How Does It Feel to Be Like a Rolling Stone? Ten Questions About Dispersal Evolution

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Abstract

This review proposes ten tentative answers to frequently asked questions about dispersal evolution. I examine methodological issues, model assumptions and predictions, and their relation to empirical data. Study of dispersal evolution points to the many ecological and genetic feedbacks affecting the evolution of this complex trait, which has contributed to our better understanding of life-history evolution in spatially structured populations. Several lines of research are suggested to ameliorate the exchanges between theoretical and empirical studies of dispersal evolution.

INTRODUCTION

Several good reviews have appeared recently on dispersal (see in particular Bowler & Benton 2005, Clobert et al. 2004, Levin et al. 2003, Olivieri & Gouyon 1997), including whole volumes devoted to the question (Bullock et al. 2002, Clobert et al. 2001, Dingle 1996). The increasing awareness of dispersal's crucial role in the context of global habitat fragmentation, climate change, and biological invasions motivates to a large extent such recent interest [see the special issue in *Science* (volume 313, issue 11) and in particular Kokko & Lopez-Sepulcre 2006]. I have organized the present review around tentative answers to ten frequently asked questions about dispersal evolution. Answers to the first five questions seek to clarify how different methodological constraints, both in theoretical and empirical studies, might affect our understanding of dispersal evolution. In particular, questions two and three set the stage by reviewing briefly the data on dispersal evolution, whereas questions four and five address the general assumptions of models and their relation to data. Answers to questions six through ten build on the previous methodological clarification and attempt to dissipate some confusion about specific selective forces acting on dispersal evolution, using both theory and data. I conclude by addressing the general successes and failures of dispersal evolution studies.

Natal dispersal: movement by which an individual leaves its birthplace to engage into mating or reproduction somewhere else

Breeding dispersal: movement between two reproduction events for the same individual

Dispersal kernel: the probability density that an individual initially at coordinates (0,0) is found at coordinates (x,y) after dispersal

Dispersal rate: rate at which individuals leave a patch of habitat, without clear specification about the distance moved once out of this patch

Local adaptation: the higher fitness of resident genotypes in their native environment relative to that of immigrant genotypes in the same environment

1. WHAT IS DISPERSAL AND WHY IS IT IMPORTANT?

I here define dispersal as any movement of individuals or propagules with potential consequences for gene flow across space. Such definition thus includes both natal dispersal and breeding dispersal. Dispersal movement comprises three stages: (*a*) departure (or emigration), (*b*) a vagrant stage, and (*c*) settling (or immigration). There is no restriction on the ploidy of the dispersing stage, including pollen dispersal. The literature often uses the terms migration and dispersal interchangeably (but see Dingle 1996). The dispersal kernel and dispersal rate are two metrics often used to summarize the consequences of dispersal movements, even though they provide an incomplete description of the dispersal process (Bowler & Benton 2005).

Dispersal holds a central role for both the dynamics and evolution of spatially structured populations, allowing the genetic cohesion of a species across space, its global persistence despite local extinction, and the tracking of favorable environmental conditions in an ever changing world. Dispersal can rescue a small population from local extinction (Brown & Kodric-Brown 1977), but by increasing synchrony in population dynamics, high levels of dispersal can also increase global extinction risk (for experimental evidence, see Molofsky & Ferdy 2005). Dispersal affects the distribution of genetic diversity through space, by increasing the proportion of total diversity contained within rather than between populations (Wright 1969). In particular, dispersal can help mitigate the effect of drift in small populations, decrease mutation load, and thereby reduce the risk of extinction (for theoretical predictions, see Higgins & Lynch 2001; for a review, see Tallmon et al. 2004). Gene flow mediated by dispersal can both impede the evolution of local adaptation (Lenormand 2002) and accelerate it (Gandon et al. 1996). Dispersal affects the evolution of speciation (see review in Barton 2001), inbreeding depression (Roze & Rousset 2003), cooperation and sociality (Le Galliard et al. 2005), and many life-history traits (e.g., Pen 2000). Finally, dispersal plays a key role in community dynamics (see review in Leibold et al. 2004). Understanding dispersal, and also its evolution, is therefore crucial to improve the management of natural populations, as illustrated by the evolutionary suicide of the rare endemic plant *Centaurea corymbosa*. Because of the high risk of dispersal in this cliff species, seed traits enhancing long-distance dispersal have been counter-selected, resulting in the absence of colonization and exchange between populations (Colas et al. 1997). Without human-assisted colonization, the long-term persistence of the species solely relies on that of six small populations, all within 3 km^2, subject to both demographic and environmental stochasticity (Fréville et al. 2004).

