CHAPTER 11

Evolution of dispersal in heterogeneous landscapes

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Abstract. Dispersal is the mechanism by which populations distribute themselves across landscapes. As such, its study is an essential aspect of spatial ecology. Habitats themselves are heterogeneous across space and time. Dispersal can reflect purely random movement or may be conditioned on properties of the environment or the presence of other organisms. Understanding what forms of dispersal confer selective advantage in what types of habitats is an issue that has recently come to the forefront of spatial ecology and its interface with evolutionary theory. The connection between ecology and evolutionary theory is usually expressed through the concepts of evolutionarily stable strategy and invasibility. There is some dichotomy in theoretical predictions of selective advantage. Dispersal of some sort is favored in a metapopulation framework. Unconditional dispersal is generally not favored in temporally constant environments in a discrete diffusion setting. Unconditional dispersal may, however, be favored in this framework if there is temporal variability in the habitat. Conditional dispersal may be favored when there is spatial variation. Such results have been extended to both reaction-advection-diffusion and integrodifference modeling frameworks. This essay will review the development of the theory of evolution of dispersal, describe the current state of understanding in the subject, and highlight important open questions and issues.

11.1 Introduction

The dispersal of organisms is clearly an important aspect of many ecological processes. It drives biological invasions, allows populations to colonize empty habitats, and allows individuals to track resources and avoid predators or competitors. It plays a significant role of the life histories of many organisms. Yet, despite the fact that

dispersal is ubiquitous, our understanding of its evolutionary causes and ecological effects is still quite limited. In their introduction to the book "Dispersal" (Clobert et al., 2001), the editors remark that "dispersal is probably the most important life history trait involved in both species persistence and evolution" and that "One of the most studied yet least understood concepts in ecology and evolutionary biology is the movement of individuals, propagules, and genes." There are a number of factors that can influence the evolution of dispersal, and correspondingly there are a number of different modeling approaches that have been used to study it. Factors that are commonly invoked to explain the evolution of dispersal can be either genetic or ecological (Gandon and Michalakis, 2001). Genetic factors include kin selection, i.e., reduction of competition between related individuals (Hamilton and May, 1977), and avoidance of inbreeding (Gandon, 1999). The main ecological factors involve environmental heterogeneity in time and/or space (McPeek and Holt, 1992). In the present article we will focus our attention on ecological factors, especially spatial heterogeneity. Most of the analysis of the ecological aspects of the evolution of dispersal has been based on ecological models rather than explicitly evolutionary models. Evolutionary conclusions typically have been drawn from ecological models by means of the notion of evolutionarily stable strategies. A strategy is said to be evolutionarily stable if a population using it cannot be invaded by a small population using any other strategy. The idea is that the strategies observed in natural systems are those that are evolutionarily stable, because they can resist invasion. If two strategies are compared and the first is found to be evolutionarily stable relative to invasion by the second while the second is not evolutionarily stable with respect to the first then the interpretation is that the first should be able to invade and displace the second. On the other hand, if neither strategy is evolutionarily stable with respect to the other then each can invade the system when rare and hence they may be expected to coexist in some sort of stable polymorphism. (The theory of uniform persistence or permanence gives a rigorous mathematical formulation for this idea; see Hutson and Schmitt (1992).) Most of the analysis we will describe in this article is motivated by the idea of evolutionary stability.

It is clear that in some sorts of temporally varying environments there should be selection for some amount of dispersal. In particular, for populations inhabiting patchy environments where they are subject to local extinctions, persistence is possible only if the population can recolonize empty patches. A collection of local populations distributed across a network of patches is called a metapopulation. The idea that local populations may be subject to extinction but that empty patches can be recolonized by individuals dispersing from other patches is the basis for patch occupancy models for metapopulations. Those models do not include explicit population dynamics; they only track the probabilities that patches are occupied. In that modeling framework dispersal is viewed as a factor in the rate of colonization so some amount of dispersal is essential to prevent extinction of the entire metapopulation. Patch occupancy models should be distinguished from discrete diffusion models which keep track of population densities but do not necessarily incorporate local extinctions or other forms of temporal variability (see Hanski (1999, 2001)). Even in the context of patch occupancy models or stochastic individual based models that allow local ex-

tinctions there are interesting questions about the evolution of dispersal, but we will not pursue those here. We refer the interested reader to Heino and Hanski (2001). For many types of plants, only seeds can disperse under normal conditions, so again the process of dispersal is tightly connected to the process of recruitment. Indeed, patch occupancy models where each patch represents a location where a single plant can grow have been widely used to study dispersal and competition in plants; see for example Tilman (1994). There are various modeling approaches that can be used to study the evolution of dispersal; see Levin et al. (2003) and Clobert et al. (2001). We will discuss the evolution of dispersal, including the effects of temporal variation, in the context of reaction-diffusion models, their generalizations, and their discrete analogues. Even in the context of reaction-diffusion or discrete-diffusion models it turns out that temporal variation can cause selection for dispersal. This phenomenon was observed by McPeek and Holt (1992) in numerical experiments on discrete diffusion, studied further in that context from the viewpoint of adaptive dynamics by Parvinen (1999), and studied analytically and numerically by Hutson et al. (2001) in the reaction-diffusion context.

