Received: 2 January 2024 | Revised: 4 June 2024 | Accepted: 7 June 2024

DOI: 10.1111/ele.14472

ECOLOGY LETTERS cnrs WILEY

LETTER

Environmental gradients mediate dispersal evolution during biological invasions

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Funding information
Division of Biological Infrastructure, Grant/Award Number: DBI-2010892; National Institute of Food and Agriculture, Grant/Award Number: 2021-09368; Office of Experimental Program to Stimulate Competitive Research, Grant/Award Number: EPS-2019528; Division of Environmental Biology, Grant/Award Number: DEB-2121980 and DEB-2230806

Editor: Jonathan Chase

Abstract

Rapid evolution of increased dispersal at the edge of a range expansion can accelerate invasions. However, populations expanding across environmental gradients often face challenging environments that reduce fitness of dispersing individuals. We used an eco-evolutionary model to explore how environmental gradients influence dispersal evolution and, in turn, modulate the speed and predictability of invasion. Environmental gradients opposed evolution of increased dispersal during invasion, even leading to evolution of reduced dispersal along steeper gradients. Counterintuitively, reduced dispersal could allow for faster expansion by minimizing maladaptive gene flow and facilitating adaptation. While dispersal evolution across homogenous landscapes increased both the mean and variance of expansion speed, these increases were greatly dampened by environmental gradients. We illustrate our model's potential application to prediction and management of invasions by parameterizing it with data from a recent invertebrate range expansion. Overall, we find that environmental gradients strongly modulate the effect of dispersal evolution on invasion trajectories.

KEYWORDS

dispersal cost, environmental heterogeneity, local adaptation, range expansion, spatial gradient

INTRODUCTION

The history of biodiversity on Earth is largely a story of invasion. From plants' colonization of land 500 million years ago to contemporary range shifts with climate change, species' geographic range expansions have repeatedly rearranged global biogeography. Though the timescale and details of these invasions vary greatly, they are underlain by the same fundamental process—the expansion of populations into previously unoccupied habitat. In recent decades, much attention has focused on the spread of introduced species as it became clear that anthropogenic movement of organisms could cause massive ecological and economic damage. Work has documented the ecological effects of invasive exotic species (Vilà et al., 2011), characterized traits that may promote invasiveness (Van Kleunen et al., 2010) and examined evolutionary processes during invasion (Colautti & Barrett, 2013; Urbanski et al., 2012). Yet, predicting the spatio-temporal dynamics of invasion itself—namely, the rate of expansion—remains difficult (Miller et al., 2020; Williams et al., 2019). From a purely ecological perspective, expansion rate can be estimated based on two population parameters: intrinsic growth rate and dispersal ability (Hastings et al., 2004). However, empirical and theoretical work increasingly show that populations can evolve rapidly during invasion, which makes predicting invasion more difficult (Andrade-Restrepo et al., 2019; Burton et al., 2010; Colautti & Lau, 2015; Fronhofer & Altermatt, 2015; Ochocki & Miller, 2017; Peischl & Gilbert, 2020; Phillips, 2015; Urquhart & Williams, 2021; Weiss-Lehman et al., 2017; Williams et al., 2016). Here we focus on two evolutionary processes that can modulate invasion dynamics on ecological timescales: dispersal evolution and local adaptation.

The evolution of heightened dispersal in leading edge populations during range expansion has been demonstrated in a variety of taxa in both experimental laboratory expansions and natural populations (Cwynar & MacDonald, 1987; Hughes et al., 2007; Ochocki & Miller, 2017; Phillips et al., 2006; Simmons & Thomas, 2004; Van Petegem et al., 2018; Weiss-Lehman

https://doi.org/10.1111/ele.14472

et al., 2017; Williams et al., 2016). This phenomenon is thought to be largely due to the process of spatial sorting, which arises from the simple fact that the most dispersive individuals will tend to aggregate at the invasion front. As long as dispersal traits are heritable, reproduction of these high-dispersal individuals will serve to increase dispersal ability at the invasion front compared to the range core (Shine et al., 2011). Spatial assortment of dispersal ability can be further augmented if individual fitness is negatively influenced by density (via intraspecific competition), such that low competition environments at the invasion front will result in high fitness of invaders (this combination of such density dependence with spatial sorting is sometimes termed 'spatial selection'). In this case, dispersal beyond the current range edge will be favoured by natural selection due to an escape from competition (Miller et al., 2020; Perkins et al., 2013; Travis et al., 2009). Such increases in dispersal can greatly increase invasion speed (i.e. distance spread in a given amount of time) compared to scenarios without dispersal evolution (Miller et al., 2020; Perkins et al., 2013; Phillips et al., 2010; Travis & Dytham, 2002).

A second fundamental evolutionary process relevant to range expansions is adaptation. Given spatial environmental heterogeneity, natural selection will favour genotypes adapted to their local environment, leading to the widespread (though not ubiquitous) phenomenon of local adaptation (Briscoe Runquist et al., 2020; Colautti & Barrett, 2013; Gorton et al., 2022; Hereford, 2009; Ittonen et al., 2022). In the context of range expansions, populations expanding across a landscape will often encounter a particular form of spatial heterogeneity, environmental gradients. Such gradients—for example in aridity, photoperiod, temperature—can result in phenotypic optima that change regularly across space. For instance, optimal phenology of bud break or flowering in plants often changes gradually across climatic gradients (Alberto et al., 2011; Gorton et al., 2022; Griffith & Watson, 2006). Such gradients and the resulting spatial variation in selection will require continual adaptation for populations to spread through these environments (Mayr, 1963). Such local adaptation is found at similar rates within both native and exotic plant species (Oduor et al., 2016), indicating that spatially varying selection may influence the dynamics of many invasive species. As gradients steepen (i.e. phenotypic optima change more quickly across the landscape), dispersal becomes more costly due to increased maladaptation in one's non-home habitat, and the 'adaptive leap' required to colonize adjacent patches increases. Evolutionary models of range dynamics show that the steepness of such gradients is a key factor determining whether or not range expansion is possible for a species (Benning et al., 2022; Bridle et al., 2019; Gilbert et al., 2017; Kirkpatrick & Barton, 1997; Polechová, 2018; Polechová & Barton, 2015).

