How Dispersal Evolution and Local Adaptation Affect the Range Dynamics of Species Lagging Behind Climate Change

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Abstract: As climate changes, species’ ability to spatially track suitable climate depends on their spread velocity, a function of their population growth and dispersal capacity. When climate changes faster than species can spread, the climate experienced at species’ expanding range edges may ameliorate as conditions become increasingly similar to those of the range core. When this boosts species’ growth rates, their spread accelerates. Here, we use simulations of a spreading population with an annual life history to explore how climatic amelioration interacts with dispersal evolution and local adaptation to determine the dynamics of spread. We found that depending on the timing of dispersal evolution, spread velocity can show contrasting trajectories, sometimes transiently exceeding the climate velocity before decelerating. Climatic amelioration can also accelerate the spread of populations composed of genotypes best adapted to local climatic conditions, but the exact dynamics depend on the pattern of climatic adaptation. We conclude that failing to account for demographic variation across climatic gradients can lead to erroneous conclusions about species’ capacity to spatially track suitable climate.

Keywords: climate gradient, demography, ecotypes, migration lag, population spread, range shifts.

Introduction

Global climate change is redistributing life on Earth, often pushing species’ ranges toward higher latitudes and elevations (Parmesan 2006; Chen et al. 2011; Pecl et al. 2017). Unless species can rapidly adapt to novel climates, their persistence will depend on their ability to track the moving geographic distribution of their suitable climates.

Moreover, the dynamics of species’ range shifts relative to each other will define the novel transient communities that characterize this era of rapid global change (Gilman et al. 2010; Alexander et al. 2016). The ecological process behind species’ range shifts is population spread, which is driven by the ability of a species’ propagules to move away from their parent (i.e., dispersal) and by the ability of those propagules to establish at a site and reproduce (i.e., demography). Understanding how these drivers of population spread are affected by climatic conditions constantly changing in space and time is key to forecasting biodiversity dynamics over the next decades.

Traditionally, most theory on population spread has been applied to understanding the advance of biological invasions (Skellam 1951; Andow et al. 1990), where populations often spread along either homogeneously favorable landscapes or spatially heterogeneous landscapes where the environmental template is temporally fixed. However, there are two problems with the application of current theory to understanding population spread during climate change. First, during climate change, regions of climate suitable for population growth are in constant directional movement (Zhou and Kot 2011; Harsch et al. 2014, 2017). Second, even within the climatically suitable regions, variation in environmental quality—be it continuous or not—is expected (Petry et al. 2016; Oldfather and Ackerly 2019), a situation with potentially large consequences for the dynamics of climate change–induced range shifts (Mustin et al. 2009).

For example, for species distributed along a climate gradient with strong effects on fecundity, a common expectation is that climatic suitability peaks at the core of a species’ range and declines toward the range edges (fig. 1A). Consequently, if a species spreads slower than the climate velocity (which we hereafter call “spread lag”), conditions experienced by individuals at the expanding range edge should become increasingly favorable, boosting fecundity and thereby accelerating spread (fig. 1B). If, however, by
cesses that can accelerate spread. However, how this mechanism interacts with other processes that can accelerate spread—dispersal evolution and local adaptation—has yet to be explored. Understanding the eco-evolutionary dynamics emerging from such interactions is critical to predicting the spread dynamics of species lagging behind climate change.

Evolutionary ecologists have long understood that if a population harbors heritable variation in dispersal capacity, spatial sorting of genotypes during spread can lead to the evolution of increased dispersal capacity at the expanding range edge and, as a result, accelerated spread (Phillips et al. 2008). We expect interactions between spread acceleration due to dispersal evolution and acceleration due to climatic amelioration. This is because climatic amelioration results from spread lags, and if dispersal evolves fast enough to prevent a substantial lag we could expect minimal climatic effects on spread dynamics. Also, because climatic amelioration is a consequence of spread lags, one might expect climatic amelioration to never accelerate spread beyond the climate velocity. By contrast, dispersal evolution, unconstrained by spread lags, might allow lagging populations to spread faster than the climate velocity, potentially leading to climatic deterioration that could slow spread.

The evolution of spreading populations may also depend on adaptation to their local environment (Leimu and Fischer 2008; Hereford 2009; Atkins and Travis 2010; Bocedi et al. 2013; Moran 2020), which potentially complicates acceleration due to climatic amelioration. Local adaptation may cause the optimal conditions for populations at range edges to differ from those of populations closer to the range core. In the extreme, leading edge populations locally adapted to a cooler climate, for example, might benefit little from warmer conditions. We might therefore expect less acceleration due to climatic amelioration with high degrees of local adaptation. We might further expect greater loss of genetic diversity during spread if locally adapted populations cannot evolve before their favored climate passes over them, ultimately contracting the species’ range (Atkins and Travis 2010; Moran 2020).

