require sampling populations through time (e.g. using museum or
herbarium specimens; Anderson *et al.*, 2008), and the third requires additional
496 experiments testing for local adaptation among populations.

Future theoretical advances will come from: exploring the potentially antagonistic
498 effects fitness declines might have on dispersal propensity vs. propagule pressure;
estimating the effects of range shifts and dispersal evolution on genetic diversity and local
500 adaptation; and exploring the circumstances under which pre-existing dispersal patterns
affect the speed and success of range shifts. Despite a surge of theory regarding dispersal
502 and species distributions, little empirical evidence exists to test theoretical predictions
(Hargreaves & Eckert, 2014). Data from natural systems on range-centre to range-edge

504 patterns in dispersal (e.g. Darling *et al.*, 2008), environmental gradients (e.g. habitat quality
and quantity), and local adaptation (e.g. Griffith & Watson, 2005, Samis & Eckert, 2009), as
506 well as the quantitative variation and adaptive potential of dispersal vs. environmental
tolerance are sorely needed to test whether existing models are on the right track.

508

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514

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632 **Supporting Information**

Additional Supporting Information may be found in the online version of this article:

634 **Appendix S1** Effect of altering σ_D , *avshift*, *K*, and kin selection

Appendix S2 Testing for fitness asymmetry at range limits methods

636 Model code available by request from the authors.

638 **Table 1** Typical parameter values. NA means there was no typical value for a given parameter as it was varied among model runs.

Parameter description	Symbol	Typical value
All models		
Rows of patches of suitable habitat	<i>nrow</i>	10
Columns of patches of suitable habitat (length of environmental gradient)	<i>ncol</i>	401
Patch-level carrying capacity	<i>K</i>	40
Maximum offspring per individual per generation	<i>R_{max}</i>	5
Mutation rate of dispersal probability, <i>D</i>	μ_D	0.05
Standard deviation of mutations in <i>D</i>	σ_D	0.05
Cost of dispersal (proportion of dispersers that die)	<i>cost</i>	NA
Columns across which fitness declines to 0 at each range edge	<i>margin</i>	NA
Mean columns of climate shift per generation during climate change phase	<i>avshift</i>	0.1
Models in which each genotype is locally adapted to a climate optimum (<i>H</i>)		
Columns from <i>H</i> across which genotype fitness declines to 0	<i>g.margin</i>	25
Mutation rate of <i>H</i>	μ_H	0.01
Standard deviation of mutations in <i>H</i>	σ_H	0.01

640 **Figure 1** Examples of range-wide fitness distributions for models with a single climate
 642 genotype (a-c), or many locally adapted climate genotypes (d). Ranges are $ncol$ (401)
 columns long, black lines show species-level fitness distributions, and grey areas indicate
 644 poor-quality habitat (relative fitness >0 but <1) defined by $margin$. (a) table-top fitness:
 uniform fitness across the environmental gradient ($margin = 0$). (b) trapezoid fitness: each
 646 range edge overlies 100 columns of declining habitat quality. (c) triangle fitness: all but the
 central column of the range is suboptimal habitat. (d) trapezoid species-level fitness as in
 648 (b) but with multiple genotypes (coloured lines), each adapted to a specific temperature
 defined by H . Genotype fitness declines to zero across $g.margin$ (50) columns on either
 650 side of H . For convenience only 13 genotypes are shown; in model runs every column from
 $g.margin + 1$ to $ncol - g.margin$ has a corresponding locally adapted H genotype.

652 **Figure 2** Six typical realizations showing evolution of dispersal propensity (D ; colour
 654 gradient) across a species' range during climate stability (left of dashed line) and
 subsequent directional climate change. Solid black lines denote the species' potential
 656 range, where fitness >0 , which is $ncol = 401$ columns long. The environmental gradient can
 be thought of as a north-south temperature gradient that warms, prompting a northward
 658 (upward) range shift. Left vs. right panels show slow vs. rapid rates of climate change
 ($avshift$). Top and middle panels show species with a single (plastic) climate genotype and
 660 compare uniform fitness vs. fitness that declines across $margin = 100$ columns toward each
 range limit. Bottom panels show a species comprised of many genotypes locally adapted to
 662 the environmental gradient, each with a tolerance of $2 * g.margin + 1 = 51$ columns. Dispersal
 $cost = 0.05$; other parameters are as in Table 1.

664

Figure 3 Effects of poor-quality edge habitat (*margin*), climate change, and local-
 666 adaptation, on the evolution of dispersal probability (*D*) for a variety of dispersal costs
 (*cost*), at *avshift* = 0.1. (a & b) models consider a single climate genotype; (c & d) models
 668 have multiple genotypes locally-adapted to climate. Leftmost panels show the species-
 level fitness distribution considered in each case; the *margin* = 0 single-genotype model is
 670 approximated by *margin* = *g.margin* = 1 under local adaptation to prevent immediate
 extinction under climate change. Subsequent panels show mean evolved *D* after 500
 672 generations of stable conditions (a & c), followed by 1000 generations of directional
 climate change and corresponding range shift (b & d). Each line shows *D* averaged across
 674 10 model runs per *cost*, excluding columns occupied in ≤ 5 runs (increased variation from
 averaging over fewer runs sometimes obscured patterns at the extreme edges).

676 **Figure 4** Effect of climate change and associated range shift on dispersal probability *D*
 across the range at five dispersal costs in four models. Points show the evolution in *D*
 678 caused by climate change (*D* after 1000 generations of range shift – *D* in generation before
 range shift) in each location along the gradient for 10 model runs per panel. Pink indicates
 680 high-quality habitat ($w = 1$), teal indicates suboptimal habitat ($w < 1$) defined by *margin*.
 (a) and (b) are single climate-genotype models with ‘table-top’ and ‘trapezoid’ fitness
 682 distributions, respectively. (c) and (d) model many locally-adapted (LA) climate genotypes
 with ‘near-table top’ and ‘trapezoid’ fitness distributions, respectively. Genotype fitness
 684 declines over 1 and 25 columns (*g.margin*) in panels c and d, respectively. Black line and
 grey shading show mean \pm 95% CI based on 30 runs; areas where CI do not overlap the

686 reference line at 0 were deemed to have experienced significant D evolution following
 climate change. The environmental gradient is $ncol = 401$ columns long.