While both dispersal evolution and local adaptation are expected to be common, we know little of how these two processes interact during range expansions (Hargreaves & Eckert, 2014). Metapopulation theory suggests that, all else being equal, spatial heterogeneity in habitat quality is generally expected to select against dispersal, because migrating individuals may end up in unsuitable habitat; that is, there is a fitness cost to dispersal (Hastings, 1983; Holt, 1985; McPeek & Holt, 1992). Conversely, dispersal can be favoured in metapopulation models when it enables individuals to escape from competition and colonize new sites (Levin et al., 1984; Olivieri et al., 1995), analogous to spatial selection as described above. Thus, dispersal evolution in a metapopulation will reflect the balance of such contrasting selection pressures (Hanski et al., 2004; Heino & Hanski, 2001). Similarly, the trajectory of dispersal evolution during range expansion will depend on the relative influences of the fitness cost of dispersal and the fitness benefit of escaping competition. Dispersal evolution is likely to then feedback on adaptation to a gradient during invasion, as higher dispersal leads to increased gene flow between populations, which can stymie local adaptation and range expansion (Kirkpatrick & Barton, 1997; Lenormand, 2002; Polechová, 2018; Slatkin, 1987). Such negative effects of gene flow may lead to further selection against dispersal as populations adapt to their local environment and the fitness cost of dispersal increases (Billiard & Lenormand, 2005; Bonte et al., 2012; Holt, 1985; Ronce, 2007). Given this prior work, we might expect that selection along environmental gradients would constrain the evolution of heightened dispersal during invasion and counteract increases in invasion speed arising from dispersal evolution.

Though scant, there are some empirical observations consistent with the idea that adaptation to novel environments can constrain the evolution of dispersal during range expansions. There was a reduced signal of dispersal evolution in flour beetle expansions across novel versus benign mesocosm landscapes (Szűcs et al., 2017; Weiss-Lehman et al., 2017), and dispersal evolution in a beetle species expanding south in the Western United states may be constrained by local adaptation to photoperiod (Clark et al., 2022, 2023). Theory has only recently begun to probe the interaction between dispersal evolution and local adaptation to gradients during range expansions and shifts. Andrade-Restrepo et al. (2019) showed that evolving dispersal induces changes in invasion tempo (wave vs. pulse) for a species expanding across an environmental gradient. Models of range shifts with climate change have shown that dispersal evolution can help rescue populations lagging behind shifting climatic isotherms (Block & Levine, 2021; Weiss-Lehman & Shaw, 2020). However, we do not know (1) how environmental gradients regulate dispersal evolution during range expansion or (2) how the process of local adaptation mediates the rate of invasion when dispersal can evolve.

Evolutionary processes acting on expanding populations are expected to often influence not only expansion speed, but also its predictability (Williams et al., 2019). Here, the question is, if we were to 'rewind the tape' multiple times, how much variability in expansion speed would there be among these different iterations of expansion? Predictability is most often quantified in practice as the variability in expansion speed among instances of simulated or experimentally replicated expansions, where high variability denotes low predictability. Theory (Phillips, 2015; Williams et al., 2019) and experiments (Ochocki & Miller, 2017; Weiss-Lehman et al., 2017) have demonstrated that for populations spreading across homogenous landscapes, evolution can increase the variability in invasion speed among expansion instances, compared to scenarios without evolution (but see Williams et al., 2016). This increased variability is thought to often be due to the fact that populations at the invasion front tend to be small, and thus are highly influenced by stochastic evolutionary processes. As small populations are repeatedly founded at the front of the expansion, alleles influencing dispersal or fitness may randomly drift (Slatkin & Excoffier, 2012) or 'surf' (Peischl et al., 2015) to high frequencies, leading each instance of an expansion to comprise a unique allelic composition at the invasion front. Conversely, we can generally expect expansion speed to become more predictable as the strength of deterministic evolutionary forces (natural selection, spatial selection) increases relative to the strength of stochastic evolutionary forces (drift, surfing) (Miller et al., 2020; Williams et al., 2019). Population genetic theory tells us that the balance between these forces will be determined mainly by effective population size and the strength of selection (Kimura, 1964; Whitlock, 2003); environmental gradients that determine fitness during range expansion will likely influence both of these factors. For example, Gilbert et al. (2017) used simulations to show that selection along an environmental gradient slowed expansion and increased population sizes at range edges, reducing the influence of drift during expansion. Furthermore, variability in expansion speed among instances arising due to random differences in dispersal allele frequencies (and thus dispersal ability) at the invasion front (e.g. Ochocki & Miller, 2017; Weiss-Lehman et al., 2017) could be counteracted by selection against dispersal due to the fitness cost of migration, such as that expected along environmental gradients.

Overall, we lack a general understanding of how environmental gradients influence expectations for dispersal evolution and adaptation during range expansion. Because of the potentially large effects of evolution on invasion rate and predictability, and the ubiquity of environmental gradients in nature, understanding the interplay of these forces would go far in building more accurate models of invasion dynamics. To that end, here we investigate the influence of an environmental gradient on the dynamics of dispersal evolution and adaptation during invasion. Our individual-based simulation model allows for the evolution of two quantitative traits: a trait conferring adaptation to an environmental gradient, and a trait controlling dispersal ability. By varying the steepness of the environmental gradient and following the demography and evolution of populations expanding across it, we ask:

1. How does the steepness of an environmental gradient influence dispersal evolution during range expansion?
2. How do the evolution of dispersal and the steepness of an environmental gradient influence the predictability of expansion speed?
3. How does dispersal evolution influence adaptation during range expansion across an environmental gradient?

MATERIALS AND METHODS

Dispersal evolution and local adaptation during invasion

We used SLiM (Haller & Messer, 2022), a forward-in-time population genetic modelling framework, to build a genomically explicit, individual-based simulation of species range dynamics in a spatially varying environment. In brief, our model simulates a population invading a new environment and tracks population demography and the evolution of dispersal and local adaptation during range expansion.

The landscape

The simulation landscape consisted of a one-dimensional array containing 1000 patches. This setup is most akin to a natural landscape that is primarily one-dimensional, such as a river corridor, mountain ridge or valley. The environment varies across space (x), producing a spatial gradient in phenotypic optima (θ) with slope b, which we vary across simulations (Figure 1a).