Here, we use theory to explore the dynamics of range shifts following spread lags for populations harboring heritable variation in either dispersal capacity or climatic niche. We examine how the interaction between dispersal evolution and climatic amelioration depends on the timing of evolution relative to the spread lag. We show that the interaction of dispersal evolution and varying demography following spread lags—each with straightforward consequences for population spread—can result in counterintuitive ecological dynamics. We then explore how the consequences of spread lags for range shift dynamics depend on the trade-offs underlying local climatic adaptation. We show that while local adaptation does not qualitatively change the effects of climatic amelioration on population spread, this masks complicated trajectories of individual genotypes that have consequences for

**Figure 1:** Why the spread velocity of species lagging behind climate change may accelerate. A. Fecundity often varies along climatic gradients, often thought to peak at the core of a species’ range and decline toward the range edges (the lollipops at the bottom of each panel represent the populations constituting the species’ range, and their sizes indicate their intrinsic fecundity; the black curves show how intrinsic fecundity varies across the climatic gradient). Hence, once the climatic gradient starts moving, the initial spread potential at the range edge should be low (the length of the gray arrow represents spread velocity). B. As the population lags behind its climate, the region of optimal conditions approaches the leading range edge, boosting potential spread. C. If this boost is insufficient to reach the climate velocity, conditions will deteriorate, spread will decelerate, and the population will decline toward extinction.
population persistence and the maintenance of genetic diversity during range shifts.

Methods

Modeling Framework

We modeled the spread of populations along a linear landscape using an integrodifference equation approach (Kot et al. 1996; Harsch et al. 2017). This approach assumes that space is continuous and time is discrete, with propagule production and dispersal occurring sequentially in each time step. Hence, integrodifference equations are particularly useful to model the spread of species in seasonal environments with distinct stages of growth and dispersal, such as annual plants, fungi, and many insects (Zhou and Kot 2011). Integrodifference equations have the following general form:

\[
N_{t+1}(x) = \int_{-\infty}^{\infty} k(x - y) g(N_t(y)) dy,
\]

where the population density at location \( x \) and time \( t + 1 \) is the sum of the propagules produced at all locations \( y \) during time \( t \) (given by the growth function \( g \)) multiplied by the fraction of propagules that disperse from \( y \) to \( x \) (given by the dispersal kernel \( k \)). One reason integrodifference equations are useful for modeling population spread is their flexibility to incorporate any kind of growth function \( g \) and dispersal kernel \( k \) (Kot et al. 1996).

We modeled the probability of propagules moving from location \( y \) to \( x \) with a two-sided negative exponential function:

\[
k(x - y) = \frac{d}{2} \exp(-d|x - y|),
\]

where the parameter \( d \) determines how fast the probability of dispersal decays with increasing distance and the mean dispersal distance is \( d^{-1} \). This function accurately describes the dispersal kernels of many species in which long-distance dispersal is rare and most propagules stay close to the parent (Willson 1993).

We modeled density-dependent production of propagules at each location with a Beverton-Holt competition model:

\[
g(N_t(y)) = \frac{\lambda N_t(y)}{1 + \alpha N_t(y)},
\]

in which the intrinsic per capita fecundity (\( \lambda \)) is reduced by competition with conspecific neighbors according to the coefficient \( \alpha \) (Hassell 1975; Watkinson 1980). Crucially, the intrinsic fecundity (\( \lambda \)) in our study is a Gaussian function of a climatic variable that changes linearly across the landscape, such as temperature along elevational or latitudinal gradients (fig. 2). Specifically, intrinsic fecundity at location \( y \) (\( \lambda(y) \)) is

\[
\lambda(y) = a \exp \left( -\frac{(y - \mu)^2}{2\sigma^2} \right),
\]

where \( \lambda \) reaches its maximum value (\( a \)) at the location of optimal climatic conditions (\( \mu \)) and decreases with distance from \( \mu \) according to the tolerance parameter \( \sigma \). Note that in our model \( \lambda \) includes the probability of successful establishment and survival until reproduction and could hence be conceived, more generally, as an intrinsic growth rate. This function is in line with traditional expectations of unimodal, symmetrical response curves of species performance along environmental gradients (Gauch and Whittaker 1972), although other types of curves are certainly common in nature (e.g., Minchin 1989).

Simulations

We simulated the spread of organisms with an annual life cycle while a climate gradient advanced through space at a constant rate. Space was represented as a continuous linear arrangement of patches. As described in the “Modeling Framework” section, in each patch seed production depended on local climate (fig. 2) and population density (eq. [3]). Offspring produced in each patch were redistributed across the landscape via a double-sided negative exponential kernel (eq. [2]). We treated population density as continuous and defined the range edge as the farthest location where population density was above a given density threshold (one individual per patch).