The effects of spatial heterogeneity on the evolution of dispersal in systems where the environment is uniform in time are rather subtle. Hastings (1983) obtained analytic results on reaction-diffusion models and their spatially discrete analogues that suggested there would be selection for slow dispersal in spatially varying but temporally constant environments. However, Hastings' results were based on assumptions about the process of dispersal and the patterns of spatial distribution of populations that it would produce that are not universally satisfied; in particular they do not hold in some models incorporating dispersal behavior that depends on environmental conditions. McPeek and Holt (1992) made a number of observations on the basis of numerical experiments on two-patch discrete-time models. They found that there was selection for slow dispersal in the spatially varying but temporally constant case if the dispersal process was independent of environmental conditions, but there was not when the dispersal process depended on environmental conditions in the right way. They also found that there could be selection for fast dispersal in environments with both spatial and temporal variation even if the dispersal process was independent of environmental conditions. (In later work, Holt and McPeek (1996) found that chaotic population dynamics can induce selection for dispersal in a manner similar to the effects of extrinsic spatiotemporal variation.) McPeek and Holt (1992) introduced the terms "conditional" and "unconditional" respectively to describe dispersal processes that do or do not depend on environmental conditions. The particular form of conditional dispersal that McPeek and Holt found to be evolutionarily stable in spatially varying but temporally constant environments has the feature that it results in an equilibrium distribution of the population where all individuals have the same fitness (as measured by reproduction rate), independent of their location, and there is no net movement of individuals at equilibrium. Such a distribution is consistent with a descriptive theory of how organisms should distribute themselves developed by Fretwell and Lucas (1970) called the ideal free distribution. Conditional dispersal that leads to an ideal free distribution of population is sometimes called "balanced dispersal." The population dynamics arising from the movement of individuals from

regions of greater fitness to regions of lower fitness by unconditional dispersal are sometimes called "source-sink" dynamics. There has been some empirical study of whether natural populations display balanced dispersal or source-sink dynamics, or perhaps neither. The empirical study in Doncaster et al. (1997) supports the view that some populations display a form of balanced dispersal; see also Cantrell et al. (2007a), Holt and Barfield (2001), and Morris et al. (2004) for additional discussion and references related to the ideal free distribution, balanced dispersal, source-sink dynamics, and the evolution of dispersal.

11.2 Random dispersal: Evolution of slow dispersal

Hastings (1983) asked whether spatial variation alone can lead to selection for increased dispersal in a spatially inhomogeneous but temporal constant environment. To that end, he envisioned a scenario where an environment was inhabited by a resident species at a stable equilibrium density, and some mutation occurred, thus introducing a small mutant population into the environment. He considered both reaction-diffusion and discrete diffusion models in continuous time as models for such a scenario. Specifically, in the reaction-diffusion case, the model for the resident population took the form

$$u_t = D\nabla \cdot [\mu(x)\nabla u] + F(x, u)u \quad \text{in } \Omega \times (0, \infty),$$

$$\frac{\partial u}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0, \infty), \tag{11.1}$$

where $u(x, t)$ is a population density, the habitat Ω is a bounded region in $\mathcal{R}^N$ with smooth boundary $\partial\Omega$, $\nabla \cdot$ is the divergence operator, ∇ denotes the gradient operator, $\mu(x) > 0$ describes how the rate of diffusion varies spatially, $D > 0$ describes the overall rate of diffusion, n is the outward unit normal vector on $\partial\Omega$, and the boundary condition means that no individuals cross the boundary of the habitat. We will refer to such boundary conditions as "zero-flux." Note that the specific form taken by zero-flux boundary conditions depends on the flux, so that zero-flux boundary conditions may involve additional terms, e.g., in cases where the dispersal terms involve advection. In (11.1) and in most of the models described in this article we interpret the local population growth rate $F(x, u)$ as being determined by the level of resources available at location x to a population living at density u. We will also use the local population growth rate as a measure of the fitness of an individual at the point x when the population density is u. Hastings assumed that the model (11.1) had a stable positive equilibrium u^* with $F(x, u^*)$ not identically zero, modeled a small invading mutant population v as satisfying

$$v_t = d\nabla \cdot [\mu(x)\nabla v] + F(x, u^* + v)v \quad \text{in} \quad \Omega \times (0, \infty), \tag{11.2}$$

also with zero-flux boundary conditions, and determined when the model predicted that the mutant population could successfully invade the resident population. The model in (11.2) was based on the assumption that the mutant population is so small that it has a negligible effect on the resident population. The main finding in Hastings

(1983) was that if the mutant differs from the resident species only by having a different dispersal rate, then it can invade when rare if and only if its dispersal rate is less than that of the resident species. Hastings obtained a similar result for a spatially discrete analogue of (11.1); we will return to that model later in our discussion of the ideal free distribution. Analogous results for the discrete-time case were obtained for the case where dispersal is unconditional (so that a hypothesis analogous to having $F(x, u^*)$ not identically zero is satisfied) by numerical experiments in McPeek and Holt (1992) and proved analytically in Parvinen (1999).

