Local adaptation and dispersal evolution interact to drive population response to climate change

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1 Introduction

Climate change is expected to dramatically reshape global biogeographic patterns as some species shift their ranges to track changing environmental conditions (CITATION). These range shifts are generally expected to proceed upwards in latitude, elevation, or both as average global temperatures continue to rise (CITATION). In fact, contemporary range shifts have already been observed in a wide range of taxa (CITATION). Such range shifts present significant challenges to current and future conservation efforts as they can result in the extinction of populations failing to track a changing climate (CITATION), the creation of novel species assemblages as not all species shift their ranges at the same rate or at all (CITATION), or both. It is therefore crucial to understand the dynamics of such climate induced range shifts to better inform current and future conservation work.

While contemporary range shifts are a relatively new phenomenon, important insights can be gained from the related but distinct process of range expansion. Range expansions have been studied for decades, leading to a robust understanding of both the ecological (CITATIONS) and evolutionary (CITATIONS) mechanisms responsible for shaping such expansions. For example, while the speed of a range expansion can be well approximated by a combination of the species' intrinsic growth rate and dispersal ability (CITATIONS), recent research demonstrates that evolution in both of these traits can have important implications for both the mean and variance of expansion speed through time (CITATIONS). As range shifts also involve a leading edge of population advance, they are likely to be affected by similar ecological and evolutionary mechanisms

1

as have been shown to drive dynamics in range expansions (CITATIONS). However, while such insights from range expansions are valuable for understanding and predicting dynamics of range shifts, it is important to recognize that these two processes have important differences as well.

In particular, range expansions and range shifts due to climate change involve fundamentally distinct initial conditions. Range expansions typically begin from the successful establishment and subsequent spread of a small, founding population as typically occurs with the range expansions of invasive and reintroduced species (CITATIONS). Such founding populations represent samples from some larger source population and as such lack any initial spatial population structure. In contrast, range shifts involve entire populations with existing spatial structure within the initially stable range (CITATION). Such spatial structure can take the form of local adaptation within the range, degree of transition in population size from range core to edge, or some combination of the two (CITATION).

These different aspects of spatial population structure have been shown to dramatically impact the response of populations to climate change (CITATIONS). For example, the nature of the gradient forming the range edge (e.g. declines in birth rates vs. increases in extinction risk) can directly change the probability of extinction a species faces during a climate driven range shift (CITATION). A population's risk of extinction during a range shift has also been related to local adaptation within the range. Specifically, a broad environmental niche (i.e. little local adaptation) can decrease a population's ability to track a changing climate if dispersal occurs in a stepping stone manner, allowing some individuals to block dispersal of better adapted phenotypes (CITATION). Local adaptation also has the potential to interact with dispersal evolution during climate change, driving increased dispersal evolution in an asexual species (CITATION). While this result was independent of the structure of the gradient forming the range edge (CITATION), this is unlikely to hold true for sexually reproducing species. As the type of gradient forming the range edge can influence the distribution of dispersal phenotypes within the range (CITATION), it is likely that this would also influence the dynamics of local adaptation in sexually reproducing species in which different locally adapted genotypes are joined via gene flow. In fact, pollen dispersal in flowering plants has been shown to dramatically reduce the likelihood of a range shift in response to climate

change (CITATION). Evolution during range shifts due to local adaptation and dispersal evolution are likely important drivers of range shift dynamics (CITATION) and it is therefore important to consider both when predicting the dynamics of populations responding to climate change.

Here, we use a complex, individual-based model incorporating evolution in both fitness and dispersal distance to determine the interaction between local adaptation and the starkness of the gradient at the range edge in driving population dynamics during climate change. Using this model, we simultaneously vary the strength of local adaptation, the starkness of the range boundary, and the speed of climate change to ascertain the relationship among them and how dispersal evolution interacts with local adaptation to help or hinder a population's ability to track a changing climate. We additionally compare the dynamics of successful versus doomed populations to understand the factors contributing to population extinction and identify warning signs for populations in danger of extinction as a result of a range shift.