We started simulations with 100 individuals in each landscape patch, or with 10 individuals of each genotype for the simulations involving dispersal evolution and local adaptation (see below). These starting populations reproduced and dispersed for 20 years under a stable climate gradient, enough time for the location of range edges to stop changing. After this initial burn-in period, climate warmed at a constant rate throughout the landscape. We recorded the location of the expanding range edge every time step (farthest location where \( N_t(x) \geq 1 \)). The difference between the location of the expanding range edge at subsequent time steps was the spread velocity for that period.

To explore how the dynamics of spread velocity and their consequences for range contraction and population persistence depend on species’ ability to track climate change, we conducted simulations for species varying in their dispersal capacity (\( d \)). The simulations were conducted in R (R Core Development Team 2016), and the code is provided in section 1 of the supplemental PDF.1

1. Code that appears in The American Naturalist is provided as a convenience to readers. It has not necessarily been tested as part of peer review.
Evolution of Dispersal

To explore the consequences of dispersal evolution simultaneous to climatic amelioration, we modified the model so that the spreading population was composed of 10 asexually reproducing genotypes varying in dispersal capacity. In contrast, all 10 genotypes had identical intrinsic fecundity ($\lambda$) and competitive tolerance ($\alpha$). That is, all genotypes produced the same number of propagules in the absence of competitors, and this number decreased in the same way with increasing densities of all other genotypes.

Before climate started changing, we let the different genotypes establish and spread across the landscape for a certain number of years under constant climate. The longer this initial simulation period, the lower the frequency of high-dispersal genotypes at the time climate started changing, since evolution in a static range tends to select against dispersal (Hastings 1983; Levin et al. 2003). In nature, other factors can select for dispersal capacity in stationary ranges, such as local interannual environmental variability (Levin et al. 1984) and inbreeding avoidance (Bengtsson 1978). Thus, the length of the period of evolution in a static

Figure 2: A. In our models of population spread, per capita fecundity in the absence of competition (gray line) was a Gaussian function of a climatic variable that changed linearly along the landscape (e.g., temperature along an elevational or latitudinal gradient; dotted line in A). B–D. In our models incorporating local climate adaptation, the population was composed of genotypes with different fecundity responses to climate (colored lines in B–D). We explored three possible relationships between local adaptation and performance elsewhere in the range. First, genotypes differed in their preferred climate but have the same maximal fecundity and niche breadth (B). Second, genotypes adapted to extreme climates had lower maximal fecundity than those adapted to climate at the range core (C). Third, genotypes adapted to extreme climates had lower maximal fecundity and broader niches than genotypes adapted to the range core (D).
range in our simulations may be more generally interpreted as conditions with varying strength of selection against dispersal.

Local Adaptation

As we did for dispersal evolution, we examined the effects of local adaptation on range shifts following spread lags by modeling the dynamics of nine asexual genotypes. To allow for local adaptation, these genotypes varied in their fecundity response to the climate gradient but were identical otherwise. More specifically, each genotype exhibited a Gaussian-shaped fecundity response to climate (eq. [4]), with different genotypes differing in the position along the climate gradient at which their fecundity was maximal (fig. 2B–2D).

We examined the consequences of three possible relationships between maximal fecundity and performance elsewhere along the climate gradient. In the simplest case, each genotype differed in their most favored location along the gradient (μ in eq. [4]) but otherwise had the same climatic niche breadth and maximal fecundity (fig. 2B). But a frequent assumption is that adaptation to environments away from a global optimum, presumably found at the range core, involves a cost and is thus associated with lower maximal performance (Atkins and Travis 2010; Moran 2020). This relationship could emerge from trade-offs between performance at high temperatures and competitive ability at moderate temperatures (Willet 2010) or between frost tolerance and growth rates (Bucher et al. 2019). We thus considered the scenario where genotypes adapted to the more extreme climatic conditions have lower maximal fecundity than those adapted to the range core (fig. 2C). Specifically, the maximal fecundity of genotype i (aᵢ) was given by

\[
aᵢ = aₓₘₓ \cdot \exp \left( -\frac{(\bar{\mu} - \muᵢ)^2}{2} \right),
\]

where \(aₓₘₓ\) is the maximal fecundity when a genotype’s preferred climate (μᵢ) is equal to the climate at the original range core (\(\bar{\mu}\)). It is also common to expect a trade-off between maximum growth rates and niche breadth (Angert et al. 2011; Sexton et al. 2017). Therefore, we considered a third scenario in which genotypes adapted to more extreme climatic conditions had lower maximal fecundity (as in the second scenario) and wider climate niches than those adapted to the range core (fig. 2D), so that tolerance parameter of genotype i (σᵢ) was equal to

\[
\sigmaᵢ = 0.5 + \frac{(|\bar{\mu} - \muᵢ|)}{2}.
\]

