

Evolution of conditional dispersal in structured populations

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Goal

To investigate the influence of population structure, both self-generated and environmentally imposed, on the evolution of conditional dispersal in asexual and sexual populations.

Background and motivation

Dispersal is a topic of paramount importance in theoretical ecology (Dieckmann et al. 1999; Levin et al. 2003) influencing species abundances and distributions, population dynamics, genetic diversity, and the evolution of reproductive isolation. While dispersal is costly, theoretical investigations have demonstrated its selective advantage in numerous situations, e.g., to avoid kin competition (Lambin 2001) and inbreeding (Perrin 2001), and to escape local catastrophes in temporally or spatially varying environments (Kun & Scheuring 1997). The majority of these theoretical models assume *unconditional* dispersal (e.g., Travis & Dytham 1998), such that dispersal is characterized by a single global variable, typically defined as the dispersal rate or as the dispersal probability during a generation. While unconditional dispersal may occur in some cases, there is ample empirical evidence that dispersal is *conditional* in many species (see, e.g., references in Travis et al. 1999). In particular, the probability of an individual emigrating from its current patch may be contingent upon local conditions.

Recently, there has been a growing interest in the development of theoretical models of the evolution of conditional dispersal (e.g., Janosi & Scheuring 1997; Travis et al. 1999; Kun & Scheuring 2006; Bach et al. 2007), wherein an individual's probability of emigration is characterized as a function of local conditions, such as the local density of conspecifics or the local availability of acceptable mates. The functional form of this conditional dependence has often been assumed *a priori*, such that only a few parameters controlling the shape of the function were allowed to evolve. For example, Travis et al. (1999) assumed a linear density-dependent dispersal strategy and allowed its slope and intercept to evolve, whereas Bach et al. (2007) assumed a sigmoidal density-dependent dispersal strategy and allowed its steepness and half-saturation density to evolve. While prescribing a particular functional form for the dispersal function may be appropriate in some cases, it can severely limit the search space of available functions, and may therefore systematically bias the search for an evolutionary stable dispersal strategy. Kun and Scheuring (2006) recently investigated a more general, three-parameter density-dependent dispersal strategy, which could capture numerous qualitatively different shapes (including linear and sigmoidal). However, even in this case, the evolving function, which in principle is infinite-dimensional, has been reduced to a three-dimensional vector-valued trait, and such low-dimensional parameterizations are known to lead to spurious outcomes in certain

situations (Dieckmann et al. 2006). In contrast, *function-valued traits* characterize phenotypic variation along a continuum, and naturally allow for the evolution of arbitrary functional relationships (Dieckmann et al. 2006). Representing conditional dispersal as a function-valued trait may therefore avoid some of the aforementioned biases and allow for the full exploration of the space of possible functional forms. Surprisingly, the formulation of conditional dispersal as a function-valued trait has yet to be undertaken.

Dispersal models typically treat space either (i) as being continuous in two dimensions with local interactions and dispersal or (ii) as a metapopulation of discrete and internally well-mixed populations coupled by dispersal. Environmental variability is often introduced as random noise with spatial heterogeneity. In contrast to random environmental variation, gradual environmental gradients along continuous spatial dimensions have also proven to be an interesting avenue of investigation (Doebeli & Dieckmann 2003; Leimar et al. 2008); e.g., environmental gradients have been shown to facilitate the evolution of reproductive isolation under parapatric conditions close to sympatry (Doebeli & Dieckmann 2003). As previous studies have demonstrated that random environmental variability plays an influential role in the evolution of conditional dispersal mechanisms, gradual environmental gradients may be expected to affect the evolution of conditional dispersal and, thus, the eventual functional form of the evolving dispersal strategy.

When studying dispersal in metapopulations, it is often assumed that the involved populations are arranged on a regular graph, typically a two-dimensional lattice with periodic boundary conditions (e.g., Travis & Dytham 1998; Travis et al. 1999; Kun & Scheuring 2006; Bach et al. 2007). However, this assumption of topological regularity is an oversimplification when populations are embedded in heterogeneous interaction networks. In particular, some populations will often be more highly connected than others. In related contexts, such as epidemiology and evolutionary game theory, the inclusion of heterogeneous interaction networks has been shown to dramatically impact ecology and evolution. For example, scale-free network structures (Barabási & Albert 1999) promote the evolution of cooperation in the graph-based prisoner's dilemma (Santos & Pacheco 2005), and hierarchical metapopulation structures promote the emergence of multiscale resurgent epidemics in the classical susceptible-infectious-recovered model of disease spread (Watts et al. 2005). In the context of conditional dispersal, the inclusion of such complex population structures has yet to be investigated.

Research questions

With this project, and its potential continuation after the summer, we plan to address a succession of research questions:

- Does the representation of the conditional dispersal rate as a function-valued trait lead to the evolution of dispersal functions not found in previous studies?
- When populations are self-structuring in continuous and homogeneous habitats, is evolution still expected to lead to density-dependent dispersal that is low below a threshold density and high above it?

- How is the evolution of conditional dispersal affected by local adaptation along environmental gradients?
- How does the evolution of conditional dispersal reconcile the mutually conflicting goals of escaping the local crowding by conspecifics and the local scarcity of acceptable mates?
- How do topological properties of complex metapopulation structures, such as assortativity and hierarchical organization, affect the evolution of conditional dispersal?