The criterion for whether or not a mutant could invade the system described by (11.1) is the instability or stability of the equilibrium $v = 0$ in (11.2). In this case and many others, the stability of such an equilibrium can be determined by a linear stability analysis. Linear second order elliptic operators on bounded domains typically have a principal eigenvalue which has a larger real part than any other eigenvalue and is characterized by having a positive eigenfunction. This eigenvalue is analogous to the principal eigenvalue of a primitive matrix. Its existence follows from the Krein-Rutman theorem, which is an extension of the Perron-Frobenius theorem on matrices to the infinite dimensional case. It turns out that second order parabolic equations with periodic coefficients also have a principal eigenvalue. See Cantrell and Cosner (2003), Section 2.5, for a discussion of principal eigenvalues. The stability or instability of equilibria in most of the models we will discuss can thus be determined by the sign of the principal eigenvalue of the linearized problem. In some cases the principal eigenvalue may be zero, so that a nonlinear stability analysis is needed. In the analysis of (11.2), Hastings showed that if $F(x, u^*)$ is not identically zero then the principal eigenvalue of the linearization of (11.2) around $v = 0$ is positive if and only if $d < D$ in (11.2). The conclusion about invasibility follows immediately.

A possible biological reason for the evolution of slow dispersal is that passive diffusion takes individuals from more favorable locations to less favorable locations more often than it does the reverse (Hastings, 1983), since it typically moves individuals from regions of high density to regions of lower density. In terms of resource matching, one consequence of random diffusion is to cause the resident species to undermatch the best resources at equilibrium. In fact, the zero-flux boundary condition in (11.1) and the divergence theorem imply that at the equilibrium u^* the integral of $F(x, u^*)u^*$ over Ω is zero, so that if $F(x, u^*)$ is nonzero at equilibrium it must change sign so that the population overmatches the resources in some places but undermatches them in others. When a slower diffusing mutant population is introduced, it can grow at locations where the resident undermatches the resources in the habitat (which would typically be the locations with the best resources), and is more likely to remain in those locations, so it can thus invade successfully. It is interesting to note that the analysis in Hastings (1983) breaks down if the assumption that $F(x, u^*)$ is nonzero at equilibrium is removed. If $F(x, u^*) = 0$ on Ω then the resident matches the resources perfectly. Furthermore, if certain technical conditions are satisfied, it can be shown that if u^* is unique for each D and there is a unique positive solution $u = K(x)$ to the equation $F(x, u) = 0$ then $u^* \to K(x)$ on the interior of Ω as $D \to 0$; see Cantrell and Cosner (2003), Proposition 3.16. In a logistic model $K(x)$

would represent the local carrying capacity of the environment. Thus, a population that diffuses sufficiently slowly will come closer to matching the available resources than one that diffuses more rapidly.

Hastings' result is a local one in the sense that it concerns only the invasion of invading species when it is rare. After the invasion of the mutant, can it drive the resident species to extinction or will it coexist with the resident species? This led Dockery et al. (1998) to consider the following continuous-time continuous-space model for two randomly diffusing competing species:

$$
\begin{cases}
u_t = \mu \Delta u + u[m(x) - u - v] & \text{in } \Omega \times (0, \infty), \\[2mm]
v_t = \nu \Delta v + v[m(x) - u - v] & \text{in } \Omega \times (0, \infty), \\[2mm]
\dfrac{\partial u}{\partial n} = \dfrac{\partial v}{\partial n} = 0 & \text{on } \partial\Omega \times (0, \infty),
\end{cases}
\tag{11.3}
$$

where $u(x,t)$ and $v(x,t)$ represent the population densities of competing species with respective dispersal rates μ and ν. The symbol Δ stands for the Laplace operator ($\Delta = \nabla^2$), which is the composition of the divergence and gradient operators and models the random dispersal of the species. The scalar function $m(x)$ represents their common intrinsic growth rates and it reflects the quality and quantity of resources available at the location x. The habitat Ω is as in (11.1). The zero-flux boundary condition in (11.3) means that no individuals cross the boundary of the habitat. The most notable feature of (11.3) is that these two species are identical except their dispersal rates.