Results

Depending on species’ dispersal capacity, population spread during climate change exhibited starkly different dynamics (fig. 3A). Species with long-distance dispersal (e.g., mean dispersal distance of 100 patches per year) spread rapidly even when fecundity at the range edge was low and thereby experienced minimal spread lag and acceleration. In contrast, species with poor dispersal lagged behind climate and experienced a period of ameliorating conditions at the expanding range edge and a consequent boost in spread velocity. Whereas this acceleration sufficed for some species to reach the climate velocity and persist indefinitely, in others dispersal capacity was too low to reach the climate velocity even when climatic conditions at the range edge were optimal. For these species, conditions at the range edge eventually started deteriorating and population spread slowed down. With ongoing climate change, these species inevitably became extinct, but the initial acceleration substantially delayed this outcome.

Even when population spread reached the climate velocity, differences in species’ dispersal capacity dictated how much climatic amelioration they required and, consequently, how much their ranges contracted (fig. 3B, 3C). For species requiring only minimal climatic amelioration at the range edge to reach the climate velocity, their eventual ranges experienced close to no contraction (fig. 3B). In contrast, a species requiring close to optimal climatic conditions to reach the climate velocity lost one-sixth of its former range width (fig. 3C).

By definition, ameliorating conditions at the expanding range edge of species lagging behind climate change can accelerate spread only to the point it reaches the climate velocity. Once this happens, the population and the climate move at the same rate, and thus conditions at the range edge remain constant. Therefore, no further spread acceleration is possible, and a species range neither contracts nor expands as long as the climate velocity remains constant. However, these dynamics can change if other mechanisms of spread acceleration, such as the evolution of dispersal, also operate.

We found that dispersal evolution in a population lagging behind climate change and otherwise headed to extinction enabled it to meet, and transiently exceed, the climate velocity (fig. 4A) as well as reexpand its range (compare fig. 4B with 4D). As in classic work on evolutionary rescue, the contraction and reexpansion of the species range caused a drop and subsequent rise in the total size of the evolving population (fig. 4C), in sharp contrast with the fate of the non-evolving population.

In contrast to the spread acceleration resulting only from climatic amelioration, simultaneous evolutionary
Figure 3: A, Spread velocity dynamics during climate change–induced range shifts of species differing only in dispersal capacity. The numbers above each line indicate the mean dispersal distance of each species. The dotted line indicates the velocity at which climate is moving across the landscape. Dispersal capacity determined whether a species could eventually reach the climate velocity and how much climatic amelioration was required for it, which in turn determined how much a species’ range contracted. B and C show the contracted ranges (solid gray) at time 50 of the climate change simulation for two species with different mean dispersal distance that reached the climate velocity (the hatched area shows the original extent of their ranges). Parameter values: number of patches = 20,000; initial climate gradient = 3–33; rate of climate change = 0.3 per year; intraspecific interaction coefficient (α) = 0.1; species’ optimal climate (μ) = 25; tolerance parameter (σ) = 1; intrinsic fecundity at the optimal climate (a) = 50.
acceleration was not bounded by the climate velocity (fig. 4A). But why did spread overshoot the climate velocity before declining thereafter? The answer stems from the fact that the population lagged behind climate change for several years before dispersal capacity significantly evolved at the leading range edge. Hence, by the time it had done so (i.e., when genotypes with the maximum dispersal capacity dominated the leading range edge), climatic conditions had significantly ameliorated. It was therefore the synchrony of greatly increased dispersal capacity and increasingly favorable climate (i.e., high fecundity) that enabled the population to exceed the climate velocity. However, spread exceeding the climate velocity eventually positioned the leading edge of the population in unsuitable climate, which decreased fecundity and slowed population spread until it equaled the climate velocity.