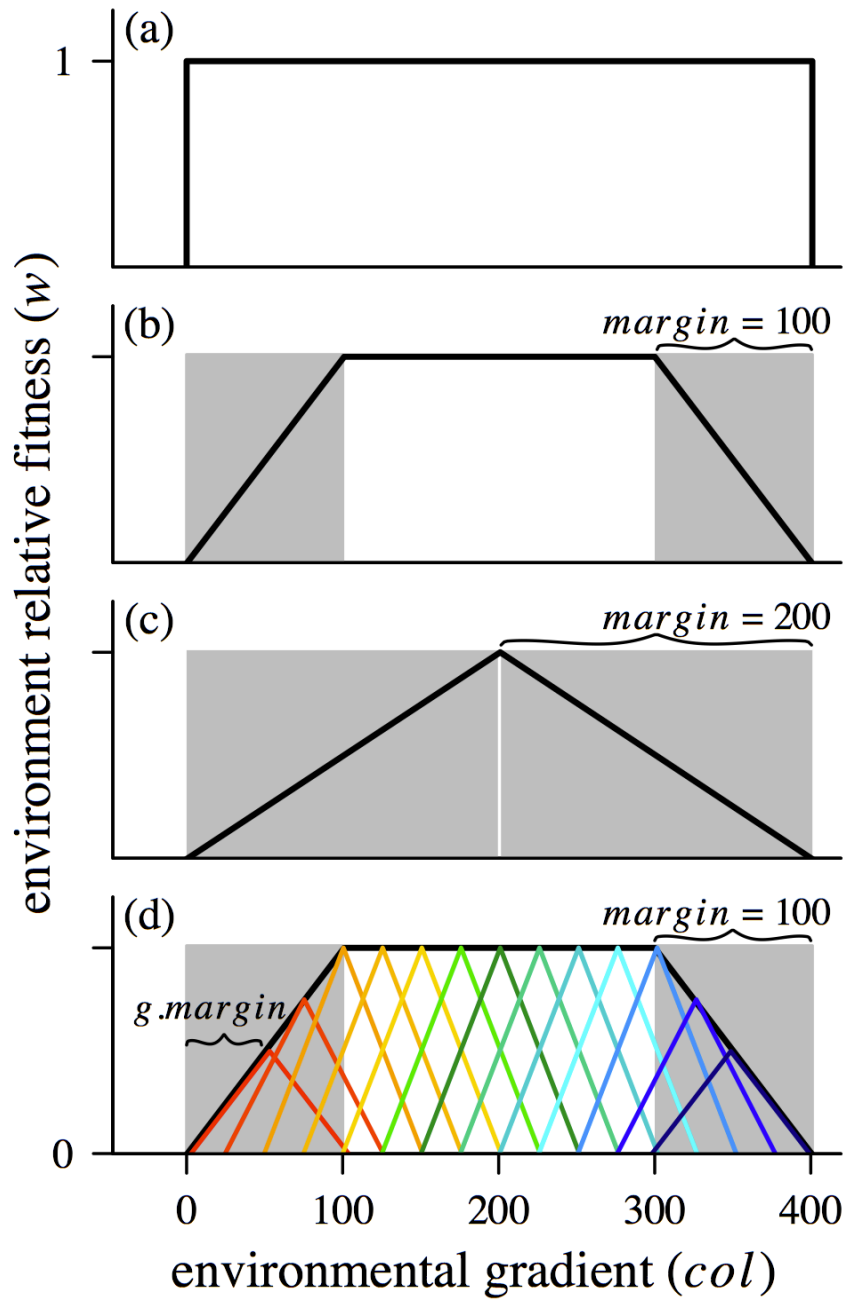
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Figure 5 The effect of poor-quality habitat at range edges (*margin*) on species extinction
 690 during climate change (range length = $ncol = 401$). Values of *avshift* resulting in 50%
 probability of extinction by the 1000th generation of climate change (following 500
 692 generations of stable climate) were estimated by logistic regression involving 200 model
 runs per data point (as organisms can only disperse 1 cell, any *avshift* > 1
 694 column/generation will eventually cause extinction given enough time). Other parameter
 values are as in Table 1.

696

Figure 6 Range-wide density (a) and dispersal probability (b) after 500 generations in a
 698 stable environment where habitat quality declines towards range limits ($margin = 100$, $cost$
 $= 0.05$, $avshift = 0.1$). Blue lines represent a dispersing population (dispersal distance = 1),
 700 grey lines represent a non-dispersing population (dispersal distance = 0). α indicates
 regions beyond the range where fitness is 0. β indicates regions where stochasticity is
 702 expected to cause extinction in the absence of dispersers from adjacent source populations
 (demographic sinks); when the population is capable of dispersal (blue line) β regions are
 704 occupied by high dispersing individuals. γ indicates regions of marginal habitat where
 fitness asymmetry selects for high dispersal. δ indicates the region of maximum fitness
 706 where high dispersal is no longer beneficial.

