

Dispersal evolution during range expansions and shifts

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Prepared using the suggested L^AT_EX template for *Am. Nat.*

Introduction

Range expansions and shifts have become ubiquitous features of modern biomes. For centuries,
3 humans have facilitated the range expansions of invasive species through travel, commerce, agriculture, and other routes (Elton, 1958), a trend that has only increased with further globalization (Hulme, 2009). In recent decades, humans have further eroded traditional biogeographic
6 boundaries through anthropogenic climate change, leading to range shifts among a wide variety of taxa (Parmesan, 2006). Understanding the dynamics of such large-scale population movements is critical to predicting ecological dynamics and conserving biodiversity in the anthropocene. Range
9 expansions in particular have long been studied in both ecological (Skellam, 1951) and evolutionary (Fisher, 1937) contexts, however recent research has emphasized the significance of interactions between ecological and evolutionary mechanisms in driving the dynamics of range expansions (Burton et al., 2010; Phillips et al., 2006; Shaw and Kokko, 2015).

In particular, rapid evolution of dispersal ability has been implicated as an important driver of range expansion dynamics in a variety of species (Alex Perkins et al., 2013; Fronhofer and Altermatt, 2015; Ochocki and Miller, 2017; Weiss-Lehman et al., 2017; Williams et al., 2016). In
15 the course of a range expansion, individuals become spatially sorted according to their dispersal abilities (Shine et al., 2011), with edge populations composed primarily of highly dispersive individuals. As edge populations are typically characterized by low population densities, resulting in
18 low intraspecific competition, individuals at the edge also tend to have high reproductive success in the absence of Allee effects or other extrinsic factors. This combination of assortative mating of
21 highly dispersive individuals with increased reproductive success at the expansion edge ("spatial selection" (Phillips et al., 2010)) can lead the evolution of increased dispersal abilities at the edge so long as at least some components of dispersal are heritable. Such evolution has been shown to

24 occur over relatively short time scales (6 – 10 generations) in laboratory experiments, leading to
higher and more variable rates of spread (Ochocki and Miller, 2017; Weiss-Lehman et al., 2017;
Williams et al., 2016).

27 Spatial selection is also expected to affect dispersal evolution in range shifts due to climate
change. In the United Kingdom, northern range margin populations of two species of bush crickets
and the speckled wood butterfly have all shown increased dispersal capabilities relative to southern
30 populations (Hill et al., 1999; Thomas et al., 2001). However, given the increasing rate of climate
change (Chen et al., 2017) and the substantial gap between current dispersal capabilities and those
necessary to keep pace with climate change in some species (Schloss et al., 2012), it is unclear
33 if dispersal evolution will be enough to rescue faltering populations. Some theoretical models
suggest that it could indeed provide a buffer, allowing populations otherwise doomed to extinction
to persist (Boeye et al., 2013), but others suggest dispersal evolution may be insufficient to rescue
36 otherwise struggling populations (Weiss-Lehman and Shaw *in revision*).

The key factor likely to determine the potential role of dispersal evolution in range shifts due to
climate change is the speed with which it occurs. If evolution of dispersal ability occurs too slowly
39 relative to the speed of climate change it cannot rescue lagging populations. Importantly, theoretical
models finding opposing results for the role of dispersal evolution in climate driven range shifts
have made different assumptions about the life history of the organisms and the nature of dispersal.
42 Some of the differences among the models, including sexual vs. asexual reproduction, haploid
vs. diploid genetics, and the number of loci encoding dispersal, have all been shown to affect the
rate of evolution due to natural selection in other traits (Goddard et al., 2005; Orr and Otto, 1994;
45 Pritchard et al., 2010; Zeyl et al., 2003). However, as dispersal evolution occurs primarily via
the spatial sorting of individuals rather than via traditional natural selection (Shine et al., 2011),
it is unclear how strongly these features might influence the evolution of dispersal during range

48 expansions and shifts. Further, to make relevant predictions for conservation in the face of climate
change, it is necessary to relate the speed of dispersal evolution in these different contexts to the
rate of climate change to better understand when it may be a relevant factor in climate driven range
51 shifts.

Here, we constructed an individual-based model to explore the role of genetic structure (ploidy
level and the number of loci encoding dispersal) and the mode of reproduction (sexual vs. asexual
54 and the role of self fertilization) in dispersal evolution in range expansions and shifts. By using a
single, common framework to explore these factors, we are able to directly compare the effect of
each on the rate of dispersal evolution and relate them to the extinction risk faced by populations
57 under varying speeds of climate change. We first explore the rate of dispersal evolution in range
expansions to quantify the time required to evolve a threshold dispersal phenotype. We then use
simulations of range shifts to quantify the extinction risk faced by a population due to climate
60 change and relate that directly to the speed with which dispersal ability is able to evolve.

