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

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Abstract

Dispersal ability will largely determine whether species track their climatic niches during climate change, a process especially important for populations at contracting (low-latitude/low-elevation) range limits that otherwise risk extinction. We investigate whether dispersal evolution at contracting range limits is facilitated by two processes that potentially enable edge populations to experience and adjust to the effects of climate deterioration before they cause extinction: a) climate-induced fitness declines toward 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-based model. We compare range-wide dispersal evolution during climate stability vs. directional climate change, with uniform fitness vs. fitness that declines toward range 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 uniform, but increased when fitness declined toward RLs, due to highly dispersive genotypes maintaining sink populations at RLs, increased kin selection in smaller 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 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 against dispersal under stable climates but for increased dispersal throughout shifting ranges, compared to cases without local adaptation. Dispersal increased at expanding RLs in most scenarios, but only increased at the range centre and contracting RLs given local adaptation to climate.
Keywords: dispersal evolution, range shift, climate change, local adaptation, individual-based simulation model, range contraction, fitness gradient, sink populations

Introduction

Modern-day climate change is already prompting widespread range shifts, through 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 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 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 among populations (Cwynar & MacDonald, 1987, Cody & Overton, 1996) and across species’ ranges (Hargreaves & Eckert, 2014). Loss of low-dispersal populations during 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 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 contractions (Hampe & Petit, 2005). Loss of trailing edge populations could thus hinder species’ persistence in a warmer and increasingly variable world.

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

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), 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 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 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 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 reducing kin competition (Hamilton & May, 1977). Indeed, empirical studies of expanding range limits have found increased dispersal at the expanding edge vs. range centre (Thomas et al., 2001, Phillips et al., 2006, Monty & Mahy, 2010).

Most models of dispersal evolution at non-equilibrium range limits consider biological invasions into unlimited and uniformly good habitat, rather than gradual expansions (or contractions) following directional climate change (Hargreaves & Eckert, 2014). Although climate-induced range shifts share some important features with invasions, namely spatial sorting, kin structuring, and competition escape that should 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 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. 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,
which might further constrain evolution of increased dispersal. Further, fitness declines can influence dispersal evolution at stable range limits (Dytham, 2009), and pre-existing 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 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 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 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, 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 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 unsuitable habitat (Simmons & Thomas, 2004). Selection against dispersal could create an ecological trap by preventing warm-edge populations from tracking their climate niche, causing their eventual extinction. However, given local adaptation to temperature, climate warming might select for increased dispersal throughout the range, as dispersive individuals from warmer regions outcompete non-dispersive individuals no longer adapted to local temperature conditions (Hargreaves & Eckert, 2014).

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 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 across a continuous environmental gradient (e.g. temperature changing with latitude or elevation), and the landscape is uniformly permeable to dispersers (no dispersal barriers). Reproductive success declines with increasing density, conferring a fitness advantage to individuals that colonize newly available habitat. We first consider two scenarios where all 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 ‘trapezoid’ to ‘triangle’ fitness distribution, with a plateau or peak of high fitness in the range centre and a linear fitness decline towards ranges edges (i.e. marginal-quality edge 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 plasticity compensates completely (scenario 1) or partially (scenario 2) for the temperature gradient within this tolerance. We then consider a third scenario: a species 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 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 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 constraints and the broad implications for range shifts under climate change.
Materials and Methods

Model landscape and growth dynamics
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 square patches arranged in \( n_{\text{row}} \) rows by \( n_{\text{col}} \) columns, where columns represented the axis of environmental variation. For simplicity we envision a temperature gradient, but the 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 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 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, left, and right), to which they were potentially connected by dispersal. Each patch had the carrying capacity \( K \). Initially, \( K \times n_{\text{row}} \times n_{\text{col}} \) individuals were assigned randomly to the \( n_{\text{row}} \times n_{\text{col}} \) patches, so that on average patches started at carrying capacity.

Individuals could produce \( R_{\text{max}} \) offspring per generation in the absence of 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 Poisson distribution with mean \( \lambda \). Reproduction was negatively density dependent. As in other models of dispersal evolution (Travis et al., 2009, Phillips, 2012), the offspring left by 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):
\[ \lambda = \frac{R_{\text{max}}}{1 + \frac{N}{K}(R_{\text{max}} - 1)} \]  

where \( \lambda \) 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.

