

Dispersal evolution during range expansions and shifts

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

Model overview

Purpose

3 Range expanding populations with heritable dispersal traits are expected to evolve increased dispersal capabilities at the expansion edge due to spatial sorting of individuals by dispersal phenotype. The spatial assortment of highly dispersive individuals at the expansion edge, combined with the
6 low intraspecific competition characteristic of edge populations, can create a feedback evolutionary process acting to increase dispersal capabilities at the edge. This phenomenon has been observed in both field and laboratory populations, leading to the prediction that such dispersal evolution
9 may help species to track changing climatic conditions via range shifts. However, many factors can influence the speed with which dispersal evolves and theoretical studies have reached different conclusions as to whether dispersal evolution will help shifting populations. Importantly, however,
12 these models were constructed with different assumptions governing the underlying genetic architecture of dispersal and the mode of reproduction. 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 defining the dispersal trait, the number of chromosome
15 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 _____ generations to reach an equilibrium distribution of genotypes. Then, we simulate a
18 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
21 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

24 shifting their range.

State variables and scales

The model tracks individuals defined by either one or two chromosome copies and a number of loci
27 defining dispersal traits. The number of chromosome copies, number of loci, 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
30 define the characteristics of the population's range. For simplicity, no variation in individual fitness or local adaptation is assumed.

Process overview and scheduling

33 The model assumes 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
36 their new patches, thus limiting the mating pool to local individuals when implementing sexual reproduction. 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
39 no restrictions are placed on the number of mates for either males or females in dioecious populations (polygynandrous 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 offspring disperse to begin the next generation.

Design concepts

Emergence

This model gives rise to several different emergent phenomena, including the spatial distribution
 48 of population abundance, genetic diversity, and dispersal phenotypes in the stable range at equilibrium. Additional emergent phenomena include the evolutionary trajectories of dispersal in expanding and shifting populations and the extinction probability of populations undergoing range
 51 shifts.

Stochasticity

Reproduction, dispersal distance, dispersal direction, and all processes related to the inheritance
 54 of loci are implemented stochastically as described below. Environmental determinants of the population range (both before and during climate change) are deterministic, however. By removing the confounding influence of environmental stochasticity, we are therefore better able to understand
 57 the genetic factors influencing dispersal evolution in range expansions and shifts.

Interactions

Individuals in all experimental scenarios interact via density dependent competition within patches.
 60 In scenarios with sexual reproduction and without obligate selfing, individuals also interact via mating within local patches. Additionally, the number of loci defining dispersal, the number of chromosome copies, and the mode of reproduction can all interact to effect the distribution of
 63 genotypes within the stable range, the time required to evolve the threshold dispersal level during range expansion, and, therefore, the probability of extinction during climate-induced range shifts.

Desired output

66 After reaching a spatial equilibrium within a stable range, each simulation will output the full de-
tails of all individuals from the latest generation. Using that output, we will simulate two additional
scenarios: a range expansion and a range shift. From the range expansion, will save aggregate data
69 on population abundance and the mean and variance of dispersal values within each patch in each
generation. Additionally, we will output the generation at which the population at the edge of ex-
pansion reaches the threshold dispersal value. From the range shift, we will similarly aggregate
72 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 re-
quired to track climate change, the simulation will continue for an additional ____ generations to
75 ensure that the population survives, and then output the full details of all individuals from the latest
generation.

Details

Initialization

78 To begin each simulation, several patches in the center of the range are populated to full carrying
capacity with individuals whose genotypes are randomly generated assuming a normal distribution
81 of allele frequencies. Populations are then allowed to grow and reach a spatial equilibrium within
the stable range for a number of generations, after which range expansion and range shift simula-
tions are performed. For the range expansion simulations, a number of individuals are randomly
84 chosen from the edge of the landscape and placed within a single patch of an empty, uniformly
habitable landscape. Due to computational restraints, we track only the leading edge of the expan-

sion (defined as ----) rather than tracking every individual in the expanding population. For the
87 range shift, the entire original population is 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, the extent of which is defined by τ . Then, at the range edges, $K(x)$ declines to 0 at a constant proportion of γ per patch. The range is then centered on 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

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

90 To simulate climate change, $\beta(t)$ is varied linearly with time at rate v (i.e. $\beta(t) = vt$). For 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 with 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 case of asexual reproduction

and sexual reproduction of monoecious individuals, the expected population size in patch x at time $t + 1$ is given by

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

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 sex ratio among 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.

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

93 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, 96 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 99 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 102 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 effects that result. In populations of dioecious

105 individuals, each reproduction event must 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
108 multiple times (polygynandry). Once parentage is determined for each reproductive event, off-
spring 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
111 of mutational effects (σ_m). 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

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

Literature Cited

- Melbourne, B. A., and A. Hastings. 2008. Extinction risk depends strongly on factors contributing to stochasticity. *Nature* 454:100.
- 117 Ricker, W. E. 1954. Stock and recruitment. *Journal of the Fisheries Board of Canada* 11:559–623.