Genetics

In our simulations, individuals were diploid and either male or female, with obligate sexual reproduction, and 10 chromosomes each 100,000 bp long. Generations were discrete. There were three mutation types: (1) neutral mutations, (2) mutations that contributed additively to a quantitative trait [i.e. biallelic quantitative trait loci (QTL) with no dominance] that determined fitness along the ecological gradient (niche trait) and (3) mutations that contributed additively to a quantitative trait determining

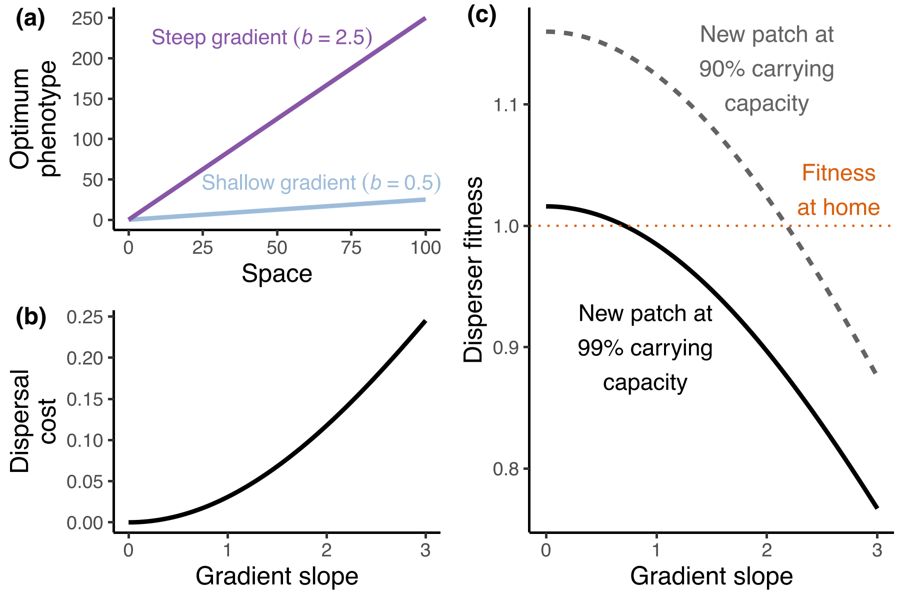


FIGURE 1 Conceptual overview of the relationships between environmental gradients, dispersal cost and fitness. (a) Illustrates the simulation landscape (showing only 100 patches), where an underlying environmental gradient across space creates a gradient in optimal phenotype, whose slope (change in optimum per patch) can range from shallow (b=0) to steep (b=3). Examples of b=0.5 and b=2.5 are illustrated. All simulated invasions start at spatial position 0. (b) Illustrates how the cost of dispersal increases with the gradient slope (b) Specifically, dispersal cost is the decrease in the probability of survival for an individual adapted to patch x dispersing to patch $x+1$, calculated as $d = 1 - \exp\left[-\frac{b^2}{2v^2}\right]$, where $v = 4$. (c) Illustrates how the expected fitness (number of offspring) of an individual dispersing one patch away decreases with the gradient slope (which influences viability fitness via maladaptation) and the population size in the new patch (which influences density dependent fecundity). Plot shows expected fitness at population densities of 99% (solid line) and 90% (dashed line) of carrying capacity. Fitness at home for a locally adapted individual will be 1, regardless of gradient slope (orange dotted line). Expected disperser fitness (y-axis) is the product of expected viability (W_i) and expected fecundity ($\frac{\hat{F}_i}{2}$, dividing by 2 as fecundity is calculated for females only; see Equations 1 and 2 in Materials and Methods).

dispersal propensity (dispersal trait). The overall mutation rate was set to 1×10^{-7} mutations per base position on a gamete per generation, and mutations were 10 times more likely to be neutral than QTLs. Results were qualitatively similar with both lower and higher mutation rates (Figure S1). The effect size for niche and dispersal QTLs were drawn from normal distributions (niche: N(0, 0.04), dispersal: N(0, 0.0004)). Mutation effect size distributions were different due to the difference in magnitude between these two traits (i.e. the niche trait might vary 0–100 across a landscape, but the dispersal trait was much smaller in magnitude to keep dispersal kernels realistic). Recombination rate was set to 1×10^{-4} (probability of a cross-over event between any two adjacent bases per genome per generation).

Mating, dispersal and population dynamics

Individual fitness was a function of both survival and fecundity. Following (Bürger & Lynch, 1995), viability fitness (the probability of survival) for an individual (W_i) was calculated as

$$W_i = \exp\left[-\frac{(z_i - \theta_x)^2}{2v^2}\right] \quad (1)$$

where θ_x is the phenotypic optimum in patch x, v is the strength of stabilizing selection (standard deviation of the fitness function; v=4 throughout), and z_i is the individual's niche trait phenotype. Thus the probability of survival is determined by the deviation of an individual's phenotypic value from the local optimum in a Gaussian stabilizing selection model, with probability of survival decreasing with increasing maladaptation.

Following viability selection, individuals dispersed according to a Poisson dispersal kernel whose mean was defined by the individual's dispersal trait phenotype, m_i (determined additively by the individual's dispersal QTL). Dispersal direction (left or right along the gradient) was unbiased and random. Landscape boundaries were reflective such that individuals could not disperse outside of the first or last patch of the simulated landscapes. There was no 'direct' cost of dispersal (e.g. an energetic cost) as implemented in some models (e.g. Travis & Dytham, 2002); the fitness cost of dispersal was due only to maladaptation.

Mating occurred after dispersal. Fecundity of female individuals was calculated as $F_i \sim \text{Poisson}\left(\hat{F}_i\right)$, where

$$\hat{F}_i = 2 + 2r\left(1 - N_{x,t}/K\right) \quad (2)$$

Thus, demographic stochasticity was included both through the survival process described above and the reproductive process described here. The maximum rate of increase (r) was set to 1.6. Fecundity was density dependent, based on the number of individuals in patch x at time t ($N_{x,t}$) and the carrying capacity of each patch (here, $K=200$ throughout). Male mates were drawn at random from the focal female's patch for each offspring individually (i.e. multiple paternity was possible). Any $\widehat{F}_i < 0$ was set to $\widehat{F}_i = 0.00001$, as the mean for a Poisson distribution in SLiM must exceed zero.

As detailed above, we modelled survival as a function of matching to the environmental optimum and fecundity as a function of density. This approach allowed us to decouple the effects of environmental gradients and density on these two fitness components, meaning that selection on the niche trait was independent of density, simplifying interpretation. In such a scenario, the probability of survival decreases in a novel environment, but if an individual survives, that novel environment does not have negative effects on fecundity. We have demonstrated such patterns across gradients in optimal phenology in *Ambrosia* (Gorton et al., 2022) and *Clarkia* (Benning et al., 2019; Benning & Moeller, 2019), and such a pattern seems likely from our and other's work on *Diorhabda* (Bean et al., 2012; Clark et al., 2023). Differential responses of fitness components to environmental variation may be prevalent in nature, given the observation that population-level demographic vital rates that result from these individual fitness components (e.g. survival, reproduction) often show differential sensitivity to environmental perturbations (Catling et al., 2024; Lyu & Alexander, 2023; Villellas et al., 2015).