Hence, our results suggest the importance of the synchrony of ameliorated climatic conditions and evolution of dispersal at the expanding range edge for spread rates that exceed the climate velocity. Indeed, depending on the duration of evolution in a stationary range prior to climate change, a suite of different spread dynamics emerged as a

Figure 4: Effects of evolution of dispersal on the dynamics of spread velocity (A), range filling (B, D), and population size (C) of a species tracking climate change. Panels compare the dynamics of populations composed of 10 genotypes that either vary in their dispersal capacity and are hence able to evolve (black lines) or not (gray lines). Genotype mean dispersal capacity varied continuously from five patches (slowest genotype) to 25 patches (fastest genotype). The populations evolved for 4,500 years in a stationary range before climate started changing. Except for the number of patches in the landscape (10,000), the tolerance parameter (σ) = 0.5, and the initial climate gradient (0–50), parameter values were the same as in figure 3.
result of differences in the relative timing of spread lags and dispersal evolution (fig. 5). When dispersal evolved rapidly because of a high initial proportion of dispersive genotypes (fig. 5A, 5D, 5G), the climate only modestly ameliorated before the population reached the climate velocity, which happened relatively soon after the onset of climate change. When dispersal evolved more slowly because of a lower initial proportion of dispersive genotypes (fig. 5B, 5E, 5H), the climate at the expanding range edge markedly improved before the population could reach its maximum dispersal capacity. As in the simulations in figure 4, the synchrony of high dispersal and better demographic performance at the expanding range edge resulted in an overshooting of the climate velocity. Finally, with even slower dispersal evolution (fig. 5C, 5F, 5I), the population lagged behind climate change long enough for the

Figure 5: A–C, Spread velocity resulting from the evolution of dispersal capacity (D–F) and intrinsic fecundity changes at the expanding range edge (G–I). The dynamics of spread velocity depend on the relative timing of spread lags and dispersal evolution, exemplified in the different columns. The longer the population evolved in a stationary range before climate change (25, 4,500, and 8,000 years in the left, center, and right columns, respectively), the lower the initial frequency of dispersive genotypes and the longer it takes them to dominate the expanding range edge. Parameter values were the same as in figure 4.
region of optimal climate to move past the expanding range edge (fig. 5I). Only then did dispersal evolution accelerate spread beyond the climate velocity, allowing the population to approach and even expand beyond its region of optimal climate (fig. 5I).

Accelerated spread of species lagging behind climate change also occurred when populations were composed of genotypes adapted to local climatic conditions (fig. 6). However, the spread dynamics of the different genotypes varied strongly depending on the pattern of local adaptation. When genotypes differed only in their optimal climate (fig. 2B), with no consequence for maximal fecundity or breadth of climatic tolerance, the spread dynamics of the entire species (fig. 6A), and of the coldest-adapted genotype, resembled those of a single genotype without local adaptation (fig. 3). This seemingly counterintuitive result makes sense in light of the Gaussian relationship between climate and the fecundity of each genotype. Thus, despite the cold range edge being dominated by the coldest-adapted genotype, conditions there were still suboptimal prior to climate change.

However, the dynamics of spread velocity for the whole population mask more complicated dynamics for individual genotypes (fig. 6A). While the coldest-adapted genotype accelerated quickly following climatic amelioration, those behind it accelerated at a slower rate. All genotypes have identical dispersal capacity and intrinsic fecundity, and thus the difference in acceleration rates is due to the high density of competitors at the leading range edges of all but the coldest-adapted genotype (see videos 1, 2, and 3, available online and described in sec. 2 of the supplemental PDF). The higher initial population density of the coldest and warmest genotypes seen in figure 6D is also a result of the lower density of competitors in the extreme climates in which only they can thrive. The decline of genotypes adapted to intermediate climates (fig. 6D)

![Figure 6: Spread velocity (upper panels) and population (lower panels) dynamics of nine genotypes adapted to their local climate, assuming different relationships between local adaptation and performance elsewhere in the range (columns, depicted graphically in fig. 2). The gray line shows the dynamics of the population as a whole, while the colored lines represent each separate genotype (colors match genotypes in fig. 2). The length of the landscape was 5,000 patches, and the mean dispersal capacity was 10 patches. Other parameter values were the same as in figure 3.](image)
lowered population density at the leading range edge of warmer-adapted genotypes coincident with their optimal climate conditions at the leading edge, which accelerated their spread so much that they transiently exceeded the climate velocity (fig. 6D; videos 1, 2, and 3). Similar results emerged when genotypes adapted to the more extreme climates had lower maximum fecundity (as depicted in fig. 2C, with results in fig. 6B, 6E). The major difference is that because of the lower fecundity of the extreme-adapted genotypes, it takes longer for the coldest-adapted genotype to reach the climate velocity (fig. 6B), while the warm-adapted genotypes all become extinct. In fact, only the coldest-adapted and the modal genotype manage to persist (fig. 6E). When genotypes adapted to extreme climates had broader climate envelopes along with lower maximal fecundity, the broad envelope of the coldest-adapted genotype made it more effective at blocking the spread of warmer-adapted genotypes. Because of their higher maximal fecundity, warmer-adapted genotypes could have reached the climate velocity had competitor densities at their leading range edge been lower (e.g., as in the scenario in fig. 6B, 6E). Eventually, this can lead to the extinction of the entire species (note the declining population size of all genotypes after time 20 in fig. 6F).