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 \( \mu_D \) 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 \( \sigma_D \) (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).

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, \( \text{cost} \), 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.

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

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 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 starting point of other models (e.g. Dytham, 2009), facilitating comparison to previous work.

2) Single climate genotype, declining fitness towards range limits

To explore the effect of declining habitat quality toward range limits we specified a number 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 ≤ margin or col ≥ (ncol−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 individual’s position along the gradient (col):

\[ w = \frac{\text{col}}{\text{margin} + 1} \quad \text{or} \quad w = \frac{\text{ncol} - \text{col} + 1}{\text{margin} + 1} \]

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

\[ \lambda = wR_{\text{max}}/\left(1 + \frac{N}{K}(R_{\text{max}} - 1)\right) \]  \[\text{[2]}\]
Note that the realized carrying capacity will be less than $K$ in these marginal regions. Elsewhere (i.e. $\text{margin} < \text{col} < \text{ncol} - \text{margin} + 1$), $\omega = 1$. We explored different values of $\text{margin}$, creating fitness distributions ranging from table top ($\text{margin} = 0$) to triangular ($\text{margin} = (\text{ncol} - 1)/2$), with a variety of trapezoid-shaped distributions in between (Fig. 1).

3) Multiple locally-adapted climate genotypes

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 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 their temperature optimum. $H$-genotypes had triangular fitness distributions; maximum fitness was experienced in column $H$, from which fitness declined linearly across a number of columns defined by $g.\text{margin}$ (Fig. 1d). All $H$-genotypes had the same temperature tolerance breadth (the triangles’ base): $2(g.\text{margin}) + 1$. To achieve the fitness distribution shown in Fig. 1d, where no genotype’s tolerance is truncated by the species’ overall tolerance, we constrained $g.\text{margin}$ to be $\leq \text{margin}$ and modelled $H$ from $g.\text{margin} + 1$ to $n\text{col} - g.\text{margin}$ (Fig. 1d). Accordingly, if $g.\text{margin} < \text{margin}$ there were genotypes locally adapted to marginal temperatures (Fig. 1d). For genotypes adapted to regions of optimal fitness (i.e. $\text{margin} < H < \text{ncol} - \text{margin} + 1$), fitness declines away from $H$ were modelled by multiplying the expected number of offspring in eq. [1] for an individual in column $\text{col}$ by the genotype-relative fitness parameter $h$. 
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 throughout the range margin, as in Fig. 1d:

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

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 throughout the range margin, as in Fig. 1d:

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

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

$$\lambda_g = mhR_{max}/(1 + \frac{N}{K}(R_{max} - 1))$$

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 ($col < g\ margin + 1$, 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.

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 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 $\mu_H$, 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 $\sigma_H$ relative to $n_{col}$ (i.e. $\sigma_H = 0.01$ is 1% of $n_{col}$), and rounded to the nearest integer. To prevent endless range expansion, $H$-values beyond the species’ original tolerance were discarded and redrawn. In other words, we assume the species currently lacks sufficient genetic variation to adapt to climates beyond those in its current range (see Discussion).

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 extinction if $g_{.margin}$ was 0 (i.e. genotypes only survived at one location), so we approximated a table-top fitness distribution using $g_{.margin} = margin = 1$.

**Climate change**

Models were run for 1500 generations; 500 generations of stable climate to allow dispersal 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 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 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’ 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, so when fitness declined toward range limits climate change improved conditions at the leading edge, and worsened conditions at the contracting edge.
Model exploration and summarization

Our intent was to explore the effects of declining fitness toward range edges and pre-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 ($K, r, \mu_D, \sigma_D$) 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.

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 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 dispersal individuals were randomly redistributed among rows within columns (i.e. environments), while maintaining the size of each patch.

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 $D$ following climate change: $\Delta D = (\text{mean } D \text{ after climate change, generation 1500}) - (\text{mean } D \text{ in last generation of stable climate, generation 500})$.

Results

Several model components affected evolved dispersal probability ($D$) consistently across fitness scenarios. The highest $Ds$ from the initial distribution of 0 to 1 were lost by the end 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 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 persisted as the range shifted and previously leading-edge locations became more central. This ‘smearing’ effect increased as $avshift$ increased, or as dispersal mutation ($\mu_D$ or $\sigma_D$), $cost$, 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 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, 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), increased kin selection ($K = 10$; Fig. S1.3), or individual selection only (Fig. S1.4).