For interpretability, in most of our results below we have transformed the spatial gradient slope, b, to represent the cost of dispersal due to maladaptation, which is the decrease in the probability of survival for an individual adapted to patch x dispersing to patch $x+1$ (Figure 1b). This dispersal cost is calculated as $d = 1 - \exp\left[-\frac{b^2}{2v^2}\right]$. Representing the steepness of the environmental gradient as the expected decrease in survival increases its applicability and estimability in empirical work, as experiments could more easily measure survival in different locations along a gradient than estimate phenotypic optima along that gradient. The realized fitness of a dispersing individual will be a function of two quantities: (1) the reduced probability of survival due to dispersing to a patch with a different phenotypic optimum (dispersal cost) and (2) the density dependent fecundity in the new patch (Figure 1c).

Simulation process

Burn-in

Each simulation started with a 20,000-generation burn-in phase. During this phase, 200 genetically uniform and perfectly adapted founding individuals were placed in the central patch of the landscape. Mating and dispersal occurred as described above, but the landscape was restricted to 11 patches (five on either side of the central patch). Every patch had a carrying capacity (K) of 200 individuals, resulting in a total landscape-wide carrying capacity of 2200. A moderate spatial environmental gradient in optima spanned the 11 patches ($b=0.5$). In the presence of an environmental gradient, dispersal will be strongly selected against due to local adaptation (e.g. Holt, 1985), unless there is some potential benefit of dispersal (e.g. colonization of a patch with low competition due to recent patch extinction). Thus, to maintain genetic variation for dispersal during the burn-in, one patch was randomly selected to go extinct every other generation. During the burn-in, mean heterozygosity of neutral mutations in the central population usually reached an equilibrium by ca. 15,000 generations. At the 20,000th generation, all individuals in the central patch migrated to the first patch of the main landscape (i.e. the 'founding event'); these two patches had the same phenotypic optimum. All other individuals were removed from the simulation.

Main simulation

Following the burn-in phase, the main simulation commenced using the specified parameters (Table S1). The landscape was expanded to 1000 patches, with the first (left-most) patch containing the founding individuals described above. The slope in phenotypic optima across the landscape was determined by b. Similar to extinction during the burn-in, 10 patches (1% of the landscape) were randomly selected for extinction each generation (regardless of whether the patch was colonized). This occasional extinction was implemented to prevent dispersal from unrealistically evolving to zero in occupied portions of the range due to persistent selection against dispersal with no possible benefit of dispersing (because all surrounding patches are at carrying capacity). Results were largely insensitive to differing extinction rates (Figure S2). Mutations arose during expansion, similar to the burn-in; simulations with no mutations during expansion (i.e. evolution via standing genetic variation only) produced quantitatively similar results (Figure S3). The simulation ended after 200 generations, or if all populations became extinct, or if the furthest landscape patch achieved a population size of at least half the carrying capacity (i.e. the species occupied the entire landscape).

Simulation runs

Our main analyses are based on 1000 simulations with values of b randomly drawn from a uniform distribution: $b \sim U(0, 3)$; we ran one batch of simulations with dispersal evolution, and one without. To explore effects of dispersal evolution and environmental gradients on the predictability of range expansion, we ran another batch of simulations at 30 values of *b*, with 50 replicate for each *b*, again with and without dispersal evolution. In simulations with no dispersal evolution, we set $m = 0.55$, which was the mean dispersal of the founding populations (after burn-in) in the simulations with dispersal evolution. We also ran sensitivity analyses to test the effects of carrying capacity, selection strength and intrinsic growth rate on model outcomes (Figure S4). To quantify the predictability of expansion speed, we report both the standard deviation and coefficient of variation ($\text{CV} = \frac{\sigma}{\mu} \times 100$) in distance spread after 200 generations of expansion.

RESULTS

Environmental gradients oppose the evolution of increased dispersal

As environmental gradients steepen, the change in phenotypic optimum between patch x and patch $x+1$ increases, increasing the fitness cost of dispersal (Figure 1). This dispersal cost introduced by environmental gradients opposes the evolution of higher dispersal at the invasion front (Figure 2; Figure S5). For interpretability, we transform the slope of the environmental gradient (x-axis in Figure 2a,b) into the dispersal cost of maladaptation, d (x-axis in Figure 2c); a dispersal cost of 0.01 equals a 0.01 decrease in the probability of survival for individuals dispersing from patch x to patch $x+1$ (see Materials and Methods; Figure 1b). Dispersal evolution at the invasion front decreases sharply as dispersal cost increases from 0 (homogenous environment) to ca. 0.01, then more gradually until a dispersal cost of ~0.1, after which there is no signal of dispersal differentiation between the range edge and core (Figure 2c). Both core and edge regions evolved decreased dispersal (relative to founding population) once dispersal cost increased sufficiently (Figure 2a). These results were quantitatively similar across a wide range of carrying capacities, selection strengths and intrinsic growth rates (Figure S4). When spatial clines in dispersal phenotypes did evolve, they persisted for many generations, even when environmental gradients led to landscape-wide decreases in dispersal over time (SI Note B; Figure S5).

Environmental gradients and dispersal evolution jointly modulate the speed and predictability of invasion

Dispersal evolution greatly increased invasion speed relative to models with static dispersal, but this phenomenon was most apparent in homogeneous landscapes with no fitness cost of dispersal (Figure 3a). With any dispersal cost, the difference in speed between scenarios with and without dispersal evolution was trivial in magnitude compared to the difference observed in homogeneous landscapes. Surprisingly, evolution of decreased dispersal led to greater expansion speed along moderate