2   Methods

2.1   Overview

2.1.1   Purpose

This model tests an evolving population's ability to track a changing climate under a variety of conditions. Specifically, populations are simulated with (1) stark or gradual range boundaries, (2) strong or weak local selection pressures, and (3) varying speeds of climate change. In all simulations, individual dispersal and relative fitness are defined by an explicit set of quantitative diploid loci subject to mutation, thus allowing both traits to evolve over time. All simulations begin with stable climate conditions for 2000 generations to allow the populations to reach a spatial equilibrium before the onset of climate change. Climate change is then modeled as a constant, directional shift in the location of environmentally suitable habitat for the population (see the *Submodels* section below). Finally, simulations end with another short period of climate stability to assess the population's ability to persist and recover after shifting its range.

2.1.2 State variables and scales

The model simulates monoecious (i.e. no defined sex) individuals characterized by spatial coordinates for their location and diploid loci for both fitness and dispersal. Space is modeled as a lattice of discrete patches overlaying a continuous Cartesian coordinate system with a fixed width along the y axis and without bounds on the x axis. To avoid edge effects along the y axis, the model employs wrapping boundaries such that if an individual disperses out of the landscape on one side, it appears at the opposite end of the same row of the landscape. Patches are defined by the location of the patch center in x and y coordinates and a patch width parameter defining the relationship between continuous Cartesian space and the discrete patches used for population dynamics (see the *Submodels* section below).

The abiotic environment is defined by a parameter denoting the center of the range, the slope of the range boundary, and the width of the range. The range can then shift in space by altering the parameter defining the range center, which is how climate change is implemented in the model. Further, a gradient of phenotypic optimum values for fitness is imposed within the range to allow for local adaptation within the range boundaries. The shape and severity of this gradient is defined by the same parameter used to set the slope of the range boundary along with one other parameter describing the strength of local selection along the gradient (greater values of this parameter will lead to steeper gradients in phenotypic optima within the range). The attached figures demonstrate the shape of the range and phenotypic optima functions and how they vary with different parameter values (see equations in *Submodels*).

2.1.3 Process overview and scheduling

Time is also modeled in discrete intervals defining single generations of the population. Within each generation, individuals first reproduce within their natal patch. After reproduction, all adults die and the offspring disperse according to their dispersal kernels (*Submodels*), resulting in discrete, non-overlapping generations. Reproduction occurs according to a stochastic implementation of the logistic growth equation taking into account the mean fitness of individuals within the patch (*Submodels*). For each offspring, two parents are randomly sampled (with replacement and weighted

4

according to their fitness) from the local population. While all individuals are monoecious, selfing is allowed only when there is a single individual within a patch. Thus, high fitness individuals may produce many offspring while individuals with relatively low fitness may not produce any. Individuals inherit one allele from each parent at each loci (except in the case of selfing when individuals inherit both copies of a single parent's alleles). Loci are assumed to segregate independently and inherited loci are subject to mutation (*Submodels*). Individual dispersal distance for each offspring is drawn from a dispersal kernel defined by their dispersal trait and the direction of dispersal is drawn from a uniform distribution. The next generation then begins with all offspring in their post dispersal locations and ready to reproduce.

2.2   Design concepts

2.2.1   Emergence

Emergent phenomena in this model include the spatial equilibrium of population abundances and trait values within the stable range, the demographic dynamics of the shifting population during climate change, and the evolutionary trajectories of both fitness and dispersal traits during climate change. These are all examined in the context of their impact on the population's ability to keep pace with the changing climate.

2.2.2   Stochasticity

All biological processes in this model are stochastic including realized population growth in each patch, dispersal distances of each individual, and inheritance of loci. Environmental parameters are fixed, however, and the process of climate change (i.e. the movement of environmentally suitable habitat through time) is deterministic. Thus, the model accounts for demographic stochasticity but ignores environmental stochasticity.

2.2.3   Interactions

Individuals in the model interact via mating and density-dependent competition within patches. Other important interactions are the relationship between dispersal evolution and local adaption,

¹²⁶ particularly in edge populations, and how this relationship impacts a population's ability to avoid

¹²⁷ extinction and track a changing climate. These interactions are examined in the context of different

¹²⁸ configurations of the initial, stable range and different speeds of climate change.

2.2.4 Desired output

¹³⁰ After each model run, full details of all surviving individuals at the last time point are recorded

¹³¹ (spatial coordinates and loci values for both traits). If a population went extinct during the model

¹³² run, the time of extinction is recorded. Throughout the simulation, certain aggregated values are

¹³³ calculated and recorded for each occupied patch including the population size and the mean and

¹³⁴ variance of allele values for each trait.

