



# The genetic signature of rapid range expansions: How dispersal, growth and invasion speed impact heterozygosity and allele surfing



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## ABSTRACT

As researchers collect spatiotemporal population and genetic data in tandem, models that connect demography and dispersal to genetics are increasingly relevant. The dominant spatiotemporal model of invasion genetics is the stepping-stone model which represents a gradual range expansion in which individuals jump to uncolonized locations one step at a time. However, many range expansions occur quickly as individuals disperse far from currently colonized regions. For these types of expansion, stepping-stone models are inappropriate. To more accurately reflect wider dispersal in many organisms, we created kernel-based models of invasion genetics based on integrodifference equations. Classic theory relating to integrodifference equations suggests that the speed of range expansions is a function of population growth and dispersal. In our simulations, populations that expanded at the same speed but with spread rates driven by dispersal retained more heterozygosity along axes of expansion than range expansions with rates of spread that were driven primarily by population growth. To investigate surfing we introduced mutant alleles in wave fronts of simulated range expansions. In our models based on random mating, surfing alleles remained at relatively low frequencies and surfed less often compared to previous results based on stepping-stone simulations with asexual reproduction.

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## 1. Introduction

Range expansions explain the wide spatial distribution of many dominant species. Unfortunately however, researchers often have only a snapshot of the extent of a recently expanded range rather than a complete spatiotemporal dataset. Genetic data have been used to elucidate processes underlying range expansions based on these snapshots, from our own planetary conquest (Ramachandran et al., 2005) to the post-glacial expansion of grasshoppers (Hewitt, 1999). Such insights, based on snapshots of genetic patterns on the landscape, are predicated on models that connect the dynamics, movement and genetics of populations. Thus, spatiotemporal genetic models are increasingly relevant as we accumulate large genetic databases. In this research we introduce integrodifference models as an alternative modeling framework in invasion genetics

with a sound mathematical and ecological basis. Integrodifference equations are discrete-time, continuous-space models that apply to range expansions in which populations have synchronized growth and dispersal stages (Neubert et al., 1995). Thus, they are useful for many herbaceous, invertebrate, and vertebrate species prone to invasion (Kot et al., 1996).

Currently, invasion models with analytical solutions for the patterns of genetic diversity that they produce are limited to the island model (Wright, 1951; Buerger and Akerman, 2011) and the stepping-stone model (Kimura and Weiss, 1964; Thibault et al., 2009; DeGiorgio et al., 2011; Slatkin and Excoffier, 2012). In the island model, subpopulations receive migrants at a constant rate from a single unchanging source population, whereas in the stepping-stone model, unoccupied demes are colonized sequentially one after another, and only receive migrants from adjacent subpopulations (Kimura and Weiss, 1964; DeGiorgio et al., 2009, 2011). Many dispersing organisms however, can move to locations beyond adjacent unoccupied areas (Levin et al., 2003) and dispersal is an important determinant of the speed of population expansion in space (Kot et al., 1996). For these reasons, neither the island nor the stepping-model in their original form is realistic in terms of population processes or dispersal (Le Corre and Kremer, 1998).

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Realism has been added in modeling studies in a variety of ways. The stepping-stone model has been amended to include more realism by incorporating logistic population growth (Austerlitz et al., 1997). The consequences of Allee effects have also been explored in haploid model systems using the reaction–diffusion framework (Hallatschek and Nelson, 2008; Roques et al., 2012). The impact of stepping-stone, diffusive, and leptokurtic dispersal on genetic patterns has been explored by Nichols and Hewitt (1994) and by Ibrahim et al. (1996) using simulations featuring logistic population growth. Other simulation studies investigated differences between the effect of stratified and diffusive dispersal on the genetic structure of maternally inherited genes (Le Corre et al., 1997) and on genetic diversity along axes of range expansion (Bialozyt et al., 2006).

Results from simulations and simple models with analytical solutions underpin our understanding of how heterozygosity within populations decreases along axes of expansion (Austerlitz et al., 1997; Le Corre et al., 1997; Nichols and Hewitt, 1994). Heterozygosity reduction in expanding populations is a consequence of genetic drift that results from population bottlenecks at the front of range expansions (Austerlitz et al., 1997). Heterozygosity loss due to genetic drift can explain how genetic diversity is reduced at the front of expanding populations, but another mechanism called allele surfing (Edmonds et al., 2004; Hallatschek et al., 2007; Hallatschek and Nelson, 2010; Lehe et al., 2012) may explain why certain alleles persist there. In allele surfing, alleles and mutations that occur near the front of population expansions are able to proliferate and achieve higher frequencies than expected in populations at equilibrium (Excoffier and Ray, 2008). Most studies of allele surfing have focused on stepping-stone models with maternally inherited alleles, which is equivalent to asexual reproduction (Edmonds et al., 2004; Hallatschek et al., 2007; Hallatschek and Nelson, 2008; Lehe et al., 2012). Therefore, the importance of allele surfing in range expansions with other mating systems and wide dispersal has not been established.