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

*Stable range, margin = 0*

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

*Shifting range, margin = 0*

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 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 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 (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 expanding edge cost scenarios seem to converge upon $D$ values that enabled individuals to keep up with climate change without overshooting the range.

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-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 (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 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 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 went extinct.

**Single climate genotype, declining fitness towards range limits**

*Stable range, margin > 0*

Introducing a fitness decline towards range limits reversed the range-wide dispersal 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 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).

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
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 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, 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 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 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 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 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.

**Shifting range, margin > 0**

Marginal edge habitat strongly affected dispersal evolution during range shifts. $D$ increased 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 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, despite higher mean $D$, increasing the proportion of marginal habitat reduced the speed of climate shift needed to cause extinction (Fig. 5).
Local adaptation to climate

Stable range

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 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).

Shifting range

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

Discussion

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

Deteriorating habitat quality is the primary theoretical explanation for range limits
(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
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
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
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-
quality, stable range margins was driven by three mechanisms. First, spatial sorting
increased dispersal in demographic sink habitats, as populations were maintained by
continual immigration of dispersers. Second, smaller realized population sizes resulted in
increased kin selection for dispersal to reduce competition among relatives (Fig. S1.4).
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
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,
whereas sacrificing offspring to a worse environment was a negligible loss.

Higher dispersal at stable range limits could provide a ‘head start’ during range
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 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 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 lost and recolonized. Whether this occurs and might be more advantageous during range shifts than selection from sink habitats deserves further exploration.

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 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 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 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 change degraded already poor-quality habitat, shifting populations further down the fitness gradient. Although introducing poor quality edge-habitat selected for greater dispersal (Fig. 3), further deterioration via climate change did not further increase dispersal (Fig. 4); climate change simply overtook individuals at the contracting edge.

Local adaptation to climate affected dispersal throughout the range, selecting against dispersal when climate was stable and for dispersal during range shifts. Local adaptation to environmental gradients may be widespread in sessile organisms (Hereford, 2009), and has been found at range-wide scales (Griffith & Watson, 2005, Colautti &
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 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 adaptation selects against dispersal in stable environments, populations may start at a dispersal disadvantage, especially if dispersal evolves slowly compared to the rate of 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 dispersal evolves freely, local adaptation may promote increasing dispersal throughout shifting ranges. This could help maintain genetic diversity by reducing founder effects, 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 local adaptation as genotypes mix and, in sexual species, interbreed.

Indeed, sexual reproduction can have profound and varied consequences for dispersal evolution and local adaptation, depending on species' mating ecology. For example, population genetic models show that strong inbreeding depression can select for increased dispersal, but that the inbreeding-avoidance benefit of dispersal is eroded by local adaptation and subsequent outbreeding depression (mating between distantly related individuals that disrupts beneficial gene associations) (Auld & Rubio de Casas, 2012). At rapidly expanding range limits, sex can impede evolution of increased dispersal if 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,
asexuality prevented the breakdown of local adaptation; in sexual species selection for increased dispersal during range shifts could degrade local adaptation over time.

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 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 imposed, species with unrestricted local adaptation simply invade the entire simulated landscape (Kubisch et al., 2013a). Although these assumptions will not be universally true, 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, 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 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 Griffith & Watson, 2005, Griffith & Watson, 2006, purple loosestrife, Colautti et al., 2010, Colautti & Barrett, 2013) demonstrate that such scenarios are biologically realistic, 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 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 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., 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
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
quantitative variation and heritability of dispersal and environmental tolerance could be
obtained, modelling their joint evolutionary response to climate change, including potential
feedbacks, would be a fascinating avenue for future work.

A primary goal of this research was to explore dispersal evolution at contracting
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
dge, 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
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
isolation might select against dispersal, as dispersers risk landing in unsuitable space
around isolated patches (Travis & Dytham, 1999). Environmental change that increases
temporal variability and extinction-recolonization dynamics might therefore select for
increased dispersal. In contrast, range contraction via permanent patch extinction (e.g.
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
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
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 contractions, and resulting dispersal evolution, at warm limits (Sunday et al., 2012).

Including habitat-quality gradients, local adaptation, and both leading and 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 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 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 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 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 second and third require sampling populations through time (e.g. using museum or herbarium specimens; Anderson et al., 2008), and the third requires additional experiments testing for local adaptation among populations.