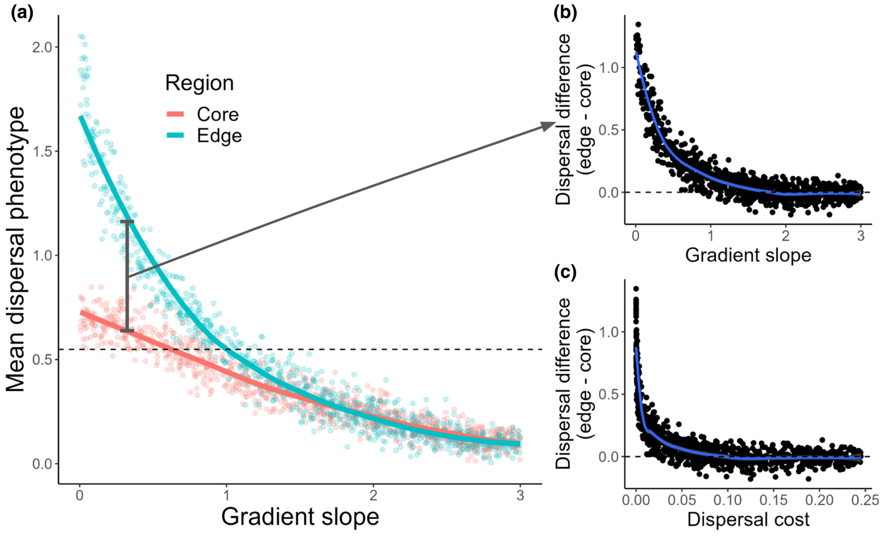


FIGURE 2 Environmental gradients oppose the evolution of increased dispersal during range expansion. Results of 1000 simulations after 200 generations of expansion [$b \sim U(0, 3)$]. (a) Illustrates the mean dispersal phenotype within core and edge regions plotted against gradient slope (*b*). Core and edge regions comprise the five most proximate and distal patches to the founding patch, respectively; each simulation is thus represented by one core point and one edge point. The dashed line signifies the mean dispersal of the founding populations at the start of expansion. (b) Depicts the difference in dispersal between the core and edge across gradient slopes, expressed as the absolute increase in mean dispersal ability of the edge relative to the core. Each point results from one simulation. To aid in interpretability, (c) shows dispersal difference plotted against dispersal cost (*d*) instead of gradient slope. Dispersal cost is a function of the slope of the gradient (*b*) and the strength of selection (*v*) and is the expected decrease in the probability of survival for an individual perfectly adapted to patch x dispersing to patch $x+1$ (Materials and Methods).

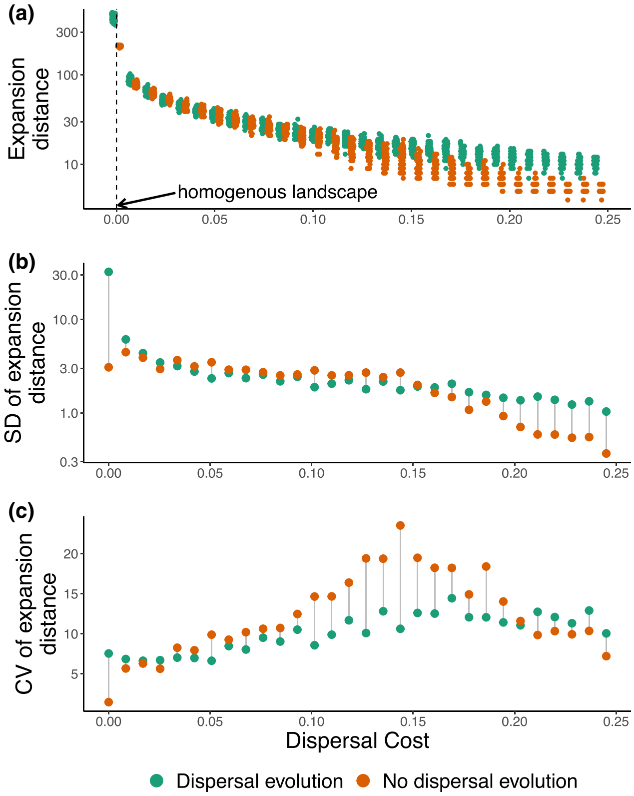


FIGURE 3 Environmental gradients and dispersal evolution jointly modulate the speed and predictability of invasion. [*Y*-axis in (a) and (b) is $\log_{10}$ transformed.] (a) Expansion distance (number of patches) after 200 generations at 30 values of dispersal cost (*d*) for scenarios with (green) and without (orange) dispersal evolution. SD (b) and CV (c) in expansion distance at 30 values of *d*, again for scenarios with (green) and without (orange) dispersal evolution. In each panel, there are 50 replicate simulations per dispersal cost bin (replicates plotted individually in (a), with among-replicate variability summarized in (b) and (c)) The first pair of points along the *X*-axis in each panel correspond to dispersal cost of zero (i.e. homogenous landscape). See also Figure S6.

to steep gradients ($d \gtrsim 0.03$) compared to scenarios with no dispersal evolution, as lower dispersal facilitated adaptation along the gradient (see next section). Along very steep gradients, the relative difference in speed between scenarios with and without dispersal evolution could be large (ca. 100% greater expansion with dispersal evolution).

In homogenous landscapes, dispersal evolution made expansion speed much less predictable (i.e. increased variability in expansion distance, as measured by SD and CV; Figure 3b,c). When dispersal could evolve, SD in expansion speed decreased sharply once there was any environmental gradient and continued to decrease gradually as gradients steepened (Figure 3b). Because mean expansion distance also decreased with gradient steepness, the effect of gradients on CV was minimal in the presence of dispersal evolution (Figure 3c). Compared to scenarios with static dispersal, dispersal evolution increased variability of expansion across shallow ($d \lesssim 0.03$) and steep ($d \gtrsim 0.2$) gradients; dispersal evolution tended to decrease variability with moderate gradients (particularly when considering CV). Scenarios without dispersal evolution had lower variability in the presence of steep gradients (Figure 3b,c) because expansion tended to stall due to adaptation failure (see next section and Figure S6). Taken together, these results suggest that a model failing to consider dispersal evolution may either under- or overestimate predictability of expansion, depending on the steepness of the environmental gradient (Box 1).

Evolution of decreased dispersal along steep gradients reduces maladaptive gene flow

Increased dispersal leads to higher gene flow, which generally increases genetic variance within populations. Thus, along shallow environmental gradients in our simulations, the evolution of increased dispersal tended to increase the amount of genetic variance in the niche trait, relative to scenarios without dispersal evolution (Figure 5a). However, as environmental gradients steepened and dispersal became more costly, dispersal evolved downward, as selection against dispersal became stronger (Figure 2a). Thus, after dispersal evolution switched from increased to decreased dispersal (roughly at the dispersal cost marked with a vertical dashed line in Figure 5), the evolution of decreased dispersal tended to lower the amount of genetic variance in edge populations relative to models with static dispersal. Lower genetic variance in the niche trait across moderate to steep gradients led to lower genetic load (i.e. fewer individuals are far from the patch phenotypic optimum), which facilitated greater adaptation (Figure 5b) and increased fitness in edge populations (Figure 5c). This decreased load is why evolution of lower dispersal increased expansion distance relative to scenarios without dispersal evolution along steep gradients (Figure 3a).