In part due to wide dispersal, many biological invasions expand quickly rather than at the evolutionary time scales typically associated with human expansion out of Africa (Ramachandran et al., 2005) or with the expansion of oak trees in Europe (Hewitt, 1999). Therefore ecologists are often interested in understanding processes that underly expansions that have occurred over ecological time scales of tens of years rather than over thousands of years. The speed at which populations expand in space is determined by demographic growth and dispersal (Kot et al., 1996) and therefore models that clearly connect invasion speeds to these population traits are essential when studying rapid range expansions. Using integrodifference equations as the basis for our investigation of the genetic signature of range expansions allowed us to compute theoretical invasion speeds from demographic growth and dispersal parameters using classic theory (Kot et al., 1996).

The primary objective of this research was to study genetic diversity patterns arising in rapid range expansions. We therefore used integrodifference equation-based models to simulate over relatively short time periods with wide dispersal kernels that overlapped many demes. We compared the relative impacts of demographic growth and dispersal on the genetic signatures of range expansions spreading at the same speed, explored the genetic consequences of varying diffusivity in expansions with identical demography, simulated anisotropic range expansions in two spatial dimensions, and compared heterozygosity patterns as well as the distribution of surfing alleles produced by simulated range expansions with a variety of dispersal kernels. As much of the previous work on allele surfing in range expansions has focused on asexual or haploid model systems, we also contrasted results from simulations with random mating to those with asexual mating.

## 2. Models

### 2.1. Population dynamics and spread models

We consider a species with Beverton–Holt population dynamics (Beverton, 1957). The species reproduces synchronously before dispersing in space according to a dispersal kernel  $k(x - y)$ , which describes the probability that an animal moves from location  $y$  to location  $x$ . The resulting integrodifference model is

$$f(N_t(y)) = \frac{R_0(N_t(y))}{1 + (R_0 - 1)N_t(y)/K}, \quad y \in \Omega, \quad (1a)$$

$$N_{t+1}(x) = \int_{\Omega} k(x - y)f(N_t(y))dy, \quad (1b)$$

where  $N_t(x)$  is the population density in space at time  $t$ ,  $R_0$  is the geometric growth parameter and  $K$  is the carrying capacity. The infinite one-dimensional spatial domain is represented by  $\Omega$ .

The dispersal kernel formulation is very flexible and a variety of dispersal behaviors can be modeled by changing it (Neubert et al., 1995). The assumption of spatially homogenous diffusive dispersal is embodied in the Gaussian dispersal kernel:

$$k(x - y) = \frac{1}{\sqrt{4\pi D}} \exp\left(\frac{-(x - y)^2}{4D}\right), \quad (2)$$

where  $D$  is the diffusion constant. Note our diffusion constant represents  $Dt$  in standard formulations of random-walk-based diffusion models (Codling et al., 2008). This diffusion constant can be derived based on the probability that an individual will jump to the right, to the left, or not move (Codling et al., 2008). Although it is tempting to use diffusion to describe all animal movement, dispersal in many species is better approximated using leptokurtic distributions (Walters et al., 2006; Skarpaas and Shea, 2007) in which individuals have a higher probability of dispersing short and long distances than in a Gaussian kernel with the same variance. Therefore, we also simulate range expansions with double exponential (Laplace) and fat-tailed kernels, both of which are leptokurtic.

The Laplace kernel, when derived based on a diffusive model with constant settling (Neubert et al., 1995), has the form

$$k(x - y) = \frac{1}{2} \sqrt{a/D} \exp(-\sqrt{a/D}|x - y|), \quad (3)$$

where  $D$  is the diffusion constant as before,  $a$  is the constant settling rate, and  $k(x - y)$  describes the distribution of settled individuals.

Fat-tailed dispersal kernels are those without exponentially bounded tails. Authors have argued based on simulation studies that longer-distance dispersal is increasingly selected for over the course of invasions leading to the evolution of fat-tailed kernels (Phillips et al., 2008). A typical fat-tailed kernel comes from Wallace (1966) and Taylor (1978) who described the relationship between distance from a release point and density of fruit flies using

$$k(x - y) = \frac{\alpha^2}{4} \exp(-\alpha\sqrt{|x - y|}), \quad (4)$$

where  $\alpha$  determines the rate of decrease with the square root of distance.

For kernels with moment-generating functions such as (2) and (3), the model equation (1) has traveling wave solutions that connect the zero equilibrium in front of the wave to the carrying capacity equilibrium at the top of the wave (Kot et al., 1996). For range expansions that have these traveling wave solutions, we can compute the minimum traveling wave speed. Locally introduced populations that grow and spread according to the Gaussian kernel (2) have a minimum traveling wave speed  $c(R_0, D) = 2\sqrt{D \ln(R_0)}$

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