2.3 Details

2.3.1 Initialization

¹³⁷ The following parameters are set at the beginning of each simulation and form the initial conditions

¹³⁸ of the model: the mean and variance for allele values of each trait, population size, location of

¹³⁹ environmentally suitable habitat, number of generations for the pre-, post-, and during climate

¹⁴⁰ change periods of the simulation, and all other necessary parameters for the submodels defined

¹⁴¹ below. Simulated populations are initialized in the center of the range and allowed to spread and

¹⁴² equilibrate throughout the range during the period of stable climate conditions. This ensures that

¹⁴³ the populations reacting to a changing climate truly represent the expected spatial distribution for

¹⁴⁴ a given range, rather than the initial parameter values used in the simulation.

2.3.2 Submodels

¹⁴⁶ **Environmentally suitable habitat** Environmentally suitable habitat is determined by the pop-

¹⁴⁷ ulation's carrying capacity as it ranges in space (K_x). The maximum achievable carrying capacity

¹⁴⁸ (K_{max}) occurs in the center of the species' range and declines with increasing distance from the

¹⁴⁹ center. Specifically, the carrying capacity at a location x is defined as a combination of K_{max} and

¹⁵⁰ a function $f(x,t)$, where $f(x,t)$ ranges from 1 in the range center to 0 far away from the center

and is defined as follows

$$f(x,t) = \begin{cases} \frac{e^{\gamma(x-\beta_t+\tau)}}{1+e^{\gamma(x-\beta_t+\tau)}} & x \le \beta_t \\ \frac{e^{-\gamma(x-\beta_t-\tau)}}{1+e^{-\gamma(x-\beta_t-\tau)}} & x > \beta_t \end{cases} \tag{1}$$

where $beta_t$ defines the center of the area of suitable habitat at time t, τ sets the width of the range, and γ affects the slope of the function at the range boundaries (See Figure 1). To understand the relationship between γ and the slope of $f(x,t)$ at the range boundary, the partial derivative of $f(x,t)$ over the spatial dimension can be shown to be

$$f(x,t) = \begin{cases} \frac{e^{\gamma(x-\beta_t+\tau)}}{1+e^{\gamma(x-\beta_t+\tau}} & x \le \beta_t \\ \frac{e^{-\gamma(x-\beta_t-\tau)}}{1+e^{-\gamma(x-\beta_t-\tau}} & x > \beta_t \end{cases} \tag{2}$$

yielding a derivative of $\pm\frac{\gamma}{4}$ at the inflection points on either side of the range center ($x = \beta_t \pm \tau$).

Population dynamics occur within discrete patches, so to calculate a K_x value for a discrete patch from the continuous function $f(x,t)$, we use another parameter defining the spatial scale of each patch (η; See Figure 1). The local carrying capacity of a patch centered on x (K_x) is then calculated as the mean of $f(x,t)$ over the interval of the patch multiplied by K_{max}.

$$K_x = \frac{K_{max}}{\eta} \int_{x-\frac{\eta}{2}}^{x+\frac{\eta}{2}} f(x,t)dx \tag{3}$$

By varying the parameters defining $f(x,t)$, we can change both the total achievable carrying capacity of the population throughout the range (by altering both τ and γ) and the slope at which K_x declines to 0 (by altering γ). We are primarily interested in the effect of altering the slope at which K_x declines at the range boundaries, however as doing so can also alter the total achievable carrying capacity of the population, we control for this confounding factor by fixing the total area under the curve $f(x,t)$. The indefinite integral of $f(x,t)$ can be shown to be

$$\int_{-\infty}^{\infty} f(x,t)dx = \frac{2ln(e^{\gamma\tau}+1}{\gamma} \tag{4}$$

which can be solved for τ. Thus, if the total area under the curve is fixed, an appropriate value of

7

168   τ can be calculated for each value of γ.

