

Dispersal and speciation in a complex habitat

Ben Haller

*Department of Biology,
McGill University, Montreal, Canada*

Goal

To investigate how speciation processes and resultant biodiversity patterns are affected by spatial environmental heterogeneity, dispersal, mate choice, and temporal environmental variability.

Background and motivation

For Darwin (1859), the origin of species was the “mystery of mysteries,” and it remains poorly understood even today. Speciation, as the process that generated much of the biodiversity in the world today, is fundamental to the nature of life on earth; it is thus clearly worthy of study in its own right. A better understanding of speciation also has consequences for conservation biology and for the mitigation of anthropogenic ecological disturbances. It has previously been shown that adaptation to a local environment together with local competition for resources can promote speciation (Heinz et al. 2009). This project will investigate the effects of spatial environmental heterogeneity and dispersal distance on speciation dynamics and the resultant biodiversity patterns. Time permitting, temporal environmental variability and the evolution of dispersal and mate choice may also be explored within this framework. This research will be conducted using an individual-based evolutionary model, building on previous work in IIASA’s Evolution and Ecology Program.

Speciation results, fundamentally, from the genetic divergence of populations. The dispersal of individuals between populations, or more precisely the gene flow that results when those dispersers interbreed with residents, is commonly thought to hinder such genetic divergence, and therefore to impede speciation, although there may be exceptions to this rule of thumb (Garant et al. 2007). Heinz et al. (2009) modeled the interaction between dispersal evolution and speciation, and found that the evolution of short-range dispersal promoted speciation. Payne et al. (in preparation) extended the model of Heinz et al. (2009) to include the evolution of conditional dispersal, which was found to inhibit speciation in sexual populations. These models involved only a linear environmental gradient, so that the effects of more complex spatial structures on speciation dynamics have yet to be explored in such a framework.

Assortative mating can promote genetic divergence by increasing the reproductive isolation of populations even when dispersal connects spatially distributed populations (Garant et al. 2007), and several theoretical models have explored this idea. Doebeli and Dieckmann (2003) found that the evolution of mate choice along an environmental gradient could lead to parapatric speciation. Yukilevich and True (2006) modeled the coevolution of dispersal and assortative mating in a “two-island” system representing secondary contact after allopatric divergence. Gavrillets and Vose (2009) observed adaptive radiation resulting from evolution in an “island colonization” model consisting of ecologically random patches, with the evolution of habitat preference and mate choice. Again, these models involved only simple or random spatial structures.

Real environments vary over time as well as in space. Species can cope with environmental variation through adaptation or range shifts. Some prior work has examined adaptation and range shifts in response to spatial or temporal variability (Kirkpatrick and Barton 1997; Pease et al. 1989; Polechová et al. 2009), but not in conjunction with the evolution of dispersal and assortative mating, and not in the context of a complexly structured spatial landscape.

The proposed research will thus synthesize previous work, while also examining scenarios that were left unexplored by previous studies. In particular, this project will examine the combined effects of both spatial structure and dispersal on speciation.

It is clear from both theoretical and empirical studies that dispersal, ecology, behavior, and adaptation are complexly intertwined (Pelletier et al. 2009), and that spatial and temporal variation in environmental conditions play an important role in driving evolution (Mathias et al. 2001; McPeck and Holt 1992). While modeling these factors in isolation is interesting, it is important also to examine them together, to understand how they interact with each other, to weigh their relative importance, and to build a broader picture of how speciation emerges from lower-level processes.

A better understanding of adaptation and speciation is of more than theoretical interest, because the factors that promote the generation of biodiversity are likely related to the factors that preserve existing biodiversity. Conservation of biodiversity in the face of rapid anthropogenic environmental change (such as deforestation, habitat fragmentation, and climate change) demands a better understanding of how environmental and ecological factors support biodiversity (Jackson and Sax 2010). Evolutionary responses to environmental and ecological change can be rapid, with important implications for conservation (Stockwell et al. 2003). Furthermore, specific conservation policies, such as assisted migration, wildlife corridors, and captive breeding programs, are precariously balanced atop our very limited understanding of the role of dispersal and gene flow in the persistence of populations, the maintenance of genetic diversity, and the promotion of local adaptation (Storfer 1999; Sutherland et al. 2004).