Methods and work plan

Work plan

The main steps in this project are as follows:

- First, we will develop an evolutionary model of conditional dispersal in a two-dimensional continuous and homogeneous habitat. Conditional dispersal will be described as a function-valued trait based on the local density of conspecifics. To avoid the confounding effects of sexual reproduction, we will initially assume that individuals reproduce, and thus inherit their phenotypic traits, asexually.
- Second, we will include an environmental gradient along which individuals can exhibit local adaptation. Conditional dispersal will be based on local environmental quality, which in turn is affected by local carrying capacity and the local density of phenotypically similar conspecifics.

Time permitting, we will extend this model as follows:

- We will include sexual reproduction and assortative mating, with conditional dispersal being based on local environmental quality and the density of acceptable mates.
- We will investigate the impact of various topological properties of metapopulation structures on the evolution of conditional dispersal.

Evolving traits

The dispersal strategy of an individual will be represented as a function-valued trait (Dieckmann et al. 2006), describing its dispersal rate (or, alternatively, its dispersal distance) in response to one or more arguments. Initially, this function will be contingent upon just a single argument: the local ratio of competition pressure to carrying capacity. Subsequently, a second argument may be included: the local density of acceptable mates.

In the presence of an environmental gradient, an individual will be assumed to possess another evolving trait determining to which location along the gradient it is best adapted (Doebeli & Dieckmann 2003).

Population structures

In the first part of this project, we will assume that individuals are located in a two-dimensional continuous habitat, in which the phenotype-dependence of carrying capacity changes along an environmental gradient (Doebeli & Dieckmann 2003). We will assume periodic boundary conditions, and in order to avoid an abrupt discontinuity in the environmental gradient at the boundaries, we will employ a smooth gradient that peaks at the center of the spatial domain and implies identical environmental con-

ditions at its two ends. Such a gradient could be described by e.g., a sinusoidal function.

Subsequently, metapopulation structure will be represented as a graph $G = (V, E)$, where V is the set of vertices, denoting individual populations, and E is the set of edges, denoting possible dispersal routes between them. For example, an individual situated in population $i \in V$ may disperse to population $j \in V$ if $(i, j) \in E$. When investigating irregular population structures, we plan to explore random graphs with varying degrees of assortativity and hierarchical metapopulation models:

- A random graph consists of N vertices, such that an edge is formed between each vertex with some probability p . Assortativity r is informally defined as the affinity with which vertices of similar degree (number of neighbors) connect to one another (see Newman 2002 for a formal definition). In *assortative* graphs ($r > 0$) vertices of similar degree are more likely to be connected to one another, whereas in *disassortative* graphs ($r < 0$) vertices of dissimilar degree are more likely to be connected to one another. The assortativity of graphs will be tuned using the method provided by Payne & Eppstein (2008).
- A hierarchical metapopulation structure, as described by Watts et al. (2005), is defined as follows. Populations are hierarchically organized on a tree, such that the probability that population i is connected to population j is given by $p_{ij} \propto \exp(-x_{ij} / \zeta)$, where x_{ij} is the distance (i.e., the number of edges along the tree) between population i and population j , and ζ is a parameter that determines the attenuation of connection probability with distance.
- Other complex metapopulation structures of practical interest could also be investigated, such as small-world (Watts & Strogatz 1998) and scale-free (Barabási & Albert 1999) graphs. Further, other relevant topological properties (such as community structure; Newman 2006) could be systematically investigated. Moreover, directed graphs could be considered, in which dispersal routes can be traversed in only one direction.

Population dynamics

Population dynamics will follow those described by Doebeli & Dieckmann (2003). An asynchronous, individual-based stochastic model will be developed in which time is continuous and generations overlap. The initial population will consist of a single, randomly chosen ancestral phenotype. Individuals will be assigned birth, death, and dispersal rates; the time lapse between these events will be drawn from an exponential distribution with a mean equal to the inverse of the sum of the event rates of all individuals. Individuals will be chosen to take part in the selected event probabilistically, in proportion to their corresponding rates. Birth and death events will be handled as by Doebeli & Dieckmann (2003). For birth under asexual reproduction, the offspring will undergo mutation with some small probability; otherwise, the offspring will inherit the parental phenotype faithfully. For birth under sexual reproduction, the offspring phenotype will be drawn from a normal distribution around the mid-parental phenotype. Under sexual reproduction, we will assume a fixed degree of assortative mating, with the mating probability between two local-adaptation phenotypes being given by a normal distribution. Initially, Gaussian competition kernels will be assumed, but the sensitivity of our results to this assumption will be tested by investigating leptokurtic competition kernels as well.

Relevance and link to EEP's research plan

This work contributes to two of the research projects of the Evolution and Ecology Program at IIASA. Specifically, investigating the interplay between population structure and conditional dispersal is relevant to EEP's projects on *Adaptive Dynamics Theory* and *Evolving Biodiversity*. As discussed in EEP's research plan, advancing general insights into spatially structured evolutionary processes (Task 1.1) and developing and applying new techniques for simplifying spatial complexity (Task 1.2) are major goals of the program. By gaining an understanding of the important influence of population structure on the evolution of conditional dispersal, the proposed research has the potential to contribute to both of these goals.

Expected output and publications

The results of this research will be communicated through co-authored publications in international scientific journals, and may be included in my Ph.D. dissertation.

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