The patterns of spread acceleration examined here depend on our assumption that species’ demography is a Gaussian function of a single climatic variable (or a suite of variables changing in synchrony). When we relaxed this assumption (results are in sec. 3 of the supplemental PDF), we found that while the general pattern of spread acceleration following climatic amelioration persists, different relationships between fecundity and the environment can produce a wide variety of spread velocity dynamics.

Discussion

The physiology and ecological interactions of most species depend on climate (Pörtner and Farrell 2008; Dell et al. 2011; McCluney et al. 2012; Gilbert et al. 2014). This often results in spatial variation in species performance along climatic gradients (e.g., Epstein et al. 1996; Petry et al. 2016). When a species range lags behind climate change (i.e., when it does not remain in constant equilibrium with its climate), the spatial variation in performance effectively moves across the species’ range, affecting the dynamics of population spread. As shown previously by Mustin et al. (2009), whenever intrinsic fecundity declines toward the edge of a species’ distribution along a climate gradient (hereafter, “species range”), lagging behind climate change can ameliorate conditions at the leading range edge, boost fecundity, and accelerate spread (fig. 3). Here, we show that climatic amelioration can interact with the evolutionary trajectories of dispersal capacity and climatic niche, resulting in complex population spread dynamics.

Our predictions about the interaction between climatic amelioration and dispersal evolution were supported by our results. For example, on their own, ameliorating conditions at the leading range edge enabled species to reach, but never exceed, the climate velocity because conditions ameliorated only for species that spread more slowly than the climate velocity. In contrast, when climatic amelioration happened in concert with dispersal evolution, overshooting the climate velocity and hence reexpanding a contracted range became possible. Interestingly, population spread exceeded the climate velocity only when maximum dispersal capacity at the range edge evolved slowly enough to temporarily coincide with substantial climatic amelioration following a spread lag (fig. 5). Consistent with our predictions, sufficiently slow dispersal evolution resulted in cycles of rising and falling fecundity at the range edge as the position of the population relative to its suitable climate fluctuated (fig. 5f). In contrast, when maximum dispersal evolved rapidly and was of sufficient magnitude, it provided enough acceleration to reach the climate velocity, and the population experienced a minimal spread lag (fig. 5a, 5d, 5g). If instead dispersal evolution had been fast but insufficient to reach the climate velocity, climatic amelioration subsequent to the dispersal evolution may have provided the additional acceleration required to reach the climate velocity. Either way, once the genotypes with the highest dispersal dominated the leading range edge, the subsequent dynamics would have followed those of the nonevolving populations shown in figure 3.

In our simulations, the rate of evolution depended only on the initial relative frequency of the genotypes varying in dispersal capacity, which depended on the length of the period of evolution in a stationary range prior to climate change. Classical theory suggests that dispersal capacity is selected against in stable ranges (Hastings 1983; Levin et al. 2003). Hence, fast-dispersing genotypes are likely to be rare and the evolution of dispersal capacity slow in regions where climate has been stable for long periods. In contrast, fast-dispersing genotypes are likely to be common in populations that more recently filled their potential ranges after a major climatic change, such as the end of the last glaciation (Cwynar and MacDonald 1987; Excoffier et al. 2009). Moreover, even within stable ranges, other factors—such as local extinction and colonization dynamics within metapopulations (Duckworth 2008; Hargreaves and Eckert 2014) and inbreeding avoidance (Bengtsson 1978)—can maintain genetic variation in dispersal strategies and partly explain the fast dispersal evolution observed in recent range shifts (Hill et al. 2011; Lindström et al. 2013). How multiple factors affecting
dispersal evolution interact during range shifts in response to climate change is an important question for future theory.

Populations are often adapted to local climatic conditions across a species range (Kawecki and Ebert 2004; King et al. 2020). Local adaptation can reduce the range-wide variation in demographic performance (Kawecki and Ebert 2004), thereby affecting spread rates following climate change lags (Mustin et al. 2009). When we simulated the spread of a population composed of genotypes with different climatic niches, we observed the same acceleration as in simulations of a single population without local adaptation. The reason is that despite varying in their optimal climates, each genotype’s fecundity was still a Gaussian function of climate, and prior to climate change the conditions at the leading range edge were still suboptimal despite the edge being dominated by the coldest-adapted genotype. While the spread dynamics of the coldest-adapted genotype followed those of a single population without local adaptation, other genotypes often failed to track climate change as a result of high competitor densities at their leading range edges. Only after intermediate genotypes had become extinct could warm-adapted genotypes catch up with climate change (fig. 6).