Dockery et al. (1998) showed that if the dispersal rate of the mutant is smaller than that of the resident species, then the mutant not only can invade but also can drive the resident species to extinction, i.e., a slower diffusing species always emerges as the winner of the competition. For nonlocal dispersions, some similar results hold (see Hutson et al. (2003)). However, when the intrinsic growth rate varies periodically in time, it is shown in McPeek and Holt (1992) for patch models and in Hutson et al. (2001) for diffusion models that the slower diffuser may not always be the winner, and faster dispersal can be selected in some situations. A challenging open problem is whether the slowest diffuser always wins the competition in the context of k competing species with $k \geq 3$ (Dockery et al., 1998).

11.3 Random dispersal vs. conditional dispersal

In reality, species do not always move randomly. As resources are often distributed heterogeneously across the habitat, a species can often sense local environment change and its movement may be affected by environmental factors such as resource distributions and population density. One of the simplest modeling approaches is to assume that organisms display taxis and can move up along the gradient of a local population growth rate. Such biased movement upward along resource gradients is an example of conditional dispersal and has been considered in Belgacem and Cosner (1995) and

Cosner and Lou (2003) for a single species. Among other things, Belgacem and Cosner (1995) and Cosner and Lou (2003) showed that conditional dispersal involving both random diffusion and directed movement up resource gradients can sometimes (but not always) make persistence of a single species more likely. For two-patch models, McPeek and Holt (1992) showed that in spatially varying but temporally constant environments certain types of conditional dispersal can be advantageous.

Hence, it is of interest to compare a random dispersal strategy with a conditional dispersal strategy such as biased movement along a resource gradient, and determine which dispersal strategy will evolve. This led Cantrell et al. (2006, 2007b) to introduce the model

$$
\begin{cases}
u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + [m(x) - u - v]u & \text{in } \Omega \times (0, \infty), \\[2mm]
v_t = \nu \Delta v + v[m(x) - u - v] & \text{in } \Omega \times (0, \infty), \\[2mm]
\mu \dfrac{\partial u}{\partial n} - \alpha u \dfrac{\partial m}{\partial n} = \dfrac{\partial v}{\partial n} = 0 & \text{on } \partial\Omega \times (0, \infty),
\end{cases}
\tag{11.4}
$$

where the two species have different dispersal strategies: the species with density v disperses only by random diffusion, the other species disperses by a combination of random diffusion and a directed movement towards more favorable habitats, where α is a positive parameter which measures the tendency of biased movement along the resource gradient. Both still satisfy zero-flux boundary conditions.

When $\alpha = 0$, from the previous section we know that the slower diffusing species always wins the competition. What happens if $\alpha > 0$? It turns out that the answer is rather delicate and depends on both the magnitude of α and the geometry of the habitat Ω.

It is shown in Cantrell et al. (2006, 2007b) that for convex habitats, the competitor that moves upward along the resource gradient may have a competitive advantage even if it diffuses more rapidly than the other competitor, i.e., a faster diffuser with some (weak) advection along the resource gradient can win the competition. It means that the advantage gained from the directed movement upward along resource gradients can compensate for the disadvantage created by faster diffusion, at least for convex habitats.

The case $\mu = \nu$ also depends on the geometry of the habitat. For convex habitats, we show in Cantrell et al. (2007b) that for small positive α, the species with density u always wins. Hence, at least for convex habitats, species with a small amount of biased movement have the advantage. That is, the dispersal strategy with some biased movement can evolve there. On the other hand, there are some nonconvex habitats, as constructed in Cantrell et al. (2007b), such that the species u always loses. It is interesting that the geometry of the habitat can play an important role in the evolution of dispersal, and this may have potential applications to the conservation of species. For example, it may be helpful in understanding how habitat fragmentation affects the loss of species.

If we further increase α, it seems that the species with density u becomes "smarter"

and hence will continue to win the competition. Surprisingly, for sufficiently large α, one often can expect that the two competing species can coexist (Cantrell et al., 2007b). In other words, strong advection upward along environmental gradients can induce the coexistence of species and provide a mechanism for the coexistence of competing species. If we interpret the competitors as different genotypes of the same species, this situation would correspond to a stable polymorphism. (In at least some species there appears to be a genetic basis for some aspects of dispersal ability; see Roff (1994).)

From the biological point of view, such coexistence results are surprising, at least at the first look. Given any pair of $\mu < \nu$, when α is positive and small, the species u always wins the competition, i.e., the slower diffuser still wins. As α increases, the species with density u has the tendency to move toward more favorable regions, so it seems to have more competitive advantage than the species with density v and should still win the competition. However, the results in Cantrell et al. (2007b) show that the "smarter" species may coexist with the other species, which is randomly diffusing with a larger random diffusion rate. A possible explanation for such coexistence is that as α becomes large, the "smarter" competitor moves toward and concentrates at places with the locally most favorable environments, leaving enough resources elsewhere for the other species to survive. Thus, there is a type of spatial segregation of the competitors which leads to coexistence. These biological intuitions are justified by some rigorous analytical results from Chen and Lou (2008) in the case when there is only one local maximum of resource density.