2. IS DISPERSAL PLASTIC?

Studying dispersal does not imply simply quantifying a single dispersal kernel, but also assessing how this dispersal kernel varies with individual, social, and ecological conditions. For instance, the heteromorphic plant *Crepis sancta* produces a larger fraction of fruits equipped with a dispersal structure when subjected to experimental nutrient depletion in the soil (Imbert & Ronce 2001). Maternal condition during gestation, such as age (Ronce et al. 1998) or parasitic load (Sorci et al. 1994), affects the dispersal behavior of juveniles in the common lizard *Lacerta vivipara* with complex interactions (Massot et al. 2002). In that same species, manipulation of the social context by either the absence of relatives (Le Galliard et al. 2003) or the presence of frustrated dispersers (Boudjemadi et al. 1999) deeply modifies the rate of dispersal but also the nature, morphology, and colonization success of the dispersers. Density affects emigration and immigration rates in animals (see Clobert et al. 2004) but also seed dispersal in plants, with effects carried over several generations (Donohue 1999). In collared flycatchers, the reproductive success of congeners is assessed by prospecting individuals, and breeding-habitat selection is based on such public information (Doligez et al. 2002).

Reviews of the literature have repeatedly shown that conditional dispersal expression does not reflect only the variation of constraints on the dispersal process, but also the great plasticity in the organism's broad response to various environmental cues during emigration, vagrancy, and immigration (Bowler & Benton 2005, Clobert et al. 2004, Ims & Hjermann 2001, Ronce et al. 2001). There are good theoretical reasons to believe that informed dispersal decisions would confer an evolutionary advantage over a blind process, unless patterns of variation in habitat quality are totally unpredictable or information acquisition is costly (Ronce et al. 2001). I invite the reader to refer to the cited reviews above for further examples and a more general discussion of the benefits and downsides of conditional dispersal (for the latter in particular, see Kokko & Lopez-Sepulcre 2006).

3. HOW FAST CAN DISPERSAL EVOLVE?

Rapid evolution of dispersal requires both the presence of heritable genetic variation for traits affecting dispersal behavior and strong selection acting on these traits.

Macroptery: proportion of individuals carrying functional wings

Evolutionary potential for dispersal is present in many natural populations. In several beetle species, wing polymorphism is under the control of a single gene with two alleles (Roff 1986). Dispersal behavior variation in the Glanville fritillary butterfly, *Melitaea cinxia*, seems to be closely associated with allelic variation at the *pgi* enzymatic locus (Haag et al. 2005). Determinism of variation for dispersal or dispersal-related traits is, however, often polygenic, with heritability typically greater than 0.3 (e.g., for a study on seed heteromorphism in *C. sancta*, see Imbert 2001; for a review in animals, see Roff & Fairbarn 2001). Donohue et al.'s (2005) work on *Arabidopsis thaliana* is unique in that they quantified how the heritability of phenotypic traits translated into the heritability of the dispersal kernel itself. Moreover, they investigated how dispersal kernels were affected by the manipulation of density and found significant genotype by environment interactions (Donohue et al. 2005). Given the predominance of conditional dispersal in nature, similar information about the genetic architecture of dispersal's response to environmental conditions would much improve our understanding of dispersal evolution.