DISCUSSION

Populations invading across a landscape may be subject to evolutionary forces that manifest on ecological timescales to alter the trajectory of invasion. Much work has focused on how environmental gradients can result in local selection influencing invasion (e.g. Kirkpatrick & Barton, 1997; Polechová, 2018), and how the evolution of increased dispersal at the expansion front can accelerate invasions (Phillips et al., 2006; Shine et al., 2011; e.g. Travis & Dytham, 2002). However, we have a limited understanding of how these two forces interact during invasion. Given that expansion speed is a function of intrinsic growth rate and dispersal ability (Hastings et al., 2004), exploring how environmental gradients influence fitness and dispersal evolution is crucial to understanding species' range expansions. Here, we showed how environmental gradients oppose the evolution of increased dispersal during invasion, leading to a strong signal of dispersal evolution only along shallow environmental gradients. We found that while evolution across homogenous landscapes can cause invasions to be highly unpredictable, spatially varying selection across environmental gradients greatly decreased the variance in invasion speed among instances in our simulations. Along steep gradients, the evolution of lower dispersal allowed increased adaptation and thus increased population growth rates, which enhanced invasion speed relative to scenarios without dispersal evolution. Overall, we find that local adaptation and dispersal evolution are deeply entwined, with potentially large influences on our understanding of invasion.

The interplay between local adaptation, dispersal cost and dispersal evolution

Local adaptation within spatially heterogeneous environments is common in both native and invasive species (Briscoe Runquist et al., 2020; Hereford, 2009; Oduor et al., 2016). We can also expect many populations to harbour genetic variation in dispersal traits (reviewed in Ronce, 2007). Given these two conditions—spatially varying selection and heritable dispersal ability—the processes of local adaptation and dispersal evolution will interact. As environmental gradients steepen and phenotypic optima become more disparate across space, the fitness cost of dispersal increases, and thus maladaptation will oppose the evolution of increased dispersal

BOX 1 Local adaptation and dispersal evolution during invasion—The *Diorhabda* range expansion

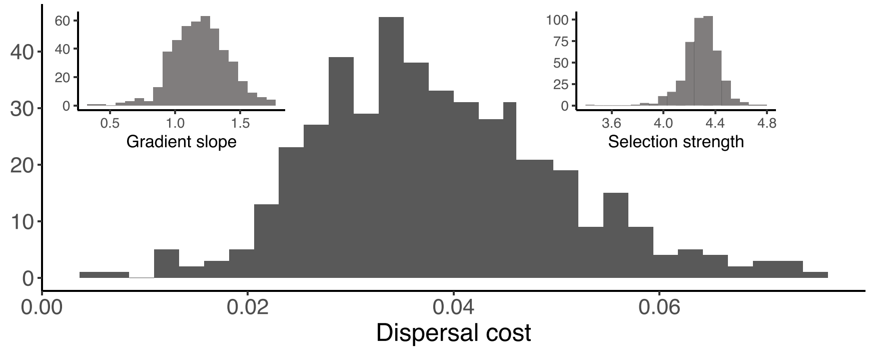
To illustrate how our model could be paired with empirical data to predict invasions and inform management decisions, we parameterized the model with data from a recent range expansion of a biocontrol agent. *Diorhabda carinulata*, the northern tamarisk beetle, was released in 2001 into the western United States for the biological control of invasive riparian shrubs in the genus *Tamarix*, called saltcedar or tamarisk (DeLoach et al., 2003). The range of the beetle was initially limited to areas north of 38° N, because it was maladapted to the daylengths (photoperiods) in the south, which are shorter midsummer than northern daylengths, and beetles initiated diapause (seasonal dormancy in insects, similar to hibernation in mammals) too early in the season (Bean et al., 2007). Because both photoperiod and the timing of the onset of winter change with latitude, there is a gradient from north to south in the photoperiod that provides the optimal cue to initiate diapause. Nearly a decade after the first releases, the beetles started to disperse southward following remote riparian corridors, enabled by beetles evolving to cue into shorter photoperiods to initiate diapause at an appropriate time in the season for the latitude (Bean et al., 2012). In 2018, Clark et al. (2022) measured dispersal traits using tethered flight mills for beetles from the core of the range and the leading edge of the expansion, reared in a common lab environment and found a modest increase in dispersal propensity and ability in beetles from the leading edge. Also in 2018, Clark et al. (2023) determined that beetles at the southern expansion front cue into shorter photoperiods compared to core beetles, such that some populations from the core and edge had become locally adapted to photoperiod. The tamarisk beetle system, showing both evolution of dispersal and local adaptation to an environmental gradient during range expansion, provides a useful system with which to parameterize our model.

We used approximate Bayesian computation (ABC) to estimate the gradient slope and strength of selection (which together describe the dispersal cost) during the tamarisk beetle range expansion. ABC is a statistical method used to estimate model parameters when likelihood calculations are intractable, by comparing simulated to observed results via a set of summary statistics (reviewed in Beaumont, 2010). We calculated three summary statistics: the difference in dispersal phenotype between edge and core populations, the difference in niche phenotype between edge and core populations, and the ratio in survival between edge and core populations in the core habitat (a measure reflecting local adaptation and the strength of selection). The observed summary statistics were calculated using data from experiments by Clark et al. (2022, 2023), where the dispersal phenotype was the mean distance flown in individual dispersal trials, the niche phenotype was the days until diapause, and survival was the proportion of individuals in diapause after the diapause cue was initiated. We used data from two tamarisk beetle populations that represented core and edge populations after range expansion ~500 km southward over ~34 generations. To estimate posterior distributions for gradient slope (b) and the strength of selection (v), we ran 60,000 simulations, sampling each parameter from a uniform prior [$b \sim U(0,2)$; $v \sim U(0,5)$]; we set intrinsic growth rate (r) in the simulations based on field experiments with a related *Diorhabda* species (Michels et al., 2010). We estimated a joint posterior of dispersal cost, d, based on $d = 1 - \exp\left[-\frac{b^2}{2v^2}\right]$ as above. Full details of analyses are in SI Note A.

BOX 1 (Continued)

ABC estimated dispersal cost during the southward tamarisk beetle expansion as a decrease in the probability of survival of ~0.038 per 48 km (Figure 4a). If there were *not* a gradient in optimal phenotype that introduced a dispersal cost (i.e. if the tamarisk beetle was expanding across a homogenous landscape), simulations suggested that expansion could have reached ~2000 km, as opposed to the observed ~500 km. Thus, local selection along a latitudinal gradient has likely slowed the tamarisk beetle expansion considerably. Simulations suggested this slowdown was attributable to both the direct negative effect of maladaptation on colonization of new habitat, and the constraint that dispersal cost placed on dispersal evolution at the invasion front (Figure 4b). These analyses demonstrate how models such as ours can be paired with empirical data to better understand and predict the course of invasion. Extensions of our model could be used to model effectiveness of different management interventions for slowing invasions.