708



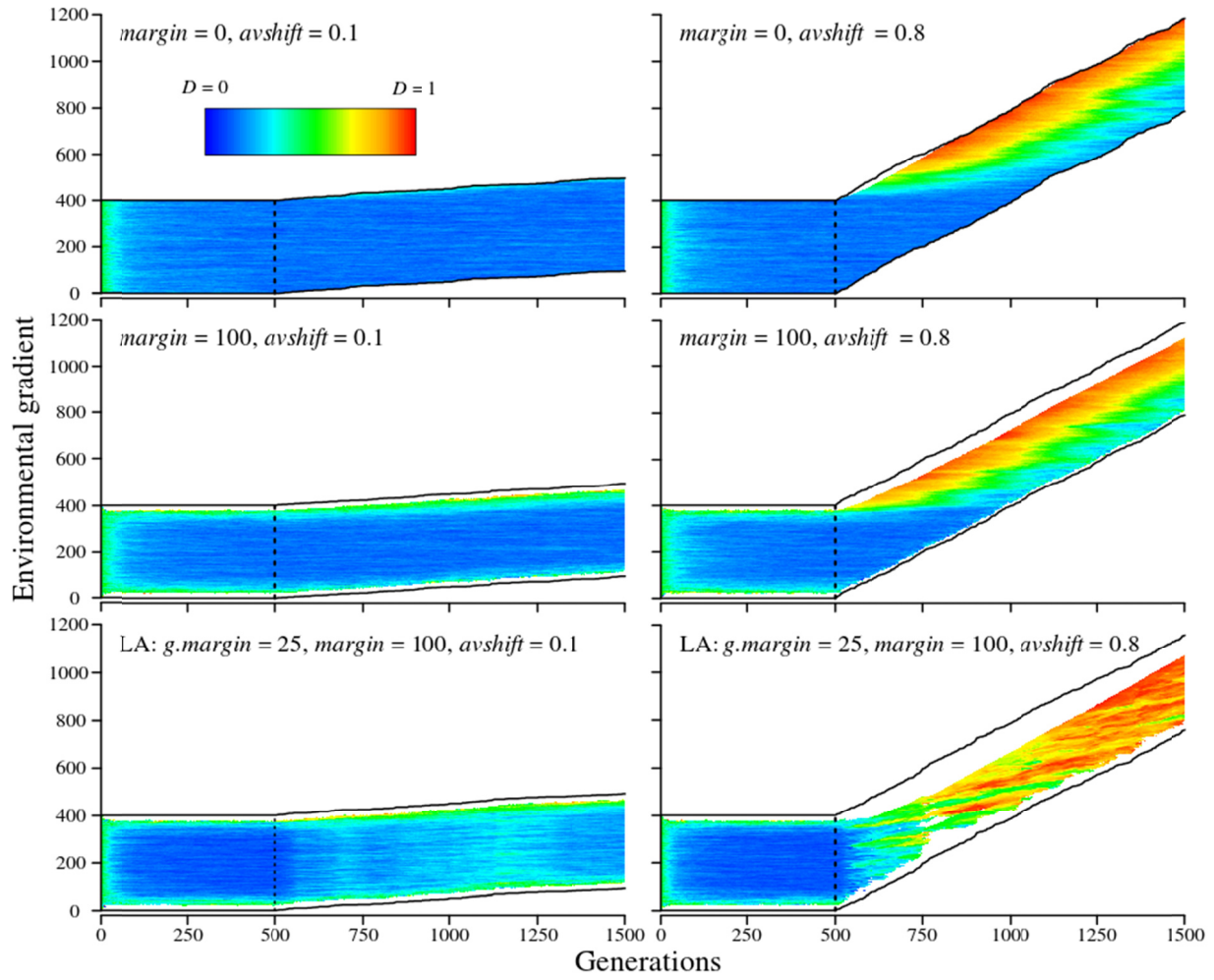
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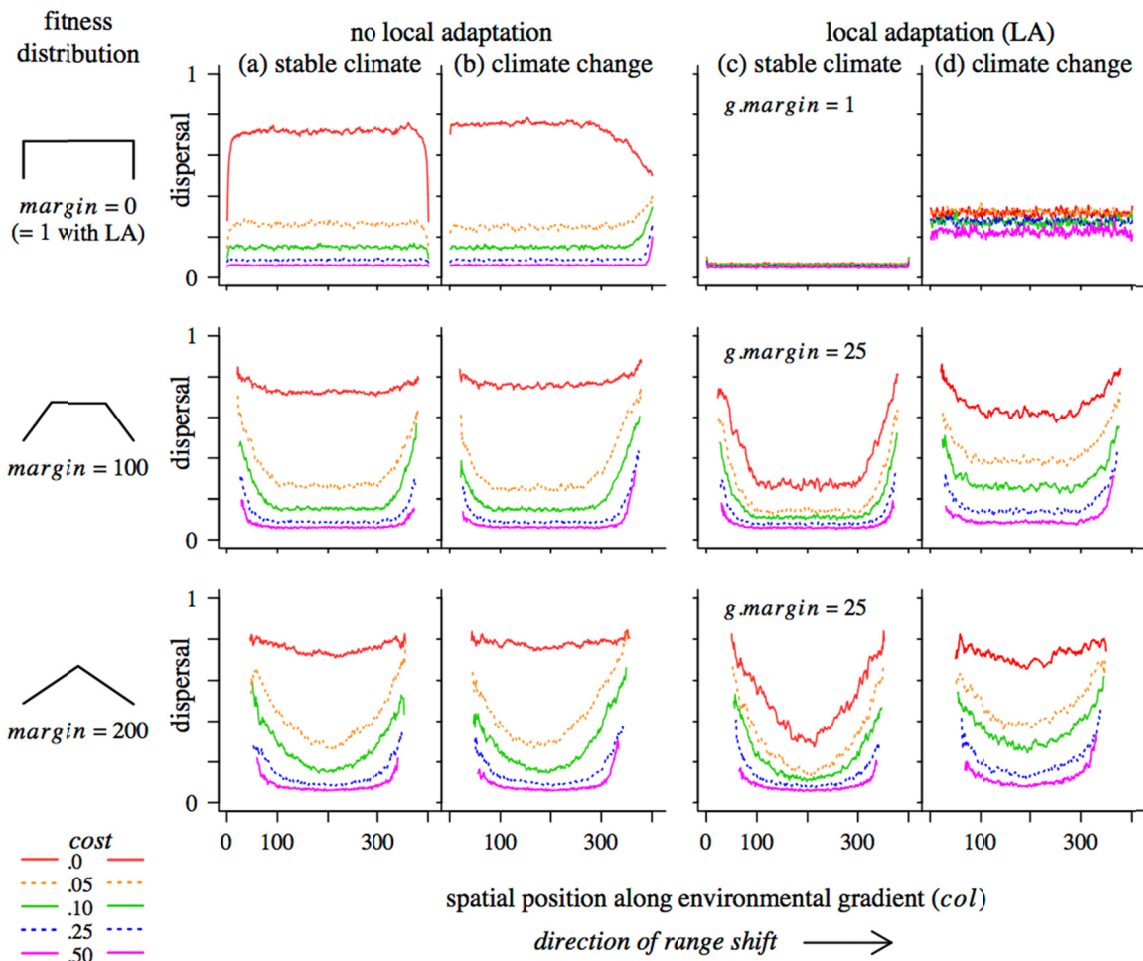
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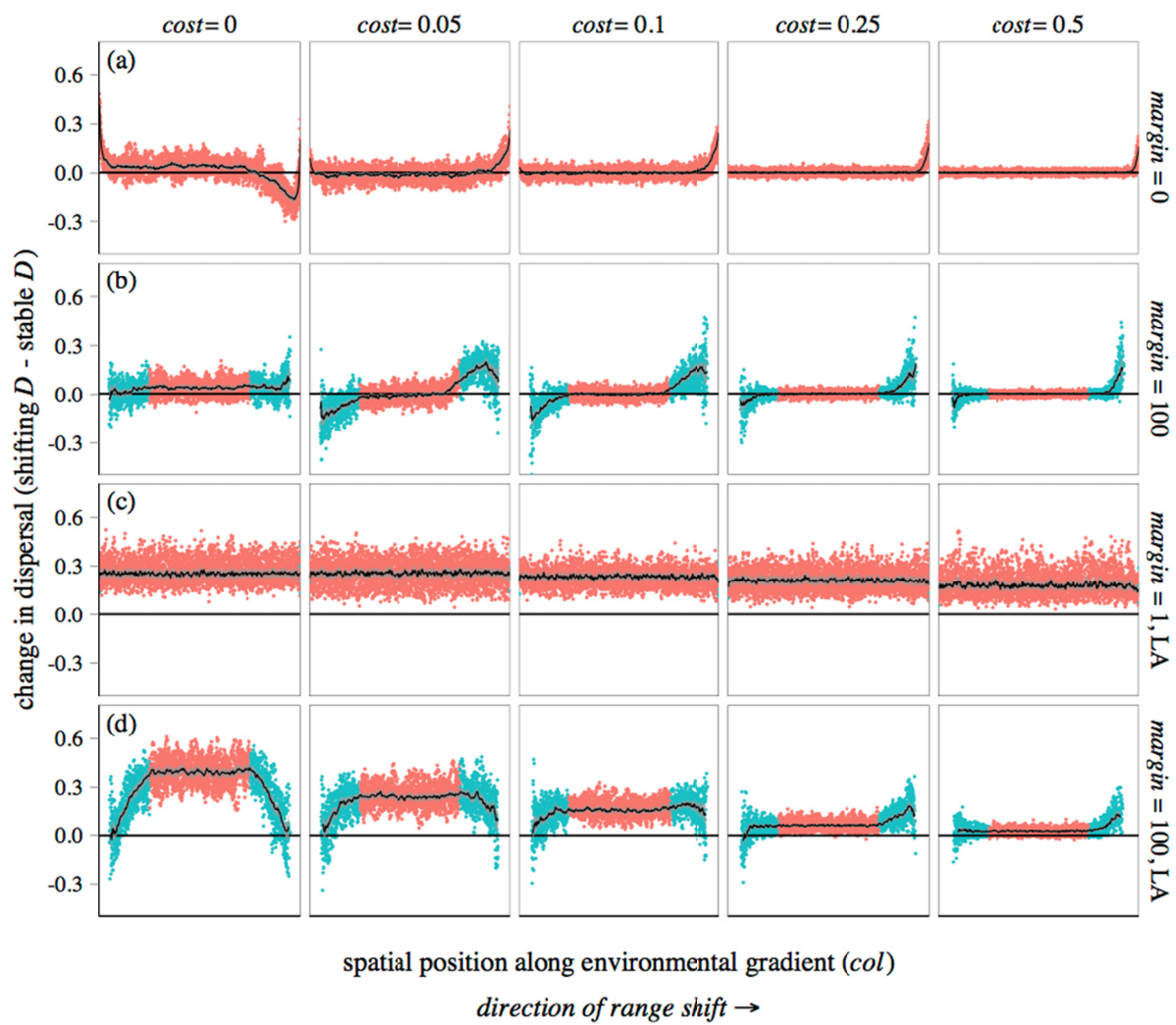