In terms of resource matching, a big difference between random diffusion and biased movement along the resource gradient is that random diffusion leads the species to undermatch the best resources, while the biased movement along the resource gradient can lead the species to better match the resources if the advection rate is suitable, or overmatch the best resources if the advection rate is too large. Whether a dispersal strategy is evolutionarily stable or not seems to rely crucially on how well the species can apply the dispersal strategy to match the resources.

11.4 Evolution of conditional dispersal

What happens if both competing species disperse by random diffusion and advection along environmental gradients? Intuitively, one possible consequence of biased movement up a resource gradient is to cause a certain degree of crowding in the favorable regions of the habitat which might change the outcome of the competition. To understand the evolution of conditional dispersal, Chen et al. (2008) considered the model:

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + [m(x) - u - v]u & \text{in } \Omega \times (0, \infty), \\ v_t = \nabla \cdot [\nu \nabla v - \beta v \nabla m] + [m(x) - u - v]v & \text{in } \Omega \times (0, \infty), \\ \mu \frac{\partial u}{\partial n} - \alpha u \frac{\partial m}{\partial n} = \nu \frac{\partial v}{\partial n} - \beta v \frac{\partial m}{\partial n} = 0 & \text{on } \partial \Omega \times (0, \infty). \end{cases} \quad (11.5)$$

When $\beta = 0$ and α is large, from the previous section we know that the two species can often coexist with each other. Hence, neither of the two dispersal strategies is the winning one. What happens if $\beta > 0$? It turns out that at least two scenarios can occur (Chen et al., 2008):

(i) If only one species has a strong tendency to move upward the environmental gradients, e.g., β is small and α is large, the two species can coexist since one species mainly pursues resources at places of locally most favorable environments while the other relies on resources from other parts of the habitat. This is the same as the case when $\beta = 0$.

(ii) If both species have a strong tendency to move upward the environmental gradients, e.g., β is large and α is even larger, it can lead to overcrowding of the whole population at places of locally most favorable environments, which causes the extinction of the species with stronger biased movement. From the biological point of view, strong biased movement along the resource gradient of both species can induce overmatching of resources for both species at places of locally most favorable environments. This is particularly disadvantageous to the species with stronger biased movement as it puts all of its bets on such places.

These results seem to imply that selection is against excessive advection along environmental gradients due to overmatching of the best resources, and they also suggest that an intermediate biased movement rate may evolve in the model.

To further understand the evolution of conditional dispersal, Hambrock and Lou (2008) recently considered the situation when the advection rates α and β are close to each other (different from the case when one is much larger than the other as in previous case), and their findings also support the conjecture that an intermediate biased movement rate may evolve in the model. More precisely, suppose that $\mu = \nu$ and if both advection rates are small, then the species with the larger advection rate always wins; if $\mu = \nu$ and both advection rates are suitably large, then the species with the smaller advection rate always wins.

Another interesting finding in Hambrock and Lou (2008) is that the evolution of random diffusion rates also depends on the magnitude of the advection rates and will change direction if the advection rates vary from small to large. More precisely, suppose that $\alpha = \beta > 0$. Then for small advection rates, the slower diffuser always wins (this is the same as the case when $\alpha = \beta = 0$). However, when the advection rates are large, the faster diffuser is always the winner in the competition.

11.5 Dispersal and the ideal free distribution

Ideal free distribution (IFD) theory describes how organisms should distribute themselves in space if they could move freely to optimize their fitness (Fretwell and Lucas, 1970). It says that individuals should locate themselves so that no individual can

increase its fitness by moving to another location. Thus, it predicts that at equilibrium the fitness of individuals should be the same in all locations, and there should be no net movement at equilibrium. (This is in contrast to the dynamics of many source-sink models where the fitness in the source is larger than that in the sink, which is typically negative, and the sink population is sustained by net movement from the source to the sink; see Pullian (1988).) McPeek and Holt (1992) observed in discrete-time discrete diffusion models that there could be selection for dispersal in spatially varying but temporally constant environments if the dispersal rates had the feature that the equilibria of the system were the same with and without dispersal. If we interpret the fitness of an individual on a given patch with a given population density as being given by the population growth rate on that patch at that density, this feature means that at equilibrium every individual would have fitness zero, which is consistent with the ideal free distribution. It turns out that such a form of conditional dispersal is evolutionarily stable in many situations, see Cantrell et al. (2007a) and Holt and Barfield (2001). To make these ideas more precise, let us consider a discrete diffusion model of the type studied by Hastings (1983):

$$\frac{du_i}{dt} = F_i(u_i)u_i + \sum_{\substack{j=1 \\ j \neq i}}^{n} [d_{ij}u_j - d_{ji}u_i] \quad \text{for} \quad i = 1, \ldots, n. \qquad (11.6)$$