Therefore we use a common theoretical framework to investigate the role of each in the evolu-
tion of dispersal in range expansions. We then relate the speed with which the dispersal phenotype
63 evolves to the likelihood of population rescue via dispersal evolution during climate induced range
shifts.

Model overview

66 *Purpose*

Here, we use a common modeling framework to disentangle the role of different factors on the
speed of dispersal evolution in moving populations. Specifically, we vary the number of loci defin-
69 ing the dispersal trait, the number of chromosome copies comprising the genome (haploid vs.

diploid), and the mode of reproduction (asexual vs. sexual). For each scenario, we simulate population dynamics within a one dimensional stable range for 5000 generations to reach an equilibrium distribution of genotypes. Then, we simulate a range expansion with individuals from the edge of the range to quantify the time it takes for the expanding populations to reach a threshold dispersal phenotype. Finally, we use the original population to simulate climate change with a speed equal to the speed of an expansion wave defined by the same threshold dispersal phenotype. We can therefore directly compare the time to evolution of the dispersal phenotype in the range expansion with the extinction probability of populations shifting their range.

State variables and scales

We track individuals defined by either one or two chromosome copies and a number of loci defining dispersal traits. The genetic structure and mode of reproduction are set at the beginning of each simulation. In sexually reproducing, dioecious populations, individuals are further delineated as male and female. Space is modeled as a linear, one dimensional array of discrete habitat patches. The carrying capacity of each patch varies and is used to define the characteristics of the population's range. For simplicity, there is no variation in intrinsic fitness among individuals.

Process overview and scheduling

We assume discrete, non-overlapping generations divided between two phases: dispersal and reproduction. Individuals first disperse from their natal patches with distance determined by their phenotypes and direction assigned randomly. After dispersal, individuals reproduce within their new patches, thus limiting the mating pool to local individuals when reproduction is sexual. The number of successful reproduction events (i.e. leading to a surviving offspring) in each patch is determined with a stochastic implementation of the classic Ricker model with parentage assigned

randomly. Individuals may contribute to multiple successful reproduction events and no restrictions
93 are placed on the number of mates for either males or females in dioecious populations (polygy-
nandrous mating). Offspring inherit alleles from their parent(s) assuming independent segregation
and a mutation process. After reproduction, all members of the current generation perish and their
96 offspring disperse to begin the next generation.

Design concepts

Emergence

99 Emergent phenomena include the spatial distributions of population abundance, genetic diversity,
and dispersal phenotypes in the stable range at equilibrium, the evolutionary trajectories of disper-
sal in expanding and shifting populations, and the extinction probability of populations undergoing
102 range shifts.

Stochasticity

Stochastic processes include reproduction, dispersal distance and direction, and inheritance of loci
105 (described below). Environmental conditions are deterministic to remove any confounding influ-
ence of environmental stochasticity on the results.

Interactions

108 Individuals in all experimental scenarios interact via density dependent competition within patches.
In scenarios with sexual reproduction and without obligate selfing, individuals also interact via
mating within local patches.

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Desired output

After reaching a spatial equilibrium within a stable range, each simulation saves the full details of all individuals from the latest generation. Using that output, we then simulate two additional scenarios: a range expansion and a range shift. From the range expansion scenario, we save aggregate data on population abundance and the mean and variance of dispersal values within each patch in each generation. Additionally, save the generation at which the population at the edge of expansion reaches the threshold dispersal value. From the range shift, we similarly aggregate data on population abundance and the mean and variance of dispersal values from each patch in each generation. If the population does not go extinct before evolving the dispersal phenotype required to track climate change, the simulation will continue for an additional 50 generations to ensure that the population survives, and then output the full details of all individuals from the latest generation.

Details

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Initialization

To begin each simulation, several patches in the center of the range are populated to full carrying capacity (K_{max}) with individuals whose genotypes are randomly generated from a normal distribution of allele frequencies. Simulations then continue for 5000 generations within the stable range to reach a spatial equilibrium, after which range expansion and range shift simulations are performed. For the range expansion simulations, K_{max} individuals are randomly chosen from the edge of the landscape and placed within a single patch of an empty, uniformly habitable landscape. Due to computational constraints, we track only the leading edge of the expansion rather than tracking every individual in the expanding population. For the range shift, the entire original population is

132 used as the environmental conditions begin to shift in space to simulate climate change.