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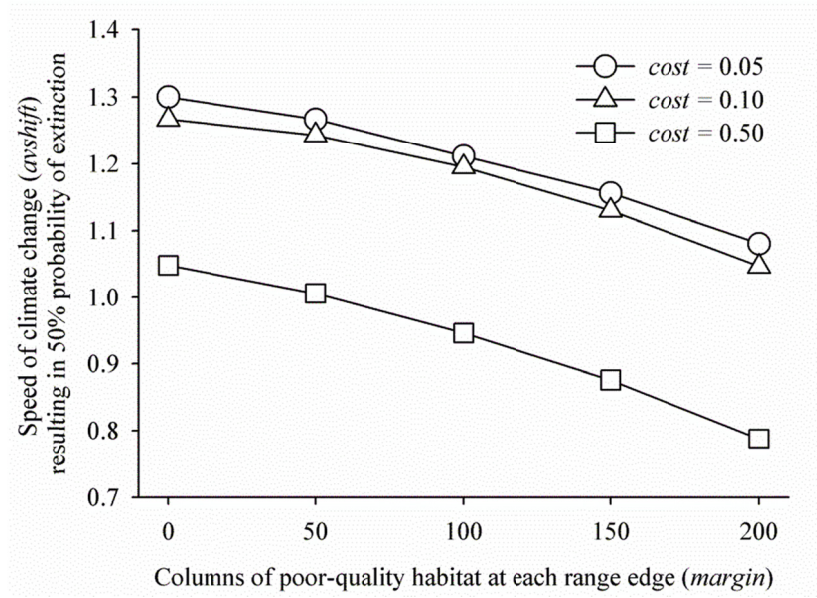
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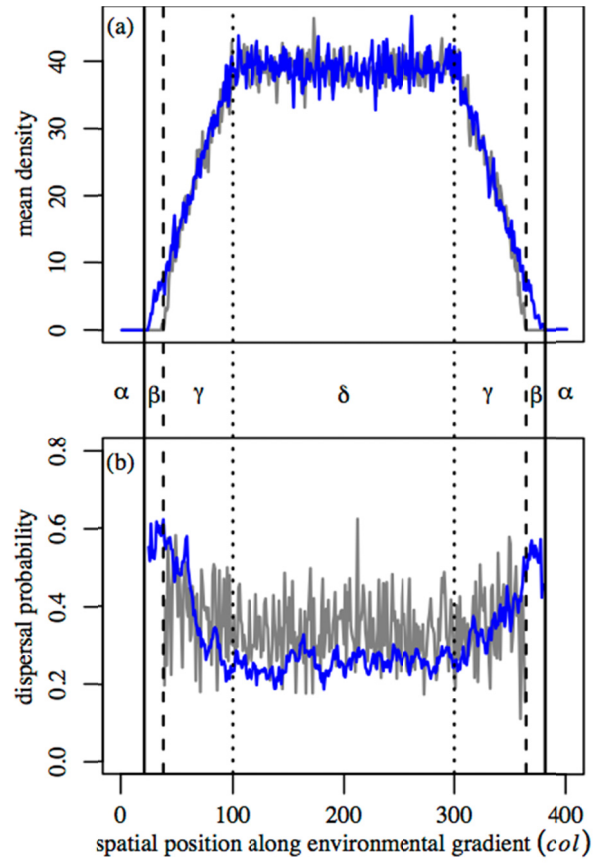
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Online Supporting Information for