Suppose that for each $i = 1, \cdots, n$, $u_i^* > 0$ is a stable equilibrium of $du/dt = F_i(u)$, so that $F_i(u_i^*) = 0$ for $i = 1, \cdots, n$, with $dF/du < 0$ for $u = u_i^*$. Suppose further that for some dispersal strategy determined by nonzero dispersal coefficients $\{d_{ij}\}$, u^* is also a positive equilibrium of (11.6). That implies

$$\sum_{\substack{j=1 \\ j \neq i}}^{n} [d_{ij}u_j^* - d_{ji}u_i^*] = 0 \quad \text{for} \quad i = 1, \ldots, n. \qquad (11.7)$$

It turns out that under these conditions the strategy defined by $\{d_{ij}\}$ is evolutionarily stable relative to strategies which do not satisfy (11.7). Furthermore, any dispersal strategy leading to an equilibrium u^{**} that does not have $F_i(u_i^{**}) = 0$ for $i = 1, \cdots, n$ cannot be evolutionarily stable; see Cantrell et al. (2007a). This result extends to some models for competition and predator-prey interactions; related results are obtained in Cressman and Krivan (2006), Kirkland et al. (2006), and Padrón and Trevisan (2006). If the model for invasibility by a small invading population (that is, the model corresponding to a discrete version of (11.2)) is linearized around zero, the resulting linear model is neutrally stable, so asymptotic stability arises from higher order effects. For a full model for two populations with competing strategies at arbitrary densities, analogous to a spatially discrete version of (11.3), (11.4), and (11.5), different strategies satisfying (11.7) have a type of neutral stability with respect to each other. This is consistent with the findings of McPeek and Holt (1992).) Since $F_i(u_i^*) = 0$ for $i = 1, \cdots, n$, all patches have the same fitness at equilibrium. Also, by (11.7), there is no net movement at equilibrium. Thus, the evolutionarily stable strategies represent forms of balanced dispersal in that they lead to a population dis-

tribution that is ideal free. Note that the condition $F_i(u_i^*) = 0$ for $i = 1, \cdots, n$, is exactly the negation of the condition that $F_i(u_i^*)$ is not identically zero relative to i imposed by Hastings (1983) and by Parvinen (1999) in results showing selection for slow dispersal in the spatially discrete case. Furthermore, the case of condition (11.7) with $n = 2$ is equivalent to the condition for evolutionary stability found by McPeek and Holt (1992). The analysis in Cantrell et al. (2007a) depends on the fact that the models are finite dimensional. The problem of extending the results of Cantrell et al. (2007a), Cressman and Krivan (2006), Kirkland et al. (2006), and Padrón and Trevisan (2006) to the infinite dimensional case is interesting and largely open.

A novel variation on these ideas was introduced by Wilson (2001) who developed a habitat occupancy model for a source-sink situation. The model has a form similar to a coupled pair of patch occupancy models, but with one model describing a source habitat and the other a sink habitat. As usual in habitat occupancy models, there must be at least some dispersal within the source patch for persistence to be possible, but the question is whether or not dispersal into the sink habitat can evolve. The source patch is assumed to have a stable equilibrium proportion p_1^* of occupied habitat in isolation, so that without dispersal there is no positive equilibrium, and the equilibrium $(p_1^*, 0)$ is stable. However, in some cases there is an evolutionarily stable dispersal strategy with nonzero dispersal that results in positive proportions of both the source and sink habitats. It turns out that under this strategy the fitness in both source and sink habitats can be seen to be zero, and "surprisingly" (Wilson, 2001, p. 30) the equilibrium proportion of occupied habitat in the source is still p_1^*. Perhaps in view of the results described previously this last feature is not really so surprising.

It is natural to ask whether an ideal free distribution of population can arise from dispersal that is conditional on local information but does not require global knowledge of the environment, as in reaction-diffusion-advection models. A version of the ideal free distribution in continuous space was introduced in Kshatriya and Cosner (2001). A dynamic model whose equilibria can be expected to fit such a distribution recently has been developed via advection-diffusion equations in Cosner (2005), under the assumptions that organisms move upward along the local gradient of fitness and that fitness varies spatially and is reduced by crowding. The model in Cosner (2005) has the form

$$u_t = -\alpha \nabla \cdot [u \nabla f(x, u)] \quad \text{on} \quad \Omega \times (0, \infty),$$

with the no-flux boundary condition

$$u \frac{\partial f(x, u)}{\partial n} = 0 \quad \text{on} \quad \partial \Omega \times (0, \infty),$$

where $f(x, u) = m(x) - u(x)$ represents the local effective growth rate of the species, $m(x)$ is the intrinsic per capita growth rate, and $u(x)$ is the population density.