(a) Parameter posterior distributions



(b) Estimated expansion distance under different scenarios

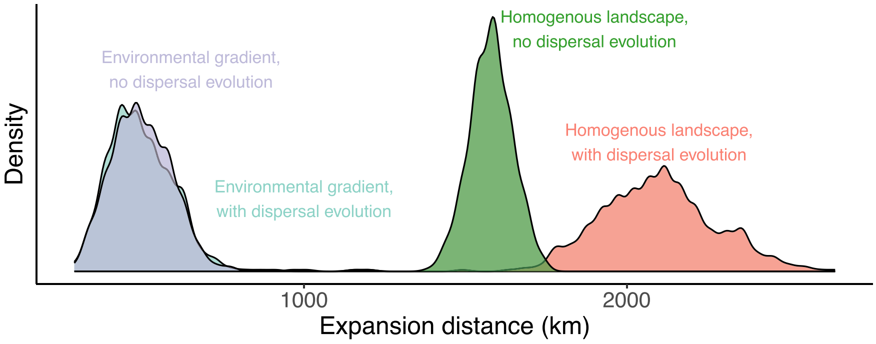


FIGURE 4 Adaptation to an environmental gradient enabled a 500 km range expansion, but slowed expansion relative to a hypothetical homogenous landscape. (a) Using approximate Bayesian computation to integrate our model with empirical data on *Diorhabda* expansion, we estimated a posterior distribution for the joint parameter, dispersal cost (d), which is calculated based on gradient slope (b) and selection strength (v) (insets). (b) Comparing expansion distances for simulations using the estimated posteriors for b and v ('Environmental gradient, with dispersal evolution'); assuming the estimated gradient but with no dispersal evolution ('Environmental gradient, no dispersal evolution'); assuming a homogenous gradient where $b = 0$ ('No environmental gradient, with dispersal evolution'); and assuming a homogenous gradient with no dispersal evolution ('No environmental gradient, no dispersal evolution'); see SI Note A for full details.

during range expansion. Gradients thus oppose spatial sorting, spatial selection and any stochastic processes leading to high dispersal at the expansion front. Consequently, environmental gradients reduce invasion speed and increase the predictability of invasion.

There are now multiple observations that support theoretical predictions of increased dispersal ability at the edge of an invading species range (Phillips et al., 2006; Simmons & Thomas, 2004; Weiss-Lehman et al., 2017). However, the phenomenon is not ubiquitous

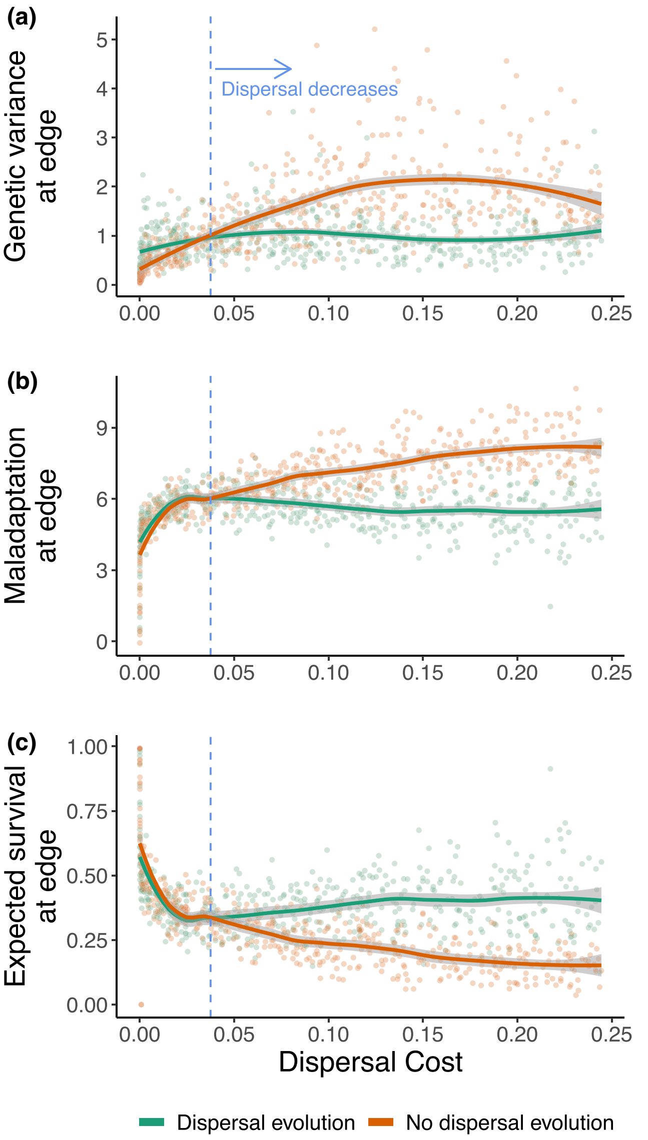


FIGURE 5 Evolution of decreased dispersal along steep gradients saves populations from maladaptive gene flow and increases expansion speed. (a) Genetic variance for the niche trait at the invasion front for simulations varying in dispersal cost (x-axis), after 200 generations of invasion, for scenarios with (green) and without (orange) dispersal evolution. (b) Maladaptation (deviation of mean niche trait from optimum) of edge population. (c) Represents the expected survival at the invasion front for the same scenarios and conditions. Expected probability of survival is calculated using the mean and variance of the population's niche trait, the optimal niche trait value, and the selection strength (SI Note C). Here, the edge population is defined as the most distal occupied patch with at least ten individuals. In all panels, each point represents data from the edge population of a single simulation after 200 generations of expansion. Coloured lines in each panel are loess regressions with 95% confidence bands. The blue vertical dashed line in all panels marks the approximate dispersal cost at which dispersal in the edge population begins to evolve downward (i.e. is lower than the dispersal of the initial founding population), estimated from the data shown in Figure 2a.

(Miller et al., 2020; Oldfather et al., 2021), and predictions for the trajectory of dispersal evolution during invasion remain elusive. Prior theory has indicated that the evolution of higher dispersal at the invasion front can be constrained by tradeoffs between dispersal and other traits (Ochocki et al., 2020), interspecific competition (Burton et al., 2010), strong Allee effects (Travis & Dytham, 2002) and availability of suitable habitat (Travis & Dytham, 1999). Our model suggests that dispersal evolution will be strongly mediated by the steepness of the environmental gradient a species is invading across. In general, large increases in the rate and unpredictability of invasions due to dispersal evolution should be limited to cases where environmental gradients are relatively shallow and the cost of dispersal is low.