Hargreaves, Bailey & Laird. 2015. Fitness declines toward range limits and local adaptation to climate affect dispersal evolution during climate-induced range shifts.

Journal of Evolutionary Biology.

Appendix S1: Effect of altering σ_D , $avshift$, K and kin selection.

Most realizations presented in the main manuscript use a rate of mutation in D (dispersal propensity) of $\sigma_D = 0.05$, carrying capacity of $K = 40$, and an average rate of climate change of $avshift = 0.1$ columns per generation. Further, all results include the effect of both individual selection (benefits accrue to the disperser) and kin selection (benefits accrue to the kin that remain behind due to density reduction, rather than to the disperser) on dispersal evolution. Here we explore the effects of modifying these components. Fig. S1.1 shows the effect of a lower mutation rate $\sigma_D = 0.005$; Fig. S1.2 shows the effect of both slower and faster rates of climate change for single-climate genotype scenarios, $avshift = 0.01, 0.05, \text{ and } 0.2$; Fig. S1.3 shows the effect of a lower carrying capacity $K = 10$; and Fig. S1.4 shows the effect of eliminating kin structuring before dispersal by randomly shuffling individuals among rows before each dispersal event. Each of these figures is directly comparable to (i.e. retains all other parameter values used in) Fig. 3 in the main text.