Cantrell et al. (2008) considered a variation on that model which also includes random diffusion as part of the dispersal process, and it has the form

$$u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla f(x, u)] + u f(x, u) \quad \text{in} \quad \Omega \times (0, \infty), \qquad (11.8)$$

with no-flux boundary conditions

$$\mu\frac{\partial u}{\partial n} - \alpha u\frac{\partial f(x,u)}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0,\infty). \tag{11.9}$$

See Grindrod (1988) for a similar model which addresses different questions. One of the main findings in Cantrell et al. (2008) is that as the rate of movement up fitness gradients becomes large and/or the rate of random diffusion becomes small, the density of organisms approximately matches the availability of resources everywhere in the habitat. This differs significantly from both unconditional dispersal by random diffusion and conditional dispersal where organisms tend to move up gradients of resource density without reference to crowding effects. Both of those dispersal strategies lead to population distributions where the density overmatches resource in some locations but undermatches it in others. This fact is the essential reason why there is selection for slow dispersal in models with purely diffusive dispersal, because for such models the only way for the equilibrium population density to approximately match the distribution of resources is for the diffusion rate to go to zero. It is also the reason why too strong a tendency to move up resource gradients without regard to crowding effects can sometimes make a population subject to invasion by another population using a different strategy.

11.6 Dispersal in temporally varying environments

In contrast to spatial heterogeneity, temporal variation in environments can sometimes select for unconditional dispersal. It can also lead to coexistence of different strategies in a stable polymorphism. Much of the work on the evolution of dispersal in time varying environments involves at least some numerical computation because analytic results are harder to obtain than in the temporally constant case. Some analytic results are derived in Hutson et al. (2001) for a reaction-diffusion model of the general form shown in (11.3) but with $m(x)$ replaced by $m(x,t)$ where $m(x,t)$ is periodic in t. In spatially homogeneous but temporally varying environments, the results of McPeek and Holt (1992) (based on numerical experiments on two-patch discrete-time discrete diffusion models) and those of Hutson et al. (2001) (obtained analytically for reaction-diffusion models) indicate that there is no selection for or against unconditional dispersal. In both of those studies the models had stable equilibria; in the case of models that support periodic or chaotic solutions the situation can be different. We will return to that case later. McPeek and Holt (1992) observed that when there is variation in time but not in space then as in the spatially and temporally constant case, there can be selection against forms of dispersal that cause the population to undermatch resources in one patch and overmatch them in the other, but there is no selection for or against uniform unconditional dispersal. In the case of environments with both spatial and temporal variability, McPeek and Holt (1992) found that if only unconditional strategies are considered then except in certain special cases, the system would evolve to a polymorphism consisting of a slow dispersal strategy and a relatively fast dispersal strategy. Hutson et al. (2001) obtained similar analytic results provided that the time average of the coefficient $m(x,t)$ over

a period is positive and some additional technical conditions are satisfied. Hutson et al. (2001) did not consider conditional dispersal. McPeek and Holt (1992) did; they found that there was selection for a specific conditional strategy that satisfied an "ideal free" or "balanced dispersal" condition analogous to (11.7). (In this situation the heterogeneity was obtained by drawing carrying capacities for discrete-logistic within-patch models at random from some distribution, so the equilibria u_i^* in (11.7) would be replaced by the means of those carrying capacities.) This is in contrast with the temporally constant case, where within the class of strategies satisfying (11.7) any number of strategies were seen in McPeek and Holt (1992) to be able to coexist in a state of neutral stability. It would be of interest to consider the evolution of conditional dispersal in the reaction-diffusion setting used in Hutson et al. (2001).

In discrete-time models variability in time does not require extrinsic variation in the environment. Such models can have periodic or chaotic dynamics without it. In Holt and McPeek (1996), it was observed that in a two-patch discrete-time model with equal growth rates on the two patches, chaotic dynamics generally favor the evolution of some amount of unconditional dispersal; if the carrying capacities of the patches are different, chaotic dynamics can support a polymorphism of slower and faster dispersal strategies. Those results were refined and extended in Doebeli and Ruxton (1997) and Parvinen (1999), where it was observed that if growth rates as well as carrying capacities differ between patches then evolutionary branching leading to a polymorphism can occur even if the population dynamics are cyclic. (In situations where patches are ecologically identical, the dispersal rate tends to evolve until the dynamics on the patches are synchronized, after which there is no more selection, so that case is special.)