In accord with recent empirical work (Ochocki & Miller, 2017; Weiss-Lehman et al., 2017), our model showed that when landscapes are homogenous, evolution will generally decrease the predictability of invasion across instances relative to scenarios without evolution (Figure 3b,c). In our model, this decreased predictability arose from genetic drift and gene surfing leading to differences among instances in dispersal allele frequencies, and thus dispersal ability, in expansion front populations (Figure S7). Such stochastic evolutionary influences were greatly dampened in the presence of an environmental gradient, as the gradient introduced a fitness cost to dispersal that effectively put an upper limit on dispersal evolution at the expansion front—an individual dispersing too far would perish due to maladaptation. In contrast to the mechanism described in Williams et al. (2019) and Gilbert et al. (2017), the decreased variance in expansion speed in the presence of a gradient was not likely due to increased population size at the expansion front in our model (Figure S8). Rather, the fitness cost of dispersal simply selected against the evolution of high dispersal, leading to large decreases in both the mean and variance of expansion speed with even a shallow environmental gradient. It is important to note that while it was processes affecting dispersal evolution that increased the variability of invasion speed in our model, variability could also increase due to evolution of other life history traits (Phillips, 2015), or random fixation of deleterious mutations (Peischl et al., 2015), or other evolutionary processes yet to be explored.

Evolution of decreased dispersal may be important for structuring species distributions

While most work addressing dispersal evolution during range expansion has focused on increases in dispersal ability, our results suggest intriguing possibilities for the evolution of decreased dispersal. When the fitness cost of dispersal is greater than the benefit of escaping competition, there will be selection against dispersal. This will be most likely in scenarios with some combination of steep gradients, high initial dispersal and/or strong local selection. During range expansion, somewhat counterintuitively, the evolution of lower dispersal along steep gradients allowed for increased expansion rates (as seen in Figure 3a where mean expansion distance is higher with the evolution of dispersal on the right tail of the figure). This is because lower dispersal reduces maladaptive gene flow, which allows local adaptation to increase the population growth rate (Figure 5). These results emphasize the fact that expansion speed is determined by the combination of dispersal and population growth rate—when reduced dispersal increases the growth rate via local adaptation, this can positively impact expected speed (see also Phillips, 2012). Thompson and Fronhofer (2019) found concordant results in that high rates of (non-evolving) dispersal stymied adaptation, range expansion and species persistence during environmental change in a metacommunity. These insights have potentially important consequences for our understanding of the 'critical environmental gradient' (a gradient so steep that range expansion is wholly prevented) in earlier range limit models with static dispersal (Polechová, 2018; e.g. Polechová & Barton, 2015). Populations may be able to spread across steeper gradients than expected if the evolution of lower dispersal rates facilitates local adaptation.

Future efforts and model extensions

Our work builds on theory exploring how environmental heterogeneity influences patterns of dispersal evolution by asking this explicitly in the context of range expansion across environmental gradients. We are currently extending the model to explore the effects of interspecific competition on eco-evolutionary dynamics during expansion. Future models could incorporate additional forms of environmental heterogeneity, such as patchiness (Hanski et al., 2004) or temporal variation in patch quality (McPeek & Holt, 1992), across continuous, two-dimensional landscapes. While our model incorporates Allee effects insofar as reproduction depends on the presence of at least one individual of the opposite sex within an individual's patch, varying the strength of these effects, (Travis & Dytham, 2002), as well as modelling various mating systems (Usui & Angert, 2024; Williams et al., 2019), would help generalize these results to even more diverse taxa. While we focused on two quantitative traits with relatively simple additive genetic architecture, an exploration of the effects of changes in heritability, genetic correlations (Duputié et al., 2012), rate of deleterious mutation (Gilbert et al., 2017) or plasticity would also be fruitful.

Predicting and managing range expansions

Future distributions of both native and invasive species are difficult to predict (Fourcade et al., 2018; Gallien et al., 2010; Rumpf et al., 2018). Our work suggests that spread (and the predictability of spread) will be strongly influenced by both dispersal evolution and adaptation to environmental gradients. For example, in our simulations with dispersal evolution, the mean and standard deviation of expansion distance decreased by approximately 80% between the homogeneous landscape and the shallowest gradient. Thus, models like ours that incorporate such evolutionary dynamics can hopefully help generate more accurate predictions of invasive species spread. Of course, in practice, we only rarely have the data needed to parameterize such predictive models—namely, dispersal ability, growth rate and gradient steepness. But these data are straightforward, if not easy, to collect. A long history of common garden and transplant studies have assessed fitness differences among populations sourced at varying distances from the planting site (Antonovics & Bradshaw, 1970; Bachmann & Van Buskirk, 2021; Colautti & Barrett, 2013; Gorton et al., 2022; Lee et al., 2003; Maron et al., 2004; Peschel & Shaw, 2023), which can be used to calculate fitness cost per unit distance (i.e. how quickly is fitness expected to decline for an individual dispersing from its natal patch). Dispersal rates can be estimated based on spread rates or dispersal trials (e.g. Clark et al., 2022).

Our model also suggests heuristics regarding expectations for range expansions that could help prioritize conservation or management actions, even in the absence of fitting a simulation model. For example, we can expect that elevational gradients will be steeper than latitudinal gradients (e.g. Bachmann et al., 2020). Thus, we may be less likely to see evolution of increased dispersal during invasion along elevational gradients. For native species where persistence during climate change will require upslope range expansion (Geppert et al., 2023), such local selection pressure could hinder the potentially positive effects of dispersal evolution in accelerating tracking of suitable habitat (Weiss-Lehman & Shaw, 2020). In general, recognition of the interplay between dispersal and local adaptation will lead to a greater understanding of species range expansions and more predictive models of spread dynamics.

AUTHOR CONTRIBUTIONS

JWB and CW-L conceived the main study design and model structure. EIC and RAH conceived the *Diorhabda* study design, and EIC collected and analysed the *Diorhabda* data. JWB performed all simulations and analyses, with all authors contributing to revisions. JWB wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

ACKNOWLEDGEMENTS

We thank two anonymous reviewers and the Weiss-Lehman lab for comments on this manuscript. This work was supported by grants from the National Science Foundation (DBI-2010892 to JWB, EPS-2019528 to CW, DEB-2230806 to CW and JWB and DEB-1930650 to RAH) and the United States Department of Agriculture (NIFA AFRI Predoctoral Fellowship 2021-09368 to EIC). Any opinions, findings and conclusions expressed in this material are those of the authors and do not necessarily reflect the views of NSF or USDA.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14472.

DATA AVAILABILITY STATEMENT

All SLiM and R code, simulation parameters, *Diorhabda* data, and the simulation results needed to reproduce the figures in this manuscript are available on Figshare (https://doi.org/10.6084/m9.figshare.c.6981030).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Benning, J.W., Clark, E.I., Hufbauer, R.A. & Weiss-Lehman, C. (2024) Environmental gradients mediate dispersal evolution during biological invasions. *Ecology Letters*, 27, e14472. Available from: https://doi.org/10.1111/ele.14472