169   Thus, γ and τ are both fixed within a given simulation and $beta_t$ (the location of the center of

170 suitable habitat) is used to simulate climate change. During the periods before and after climate

171 change β_t is constant, but to simulate climate change it varies with time as follows

$$\beta_t = \nu\eta(t - \hat{t}) \tag{5}$$

172 where ν is the velocity of climate change per generation in terms of discrete patches, η is the

173 spatial scale of each patch, t is the current generation, and $\hat{t}$ is the last generation of stable climatic

174 conditions before the onset of climate change.

175 **Local adaptation**   To allow an arbitrary degree of local adaptation within the range, the local

176 phenotypic optima $(z_{opt,x})$ is set as follows

$$z_{opt,x} = \lambda(x - \beta_t) \tag{6}$$

177 where λ defines the strength of local selection with values close to 0 resulting in little to no change in

178 phenotypic optimum across the range and values of greater magnitude resulting in large differences

179 in phenotypic optima across the range. Individual fitness $(w_{i,x})$ values are then calculated according

180 to the following equation assuming stabilizing selection

$$w_{i,x} = e^{\frac{-(z_i - z_{opt,x})^2}{2\omega^2}} \tag{7}$$

181 where ω defines the strength of stabilizing selection and z_i is an individual's fitness phenotype

182 (CITATION). All loci are assumed to contribute additively to the phenotype with no dominance

183 or epistasis, meaning an individual's phenotype is simply the sum of the individual's allele values

184 for the fitness trait.

185 **Population dynamics**   Population growth within each patch is modeled with a stochastic imple-

186 mentation of the classic Ricker model (CITATIONS). To account for fitness effects on population

growth, expected population growth is scaled by the mean relative fitness of individuals within the patch ($\bar{w}_x$). The expected number of new offspring in patch x at time $t + 1$ is then given by

$$\hat{N}_{t+1,x} = \bar{w}_x F_{t,x} \frac{R}{\psi} e^{\frac{-RN_{t,x}}{K_x}} \tag{8}$$

where $F_{t,x}$ is the number of females in patch x at time t, R is the intrinsic growth rate for the population, ψ is the expected sex ratio of the population, $N_{t,x}$ is the number of individuals (males and females) in patch x at time t, and K_x is the local carrying capacity based on the environmental conditions. To incorporate demographic stochasticity, the realized number of offspring for each patch is then drawn from a Poisson distribution.

$$N_{t+1,x} \sim Poisson(\hat{N}_{t+1,x}) \tag{9}$$

Parentage of the offspring is then assigned by random sampling of the local male and female population. The sampling is weighted by individual fitness and occurs with replacement so highly fit individuals are likely to have multiple offspring while low fitness individuals may not have any. Each offspring inherits one allele per locus from each parent, assuming no linkage among loci. After reproduction, all members of the previous generation die and the offspring disperse to begin the next generation.

Mutation   Inherited alleles are subject to mutation such that some offspring might not inherit identical copies of certain alleles from tlheir parents. The mutation process is defined by two parameters for each trait T: the diploid mutation rate (U^T) and the mutational variance (V_m^T). Using these parameters along with the number of loci defining trait T (L^T), the per locus probability of a mutation is

$$\frac{U^T}{2L^T} \tag{10}$$

Mutational effects are drawn from a normal distribution with mean 0 and a standard deviation of

$$\sqrt{V_m^T U^T} \tag{11}$$

By defining the mutation process in this manner rather than setting a probability of mutation and mutational effect directly, similar mutational dynamics can be imposed regardless of the number of loci used in the simulation.

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 dispersal distance and is given by

$$d_i = \frac{D\eta e^{\rho \Sigma L^D}}{1 + e^{\rho \Sigma L^D}} \tag{12}$$

where D is the maximum expected dispersal distance in terms of discrete patches, η is the spatial scale of discrete patches, ρ is a constant determining the slope of the transition between 0 and D, and the summation is the sum of all alleles contributing to dispersal. Thus, as with fitness, 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. The direction of dispersal is drawn from a uniform distribution bounded by 0 and 2π. If a dispersal trajectory takes an individual outside the bounds of the landscape in the y axis, the individual reappears at the same x coordinate but the opposite end of the y axis, thus wrapping the top and bottom edges of the landscape to avoid edge effects. Dispersal occurs from the center of each patch and the individual's new patch is then determined according to its location in the overlaid grid of η x η patches (see Figure 1).

2.4   Simulation descriptions

To explore the interacting role