We further found that adaptation to local climates may have different effects on spread depending on the relationship between a genotype’s maximum fecundity and performance elsewhere in the range. It is common to assume that adaptation to extreme conditions means lower maximum performance (Atkins and Travis 2010; Moran 2020). For example, the survival of intertidal copepods at high, stressful temperatures trades off with their competitive ability at lower temperatures (Willett 2010), and the leaf frost resistance of herbaceous plants trades off with their growth rates (Bucher et al. 2019). Although such a trade-off affected spread in our simulations, it did not fundamentally change our findings relative to cases where species simply differed in their optimal climate (with no cost in terms of maximal fecundity). By contrast, we did find differing results when assuming a trade-off between maximum performance and niche breadth (fig. 6C, 6F; Angert et al. 2011; Sexton et al. 2017). When the coldest-adapted genotype also had wide thermal tolerance, its competitive effect on other genotypes was more severe, overall hampering population spread and leading to greater losses of genetic diversity. This blocking of the spread of otherwise well-adapted genotypes due to competitive interactions is akin to the boxcar effect described for interactions among different species tracking climate change (Urban et al. 2012). In sum, although local adaptation could complicate dynamics at the level of the genotype, in general it did not preclude spread acceleration due to climatic amelioration.

One important qualifier to these findings is that the genotypes in our simulations reproduce only asexually, and thus our populations were composed of individuals that possess discrete trait values passed on to offspring with perfect heritability. Sexual reproduction would result in more continuous variation in climatic niches and would allow for the replenishment of individuals with intermediate trait values if such individuals were being selected against. While models with sexual reproduction represent an avenue for future work, existing models of climate change–induced range shifts that account for local adaptation and include sexual reproduction often result in dynamics similar to those found here. These dynamics include competitive blocking by cold-adapted individuals (Atkins and Travis 2010) and the loss of centrally adapted genotypes (Bocedi et al. 2013).

Range-Wide Demographic Variation and Consequences for Climate Change–Induced Range Shifts

Our results suggest that field studies characterizing both demographic patterns along climatic gradients and how they have changed with recent climate change would be of great importance for understanding possible climate-driven acceleration. In one of the only examples of such work, Petry et al. (2016) showed that (1) the fecundity of the perennial herb Valeriana edulis decreases up its elevational range in the Rocky Mountains of Colorado because of an underlying moisture gradient (drier at higher elevations) and that (2) fecundity at the leading range edge has increased over the last three decades as a consequence of increasing aridification. This suggests that the spread of this population has been accelerating since recent climate change began and will likely continue to do so (Petry et al. 2016).

Notwithstanding this example, it remains unclear how often and to what extent changes in the spatial pattern of demography across species ranges lead to accelerated spread in nature. There is both theory (Brown 1984) and empirical evidence (e.g., Martinez-Meyer et al. 2013; Van Couwenberghe et al. 2013) suggesting the generality of a unimodal pattern of species performance along important climatic gradients. However, this pattern maps onto species’ geographic ranges in complex ways, and both fecundity and other demographic rates are often as high or higher at the edge as in the core of the range (Sexton et al. 2009; Pironon et al. 2017). Indeed, geographic and climatic limits are often not the same (Oldfather et al. 2020). Moreover, multiple environmental factors typically influence species demography, and they will not all change synchronously with climate change. Therefore, spread dynamics in nature will necessarily be more complicated than the dynamics modeled here, but the main
demographic patterns remain. In section 3 of the supplemental PDF, we show spread dynamics when species fecundity is not a simple Gaussian function of climate and when it depends either on two climatic gradients shifting asynchronously (e.g., temperature and moisture) or on one shifting climatic gradient and one fixed abiotic template (e.g., soil quality).

The frequently observed but theoretically unexpected pattern of constant species’ performance across their range may have several explanations, each with different implications for population spread dynamics. First, for some species, different vital rates vary independently across climatic gradients (Doak and Morris 2010; Oldfather and Ackerly 2019), so that even if one rate is high at the range edge, another may be limiting population growth. Only the net effect of these changes on species’ population growth rates will ultimately impact spread rates (Gaston 2009).

Second, throughout their ranges, species are often restricted to locations with a suitable microclimate (Gilman 2005). While species’ demography at each of those locations may be the same, a decrease in the availability of suitable microsites along large-scale climatic gradients can generate range limits (Holt and Keitt 2000). Indeed, patterns of species occupancy, which could reflect the availability of suitable microclimates, often become patchier toward the range edges of both plants (Boucher-Lalonde et al. 2012) and animals (Boucher-Lalonde et al. 2014). Therefore, fecundity averaged across successive geographic bands (including both favorable and unfavorable microsites) would decline with increasing proximity to the range edge (Pironon et al. 2017), with consequences for spread velocity dynamics similar to those described by our models.