Research questions

The goal of this project is to improve our understanding of the process of parapatric speciation in heterogeneous environments. Previous research has established that a linear environmental gradient can drive speciation through the evolution of dispersal and mating distance (Heinz et al. 2009) and through the evolution of assortative mating (Doebeli and Dieckmann 2003). In this project, I will address the following questions:

- What effect does nonlinear variation of environmental conditions at different spatial scales have on local adaptation, range limitation, population persistence, and speciation?
- How do dispersal and mate choice coevolve and drive speciation, under different patterns of spatial variation?
- What effect does temporal variability have on these evolutionary dynamics, for different rates, magnitudes, and patterns of environmental change?

Methods and work plan

The starting point for this research project is the individual-based spatially explicit model of Heinz et al. (2009). Briefly, this model simulates the evolution of individuals that inhabit a two-dimensional space in which environmental conditions vary along one spatial dimension, forming a linear ecological gradient, while the other spatial dimension is ecologically neutral.

Each individual has three genetic traits: an ecological trait that governs the individual's fitness at any given position along the ecological gradient, a dispersal trait that governs its natal dispersal distance, and a mating trait that governs the strength of its preference for spatially proximate mates over more distant mates. I intend to work with both an asexual and a sexual model version (the asexual version does not include the mating trait). Individuals are born at a constant rate, and die at a rate that depends on the strength of competition exerted by other individuals in the environment, so that selection is frequency-dependent. Offspring inherit parental traits with mutation. For different strengths of competition and slopes of the environmental gradient, evolutionary outcomes range from a homogenized mixture of long-range dispersers to distinct "species" that maintain separate identities on the landscape through short-range dispersal and a strong preference for local mates.

Prior to the YSSP, I have already replicated the results by Heinz et al. (2009), to establish a baseline and platform upon which I will build. During the YSSP, I will modify this model to address the stated research questions. Work will proceed in four stages, allowing the investigation of as many questions as time permits.

In the first stage, natal dispersal distance and mating distance will be held constant, so that only the ecological trait is allowed to evolve. Nonlinear spatial heterogeneity will be modeled by letting the local carrying-capacity density of the environment change among locations according to four parameters: the average slope and curvature of the gradient's deterministic component, as well as the amplitude and spatial autocorrelation distance of the gradient's stochastic component. On this basis, I will characterize the spatial structures and dispersal distances for which speciation can occur.

In the second stage, the evolution of dispersal and mating distance will be enabled. Different types of spatial variation may be expected to promote the evolution of different types of dispersal and mating behavior, with consequences for the likelihood of speciation under different spatial structures.

In the third stage, the evolution of assortative mating will be added to the model, by integrating a trait that governs the strength of assortative (or disassortative) mating (Doebeli and Dieckmann 2003). Mate choice will be based either upon the ecological trait or upon an additional ecologically neutral marker trait. These mating traits will either replace or supplement the mating-distance trait of the Heinz et al. (2009) model, which does not permit the evolution of assortative mating. This extension will allow exploration of the joint evolution of dispersal and assortative mating under different spatial structures, and of the way in which this evolution promotes or hinders speciation.

In the fourth stage, time permitting, temporal environmental variability will be modeled. Oscillations in local carrying capacity may be used to simulate seasonal variation, while gradual linear change in carrying-capacity densities could simulate climate change. We will assess the effects of these temporal patterns on speciation, dispersal evolution, and mate-choice evolution.

There are different ways to detect speciation, since speciation is really a process, and not just an instantaneous event. The lines drawn between species therefore depend on the considered species concept and other arbitrary choices (Coyne and Orr 2004). To add an additional perspective to these decisions, I will incorporate unlinked neutral loci. These loci will be subject only to genetic drift, not to natural selection, and will therefore be useful in diagnosing the degree of reproductive isolation between different populations in the model, even though

neutral loci cannot always be used to diagnose speciation reliably (Thibert-Plante and Hendry, in press). Alternative quantitative methods for diagnosing the reproductive isolation of populations may thus be explored for comparison.

Relevance and link to EEP's research plan

This project extends work previously done as part of EEP's research projects on *Evolving Biodiversity* and *Adaptive Dynamics Theory* (e.g., Doebeli and Dieckmann 2003; Heinz et al. 2009; Payne et al., in preparation). It will contribute to the goal of distinguishing the key ecological factors that promote and hinder biological diversification.

Expected output and publications

The results of this research project will be published as a coauthored paper in an international scientific journal. I also expect this work to be a part of my PhD thesis.

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