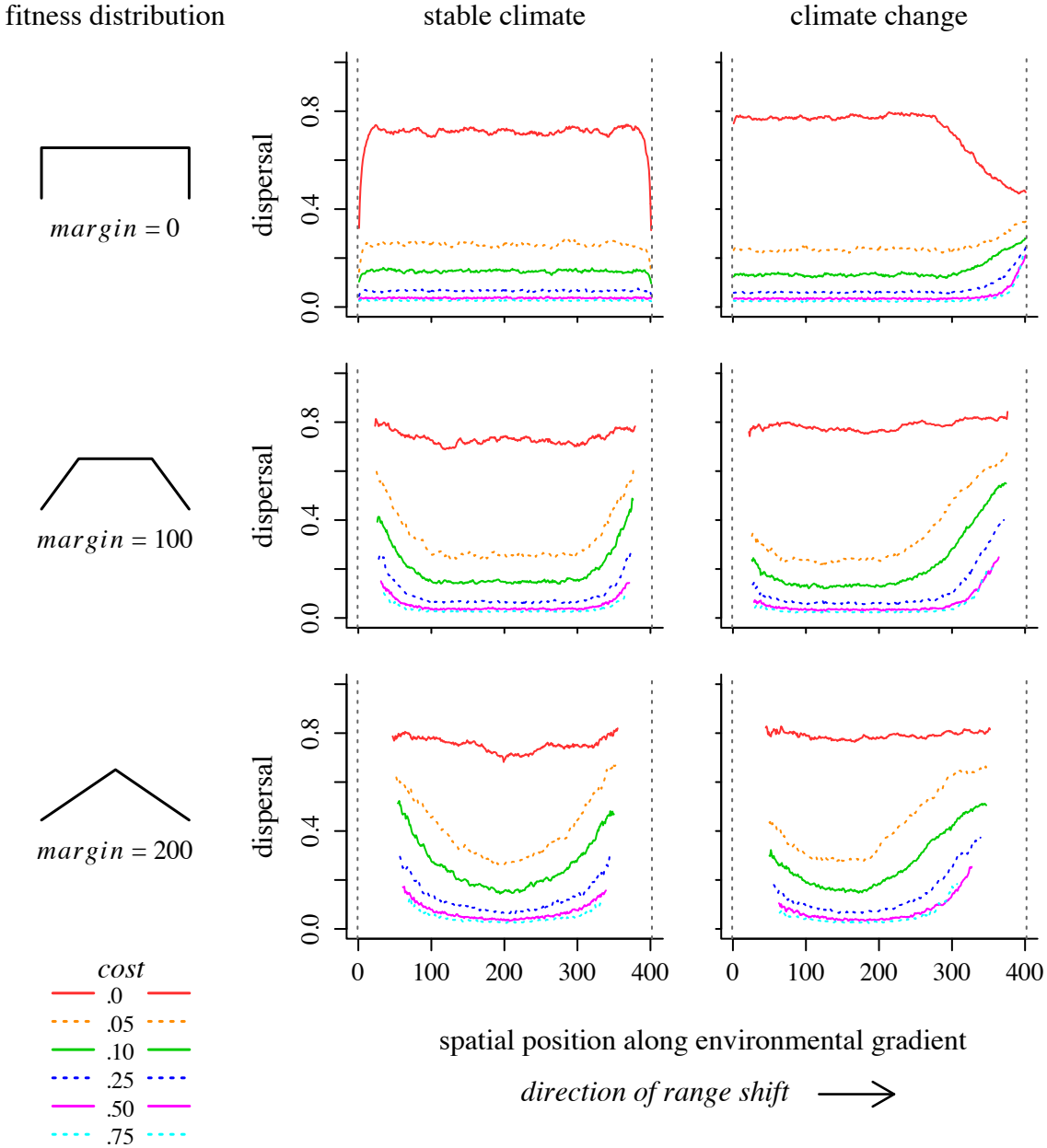


Fig. S1.1 Effect of a lower mutation rate on the evolution of dispersal probability (D) during climate stability and subsequent climate change ($avshift = 0.1$) for various amounts of poor-quality edge habitat ($margin$). Model realizations are for a single climate genotype as in Fig. 3a & b, but use $\sigma_D = 0.005$ instead of 0.05 and have an extra level of dispersal cost (0.75). Dashed lines show absolute range limits beyond which fitness = 0.

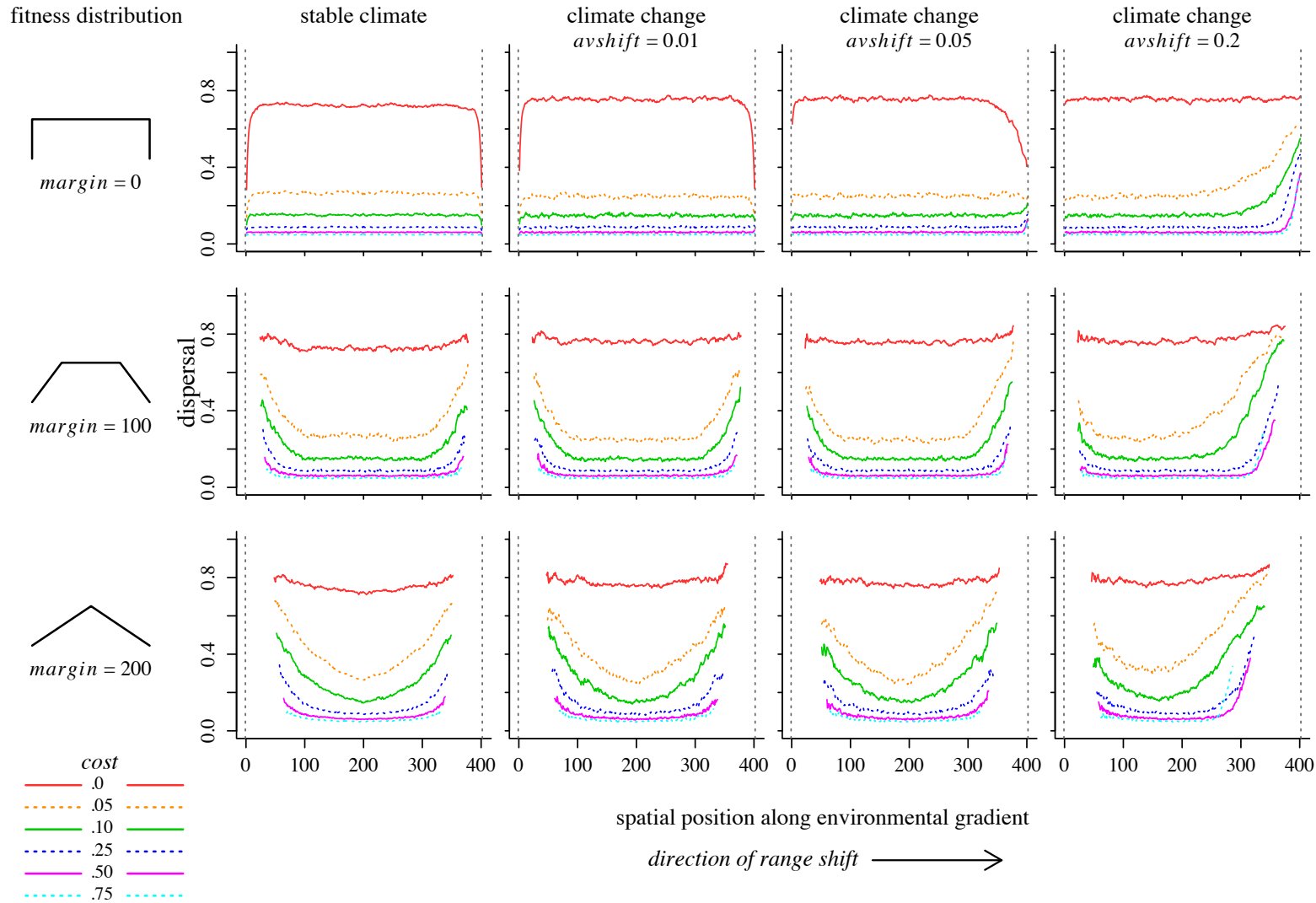


Fig. S1.2 Effect of the rate of climate change (*avshift*) on the evolution of dispersal probability for varying amounts of poor-quality edge habitat (*margin*). Model realizations are directly comparable (i.e. use same parameters except for *avshift*) to those in Fig. 3 (which use *avshift* = 0.1), and have an extra level of dispersal *cost* (0.75).