Finally, the range edge of some species is not characterized by a gradual decline in species’ performance but rather by an abrupt drop once a threshold climatic condition (e.g., frost) is reached (Cavanaugh et al. 2014; Kollas et al. 2014). This would result in relatively homogenous fecundity across a certain window of the climatic gradient and close to zero fecundity elsewhere. For these species, no climate-induced spread acceleration is expected, and the moving-habitat modeling approach developed by Zhou and Kot (2011) might better describe spread dynamics.

Limitations of Modeling Results

Our modeling results come with three main caveats. First, our models assume that species performance is largely driven by a single environmental gradient that changes linearly in space. In nature, patterns of population performance across species’ ranges are often complex because they depend on different environmental variables with contrasting spatial patterns and scales of spatial autocorrelation (Pironon et al. 2017). However, since climate change drives range shifts primarily along climatic gradients, the theory and predictions we developed here are a valuable first approximation to understanding how the pattern of fecundity across space and time influences range shifts in response to climate change (but see sec. 3 of the supplemental PDF).

Second, we model only one species and therefore ignore the effects of interspecific competition. The realized variation in species demography across climatic gradients is key to our results, and interspecific competition can certainly affect this pattern and sometimes even limit species distributions (Ettinger et al. 2011). However, as long as different species change their distributions synchronously, the climate dependency of fecundity in our model can implicitly account for the effects of interspecific interactions. In contrast, asynchronous species range shifts would disrupt the correlation between climate and species performance (Alexander et al. 2016) and would therefore require explicit modeling of the competitors. To some extent, we have already made the first steps in this direction, as our simulations with locally adapted genotypes could be viewed as simulations of different species experiencing spread acceleration due to climatic amelioration.

Finally, using clonal populations to model local adaptation and the evolution of dispersal assumes that there are no new mutations in the population and that climate or dispersal traits have perfect heritability. Additionally, the continuous nature of population size in our models implies that there is no demographic stochasticity and no genetic drift. Moreover, it means that all genotypes are present everywhere in the landscape, albeit at very low densities. In addition, we did not consider any trade-offs among dispersal capacity and other traits (Simmons and Thomas 2004; Burton et al. 2010); these can also affect the selection pressure on dispersal in static ranges and therefore the initial frequency of fast dispersers. While violations of these assumptions are unlikely to affect our qualitative results, they could alter the modeled rates of dispersal evolution: imperfect heritability, genetic drift, and the absence of certain genotypes from regions of the species range would all slow down the rate of evolution.

Determining the degree to which these caveats constrain the relevance of our results to range shifts in nature requires further empirical investigation. As a first step, researchers could build on microcosm experiments that have examined the causes and consequences of dispersal evolution during range expansion (Fronhofer and Altermatt 2015; Williams et al. 2016; Ochocki and Miller 2017; Weiss-Lehman et al. 2017). These previous experiments, for simplicity, have focused on spread over landscapes with fixed environmental templates. However, our results suggest that by ignoring the movement of the environmental gradients that underlie species’ ranges, previous
experiments have missed eco-evolutionary processes that may shape range dynamics during climate change. Experiments that simulate the directional movement of environmental gradients characteristic of current climate change can be used to test our models’ predictions as well as the generality of previous experimental results.

Conclusions

We show that even simple and intuitive processes of spread acceleration, such as dispersal evolution and climatic amelioration following spread lags, can interact to produce unexpected ecological dynamics during range shifts driven by climate change. While climatic amelioration cannot accelerate spread beyond the climate velocity, its interaction with dispersal evolution can lead to surprising dynamics in which spread transiently exceeds climate velocity, leading to range reexpansion. These dynamics are not fundamentally altered by local adaptation to climate, but competitive interactions among genotypes can lead to the loss of genetic diversity during spread. Taken together, the results of this work suggest that population spread rates during climate change are intrinsically dynamic, and failing to account for the eco-evolutionary processes behind those dynamics may greatly misidentify species’ ability to track climate change.

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Statement of Authorship

S.B. and J.L.M conceptualized the study. S.B. performed the simulations, created the figures, and wrote the manuscript, with input from J.L.M.

Data and Code Availability

There are no data for this article. All code is provided in section 1 of the supplemental PDF.

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"This is the largest American batrachian, the skull measuring a foot wide by eighteen inches long. It was very abundant, constituting with the reptilian genus Dimetrodon, the most prominent type of the Permian fauna in this country." Figured: “Eryops megacephalus Cope.” From “The Batrachia of the Permian Period of North America” by E. D. Cope (The American Naturalist, 1884, 18:26–39).