Future theoretical advances will come from: exploring the potentially antagonistic 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 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 and species distributions, little empirical evidence exists to test theoretical predictions (Hargreaves & Eckert, 2014). Data from natural systems on range-centre to range-edge
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 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.

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**References**


Niemela, J. & Spence, J. R. 1999. Dynamics of local expansion by an introduced species:


### Supporting Information

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

- **Appendix S1** Effect of altering $\sigma_D$, $avshift$, $K$, and kin selection
- **Appendix S2** Testing for fitness asymmetry at range limits methods

Model code available by request from the authors.
Table 1  Typical parameter values. NA means there was no typical value for a given parameter as it was varied among model runs.

<table>
<thead>
<tr>
<th>Parameter description</th>
<th>Symbol</th>
<th>Typical value</th>
</tr>
</thead>
<tbody>
<tr>
<td>All models</td>
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<td></td>
</tr>
<tr>
<td>Rows of patches of suitable habitat</td>
<td>nrow</td>
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</tr>
<tr>
<td>Columns of patches of suitable habitat (length of environmental gradient)</td>
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</tr>
<tr>
<td>Patch-level carrying capacity</td>
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</tr>
<tr>
<td>Mutation rate of dispersal probability, D</td>
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</tr>
<tr>
<td>Standard deviation of mutations in D</td>
<td>\sigma_D</td>
<td>0.05</td>
</tr>
<tr>
<td>Cost of dispersal (proportion of dispersers that die)</td>
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</tr>
<tr>
<td>Columns across which fitness declines to 0 at each range edge</td>
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</tr>
<tr>
<td>Mean columns of climate shift per generation during climate change phase</td>
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</tr>
<tr>
<td>Models in which each genotype is locally adapted to a climate optimum (H)</td>
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<td>Columns from H across which genotype fitness declines to 0</td>
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</tr>
<tr>
<td>Mutation rate of H</td>
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</tr>
<tr>
<td>Standard deviation of mutations in H</td>
<td>\sigma_H</td>
<td>0.01</td>
</tr>
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</table>
Figure 1 Examples of range-wide fitness distributions for models with a single climate 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 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 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 (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 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.

Figure 2 Six typical realizations showing evolution of dispersal propensity (D; colour gradient) across a species’ range during climate stability (left of dashed line) and subsequent directional climate change. Solid black lines denote the species’ potential 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 (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 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 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.
Figure 3 Effects of poor-quality edge habitat (margin), climate change, and local-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 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 approximated by margin = g.margin = 1 under local adaptation to prevent immediate extinction under climate change. Subsequent panels show mean evolved D after 500 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 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).

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 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 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 distributions, respectively. (c) and (d) model many locally-adapted (LA) climate genotypes with ‘near-table top’ and ‘trapezoid’ fitness distributions, respectively. Genotype fitness declines over 1 and 25 columns (g.margin) in panels c and d, respectively. Black line and grey shading show mean ± 95% CI based on 30 runs; areas where CI do not overlap the
reference line at 0 were deemed to have experienced significant $D$ evolution following climate change. The environmental gradient is $ncol = 401$ columns long.

**Figure 5** The effect of poor-quality habitat at range edges (margin) on species extinction 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 generations of stable climate) were estimated by logistic regression involving 200 model runs per data point (as organisms can only disperse 1 cell, any $avshift > 1$ column/generation will eventually cause extinction given enough time). Other parameter values are as in Table 1.

**Figure 6** Range-wide density (a) and dispersal probability (b) after 500 generations in a 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), grey lines represent a non-dispersing population (dispersal distance = 0). $\alpha$ indicates regions beyond the range where fitness is 0. $\beta$ indicates regions where stochasticity is expected to cause extinction in the absence of dispersers from adjacent source populations (demographic sinks); when the population is capable of dispersal (blue line) $\beta$ regions are occupied by high dispersing individuals. $\gamma$ indicates regions of marginal habitat where fitness asymmetry selects for high dispersal. $\delta$ indicates the region of maximum fitness where high dispersal is no longer beneficial.
Appendix S1: Effect of altering $\sigma_D$, $avshift$, $K$ 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, 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 \((\text{avshift} = 0.1)\) for various amounts of poor-quality edge habitat \((\text{margin})\). 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).