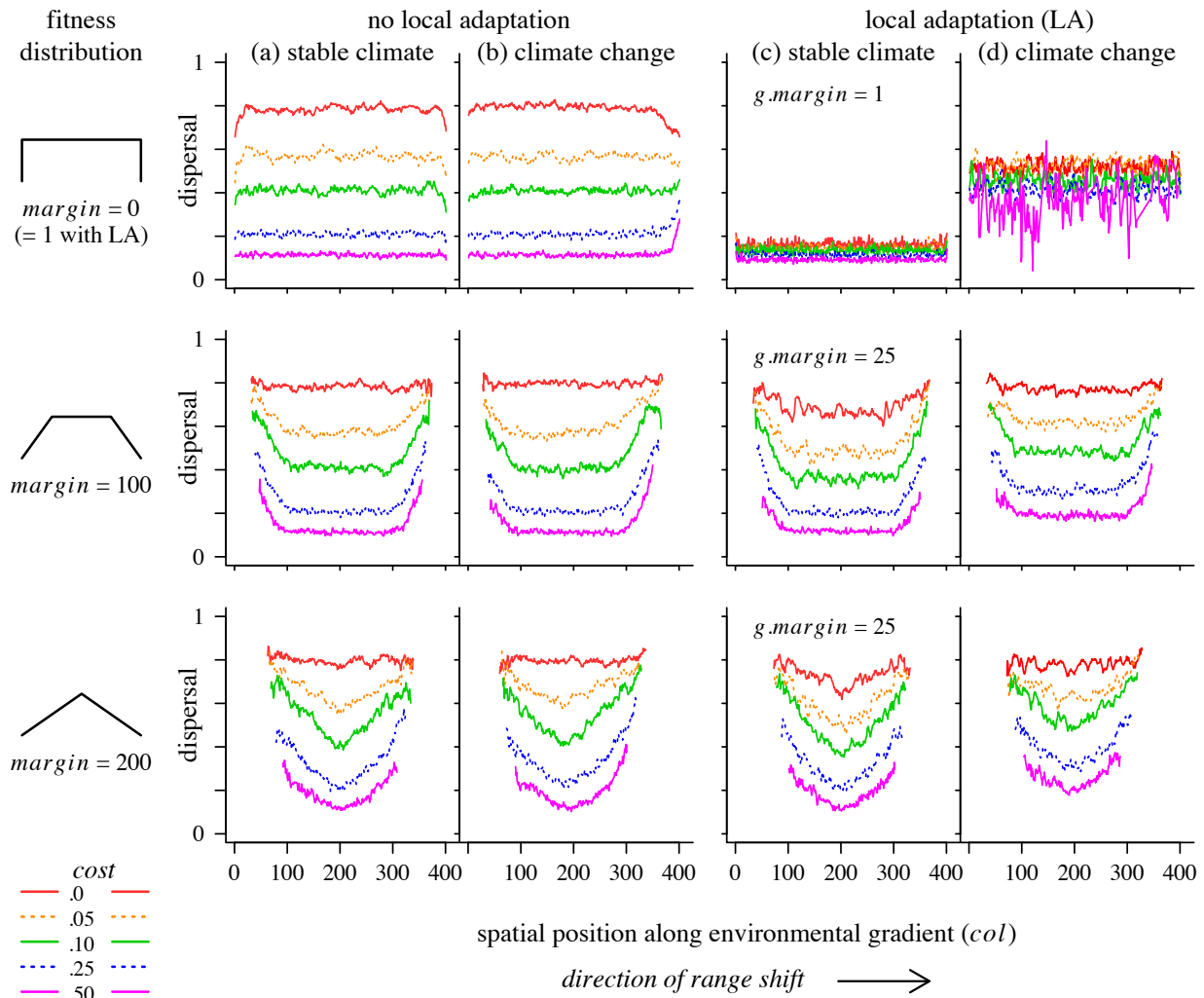


Fig. S1.3 Effect of a lower carrying capacity on the evolution of dispersal probability (D) during stable climates and subsequent climate change ($avshift = 0.1$) for various amounts of poor-quality edge habitat ($margin$). Model realizations are as in Fig. 3, but use $K = 10$ instead of 40; lower K generally increases D (compare to Fig. 3).