Submodels

Defining the abiotic environment. Environmental conditions in each patch are defined by the carrying capacity, $K(x)$. To simulate range boundaries, we assume that $K(x)$ is set to a constant, maximum value, K_{max} , throughout the core of the range (defined by τ). At the range edges, $K(x)$ declines to 0 at a constant proportion of γ per patch. The range center is defined by β , which is held constant for the initial simulations of a stable range and then shifted linearly to simulate climate change (see below). More precisely, the carrying capacity of each patch is given by

$$K(x) = \begin{cases} \max(0, (1 - \gamma(\beta(t) - \tau - x))K_{max}) & x < \beta(t) - \tau \\ K_{max} & \beta(t) - \tau \leq x \leq \beta(t) + \tau \\ \max(0, (1 - \gamma(x - \beta(t) - \tau))K_{max}) & x > \beta(t) + \tau \end{cases} \quad (1)$$

To simulate climate change, $\beta(t)$ is varied linearly with time at rate v (i.e. $\beta(t) = vt$). For
 135 simulations of range expansion, the environmental conditions are simplified to a homogenous landscape of patches all with carrying capacities of K_{max} .

Local population dynamics. Population growth within each patch is modeled as a stochastic implementation of the classic Ricker model (Melbourne and Hastings, 2008; Ricker, 1954). Importantly, this equation can account for asexual reproduction or sexual reproduction with explicit males and females (Melbourne and Hastings, 2008). In the simpler cases of asexual reproduction and sexual reproduction of monoecious individuals, the expected population size in patch x at time $t + 1$ is given by

$$\hat{N}_{t+1,x} = N_{t,x} \text{Re}^{\frac{-RN_{t,x}}{K(x)}} \quad (2)$$

where $N_{t,x}$ is the current population size of patch x , R is the intrinsic growth rate, and $K(x)$ is the carrying capacity of patch x . When modeling population growth of sexually reproducing, dioecious individuals, the expected population size in patch x at time $t + 1$ becomes

$$\hat{N}_{t+1,x} = F_{t,x} \frac{R}{\psi} e^{\frac{-RN_{t,x}}{K(x)}} \quad (3)$$

where $F_{t,x}$ is the number of females in patch x at time t and ψ is the expected ratio of female offspring. To account for demographic stochasticity, the expected population size is then used to generate the realized population size in the next generation from a Poisson distribution.

$$N_{t+1,x} \sim \text{Poisson}(\hat{N}_{t+1,x}) \quad (4)$$

This realized population size in the next generation can also be thought of as the number of successful reproduction events in the current generation. For each of these successful reproduction events, parentage is assigned randomly, according to the mode of reproduction. For asexual reproduction, a single individual is drawn randomly and with replacement (thus allowing for multiple offspring from a single individual) from the local population for each successful reproduction event. For sexual reproduction events, parental pairs are formed according to the nature of individuals in the population (monoecious or dioecious) and the probability of self fertilization (ω). In populations of monoecious individuals, a single parent is first randomly selected from the local population. With probability ω the individual self fertilizes and with probability $1 - \omega$ a second individual is required. If no other individual is present in the patch, then the reproduction event fails. Thus, by varying the value of ω , we can simulate populations ranging from obligate selfing to obligate outcrossing and the resultant mate finding Allee effect. In populations of dioecious individuals, each reproduction event must include both a male and female parent, imposing an even greater mate finding Allee effect in these populations. Males and females are selected randomly and with replacement from the population for each reproduction event and both males and females can mate

multiple times (polygynandry).

153 Once parentage is determined for each reproductive event, offspring inherit alleles from their
parent(s), assuming no linkage among loci and a mutation process defined by two parameters:
the per allele probability of mutation (v_m) and the standard deviation of mutational effects (σ_m).
156 Thus, when a mutation occurs with probability v_m , the new allele value is drawn from a normal
distribution with mean equal to the original allele value and a standard deviation of σ_m).

Dispersal. Finally, individuals disperse according to an exponential dispersal kernel defined by
each individual's dispersal phenotype. An individual's dispersal phenotype is the expected disper-
sal distance and is given by

$$d_i = \frac{\hat{d}e^{\rho\Sigma L}}{1 + e^{\rho\Sigma L}} \quad (5)$$

where \hat{d} is the maximum expected dispersal distance in terms of discrete patches, ρ is a constant
determining the slope of the transition between 0 and \hat{d} , and the summation is taken across all al-
leles contributing to dispersal. Thus, loci are assumed to contribute additively with no dominance
or epistasis. The expected dispersal distance, d_i is then used to draw a realized distance from an
exponential dispersal kernel and direction (forward or backward in the linear landscape) is deter-
mined randomly. Since the dispersal phenotype is the expected value of the exponential dispersal
kernel, it can be used directly to calculate the two dimensional diffusion coefficient of population
spread (D). Specifically, since d_i^2 represents the mean squared displacement of an individual with
dispersal phenotype d_i , the one dimensional diffusion coefficient can be calculated as

$$D = \frac{1}{2}d_i^2 \quad (6)$$

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