11.7 Future directions

It would be of interest to study the evolutionary stability of ideal free dispersal relative to other conditional dispersal strategies in spatially varying but temporally constant environments. Using the modeling approach of Cantrell et al. (2006, 2007b), Chen and Lou (2008), and Dockery et al. (1998) in that context would lead to a system of the form

$$\begin{cases} u_t = \nabla \cdot [\mu\nabla u - \alpha u\nabla f(x,u+v)] + uf(x,u+v) & \text{in } \Omega \times (0,\infty), \\ v_t = \nabla \cdot [\nu\nabla v - \beta v\nabla g(x,u+v)] + vf(x,u+v) & \text{in } \Omega \times (0,\infty), \end{cases} \tag{11.10}$$

with no-flux boundary conditions

$$\mu\frac{\partial u}{\partial n} - \alpha u\frac{\partial f(x,u+v)}{\partial n} = \nu\frac{\partial v}{\partial n} - \beta v\frac{\partial g(x,u+v)}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0,\infty), \tag{11.11}$$

where $f(x,w) = m(x) - b(x)w$ (or perhaps some other or more general form of population growth term with crowding effects) and g represents part of an alternate dispersal strategy. For example, $g = 0$ would correspond to unconditional dispersal by simple diffusion, $g = m$ would correspond to advection up resource gradient

without consideration of crowding, $g = -(u + v)$ would correspond to avoidance of crowding without reference to resource distribution, and $g = m - \delta(u + v)$ or $g = m - \delta b(x)(u + v)$ would correspond to a combination of advection up resource gradient and avoidance of crowding.

Many of the results on dispersal in spatially and temporally varying environments or for populations with chaotic dynamics have been obtained through numerical simulation. It would be of interest to extend the range and scope of rigorous analytic results in that area. As noted previously, McPeek and Holt (1992) found that in spatially and temporally varying environments, selection typically favors a certain specific fixed conditional dispersal strategy. It would be of interest to try to see if something similar is true in other types of models. It would also be of interest to examine dispersal strategies which themselves could include variation in time, such as movement along the gradient of a temporally varying resource. Ultimately it might be possible to connect ideas about the evolution of local dispersal in temporally and spatially variable environments to the evolution of migration.

All of the models we have described so far operate on a single trophic level and treat the resource upon which the focal species depends as being extrinsically determined. It is natural to ask how including explicit trophic interactions where the resource itself is dynamic and may even coevolve with the consumer might influence the predictions of models for the evolution of dispersal. In Schreiber et al. (2000) it was shown that in a discrete-time patch model for a host-parasitoid system with coevolution of patch selection, a version of the ideal free distribution is evolutionarily stable. In Cantrell et al. (2007a), balanced dispersal leading to an ideal free distribution was shown to be evolutionarily stable in discrete-diffusion models for predator-prey systems provided that the model incorporates some type of self limitation or intraspecific competition by the predators. It would be of interest to examine extensions of models along the lines of (11.3), (11.4), (11.5), or (11.10) where the resource was explicitly modeled as a dynamic variable and the dispersal strategies of the consumers might include various forms of preytaxis. Two sorts of dispersal that organisms may use to track resources are movement upward along resource gradients and area-restricted search or kinesis, where organisms slow down their movements in regions where resources are dense but speed them up where resources are rare; see Farnsworth and Beecham (1999) and Kareiva and Odell (1987). To compare dispersal strategies for the consumers in such a setting one would use models similar to the following:

$$
\begin{cases}
u_t = \nabla \cdot [\mu(w)\nabla u - \alpha u \nabla f(u + v, w)] + u(eh(u + v, w) - d), \\
v_t = \nabla \cdot [\nu(w)\nabla v - \beta v \nabla g(u + v, w)] + v(eh(u + v, w) - d), \quad (11.12) \\
w_t = \nabla \cdot [\rho \nabla w] + (m(x) - w)w - (u + v)h(u + v, w)
\end{cases}
$$

in $\Omega \times (0, \infty)$ with no-flux boundary conditions

$$
\mu(w)\frac{\partial u}{\partial n} - \alpha u \frac{\partial f(u + v, w)}{\partial n} = \nu(w)\frac{\partial v}{\partial n} - \beta v \frac{\partial g(u + v, w)}{\partial n} = \frac{\partial w}{\partial n} = 0 \quad (11.13)
$$

on $\partial \Omega \times (0, \infty)$. In (11.12) and (11.13) u and v are consumers that are ecologically

identical except for their dispersal strategies, w is a resource, and h is a functional response. The diffusion rates for u and v are allowed to depend on w to model area-restricted search. The dispersal terms f and g could incorporate advection up the gradient of w, or of h, or down the gradient of $u + v$. Clearly there are many reasonable variations on the general form shown in (11.12). It would also be possible to model coevolution of dispersal by the consumer and the resource, but that would require a model with four equations. Incorporating trophic interactions more widely into models for the evolution of dispersal would be an interesting but challenging direction for future research.

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11.9 References

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