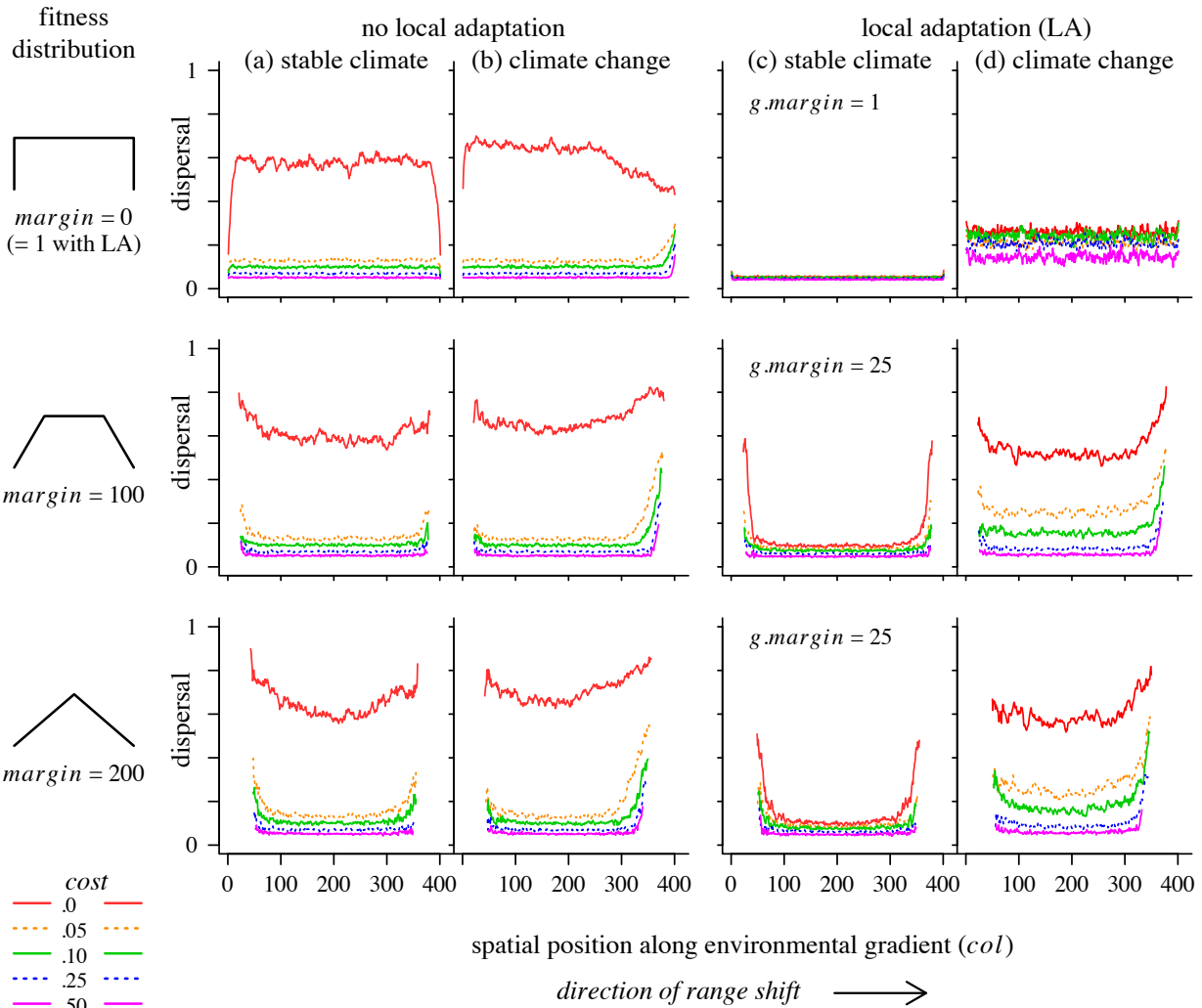


Fig. S1.4 Range-wide evolved dispersal probability (D) arising from individual selection only. Kin selection was eliminated using the method of Poethke *et al.* (2007), homogenizing kin structure within each *col* before every dispersal event. Rows show effect of poor-quality edge habitat (*margin*), columns show effect of climate change and local adaptation to the climate gradient. Model realizations use the same parameters as those in Fig. 3, thus differences between the figures show the effect of kin selection. Eliminating kin selection reduces D (i.e. D in Fig. S1.4 are generally lower than those in Fig. 3).

Appendix S2: Testing for fitness asymmetry at range limits methods

We tested for a fitness asymmetry in dispersal strategy near range edges using a simplified scenario that calculated the expected reproductive success of a single individual over two generations under two contrasting scenarios: 1) all the individual's offspring remained in the natal patch, and 2) all offspring moved into adjacent patches, half to a better patch and half to a worse patch. As we were only interested in tracking the outcome of a single individual, we simplified by holding the rest of the population constant, in both the number of individuals and their position, over the two generations for which reproductive success was tracked. The spatial distribution of that fixed surrounding population was taken from a typical full simulation run for 500 generations in a habitat where fitness declines towards range edges ($margin = 100$). To estimate the individual's reproductive success, we calculated the expected number of offspring (λ) using equation 2 from the full simulation model. For scenario 1 (no dispersal), offspring were placed in the same spatial location from which the parent individual originated and the expected number of offspring originating from the first generation offspring was calculated. Total reproductive success was calculated as the combined total of all offspring from two generations of reproduction. Scenario 2 was calculated similarly, but instead of placing offspring in the natal location, half were placed one cell to the left of the parent location and half one cell to the right. For both dispersal scenarios, an individual's expected total reproductive success was calculated for 10 locations in optimal habitat (optimal), 10 locations in the middle of the marginal habitat (marginal), and 10 locations at the edge of the habitable range (range limit) (Fig. S2.1).

At the range limit, reproductive success is greater for the scenario where offspring disperse compared to the scenario where offspring do not disperse (Fig S2.1). While a trend for

the benefit of having dispersing offspring is also seen in other parts of the range, the effect size is much smaller (e.g. in marginal habitat) or negligible (e.g. in optimal habitat). This clear effect of dispersing offspring close to the range limit indicates that the benefits gained by the offspring that disperse into better-quality habitat outweigh the fitness losses experienced by the other half of offspring that disperse into worse habitat – a fitness asymmetry.

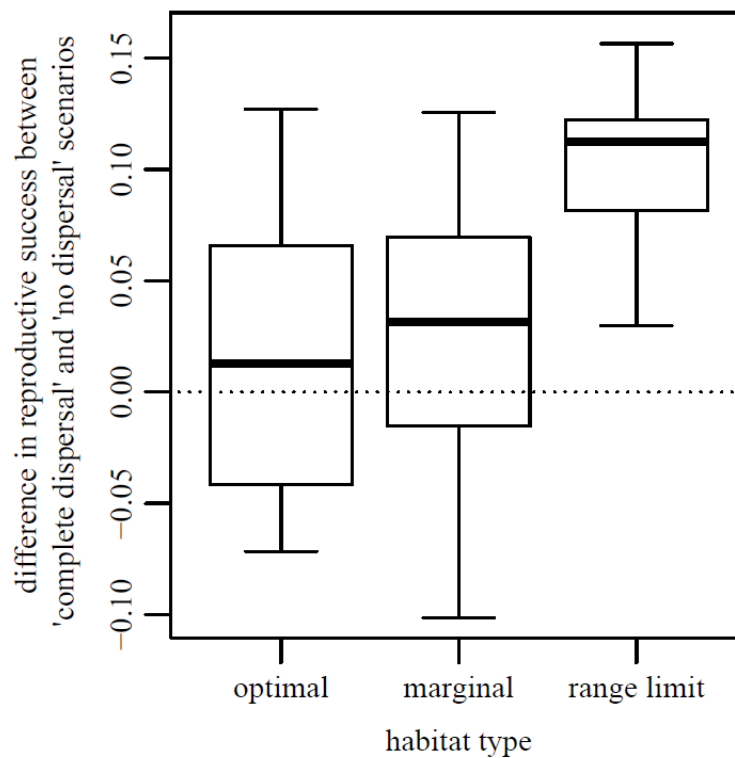


Fig. S2.1 Differences in the total reproductive success of individuals with dispersing offspring compared to individuals whose offspring all remain at their natal location. Data are grouped by habitat type. Bold lines indicate the medians, the edges of the boxes indicate the upper and lower quartiles, and “whiskers” indicate the most extreme values (N=10 for each habitat type).