In agreement with measures of heritability, the response of dispersal traits to artificial selection can be fast (see review in Roff & Fairbarn 2001). Genetic variation for dispersal propensity in short-lived organisms, such as *Caenorhabditis elegans*, also allows in vitro evolution experiments, in which characteristics of artificial patchy landscapes are manipulated (Friedenberg 2003). Evidence for the short-term evolution of dispersal in nature comes from specific situations, such as oceanic islands (Denno et al. 2001, Roff 1990), variation in landscape fragmentation (Hanski et al. 2004, Hill et al. 1999, Schtickzelle et al. 2006), ecological succession (Olivieri & Gouyon 1985, Peroni 1994), and biological invasions (Phillips et al. 2006). For instance, Simmons & Thomas (2004) found genetic changes in both the mean macroptery and, more interestingly, its response to population density in expanding edge populations of two bush crickets. Many of the examples above do not elucidate entirely the relative role of genetic changes and plasticity in explaining fast phenotypic changes (e.g., less than ten generations in Cody & Overton 1996). Empirical quantification of the strength of selection acting on dispersal traits in natural populations is almost entirely lacking (but see Donohue 1999).

4. WHICH MODEL ASSUMPTIONS MATTER?

Models of dispersal evolution widely differ in their assumptions, methodology, and ways to describe the dispersal process. The diversity of theoretical approaches sometimes makes the synthesis of their conclusions or the comparison with empirical data quite difficult. Yet different models have also shed light on different evolutionary forces acting on dispersal, unraveling the complex nature of this trait responding to multiple selection pressures (Ronce et al. 2001). Modeling choices, motivated by technical reasons or convenience, can have deep consequences in terms of potential selective forces at stake in the model, which is not always acknowledged with sufficient clarity (Ronce et al. 2001). I discuss in particular four important assumptions about landscape structure, namely the total number of sites between which dispersal occurs, the number of individuals per site, their spatial organization, and the extent of intrinsic spatial heterogeneity in habitat quality in the landscape.

A simplifying assumption frequently made in analytical models for technical reasons is that of an infinite number of sites harboring individuals in the landscape. When the number of sites is finite but large, model results converge quickly toward this limiting case (see, for instance, Rousset 2006). Such an assumption is particularly convenient when modeling stochastic demographic dynamics, as it allows the elimination of stochasticity at the global metapopulation scale and simplifies greatly the analysis (see, e.g., Rousset & Ronce 2004). For that very reason, however, it means that dispersal has no bet-hedging effect in models making this assumption (see discussion in Ronce et al. 2001 and in Section 8). Some analytical models and deterministic simulations also manipulate population densities rather than discrete numbers of individuals in each site, which implies the neglect of stochastic processes related to finite local population size. Consequently, such models ignore spatial genetic structure due to drift and the associated kin-selection phenomena affecting dispersal evolution (see Ronce et al. 2001 and Section 6). They should, however, provide a limiting case toward which stochastic models converge when local population size increases (see Gandon & Michalakis 1999). Convergence, however, is not always checked with accuracy.

Stochastic demographic dynamics: variation in population numbers either due to environmental or demographic stochasticity

Metapopulation: a set of discrete populations connected by dispersal

Bet-hedging: a strategy that reduces the variance of its gains through time, thereby increasing the geometric mean of its gains

An apparent paradox of many dispersal evolution models is their absence of an explicit description of space. Dispersal is often described through an emigration rate out of a given spatial unit harboring a variable number of individuals, and migrants are distributed randomly across the landscape. Such an island model of migration may describe correctly dispersal in some biological systems, but its popularity among modelers results essentially from its analytical tractability. Analytical descriptions of the evolution of space-limited movements have been developed, however (Bolker & Pacala 1999, Comins 1982, Ezoe 1998, Gandon & Rousset 1999, Le Galliard et al. 2005, Rousset & Gandon 2002), including two-patches models (Billiard & Lenormand 2005, Leturque & Rousset 2002, McPeek & Holt 1992), but they often remain mathematically difficult. With the emergence of increasingly powerful computers, individual-based, spatially explicit simulations of dispersal evolution have recently become popular (Heino & Hanski 2001, Hovestadt et al. 2001, Murrell et al. 2002, Travis & Dytham 2002). Fortunately, main qualitative conclusions of spatially implicit models about dispersal evolution, including those assuming global dispersal, still hold when put in a spatial context (see, for instance, the comparison of Gandon & Michalakis 1999 and Heino & Hanski 2001 in Ronce & Olivieri 2004). The main difficulty in such theoretical predictions is evaluating their relevance for empirical measures of dispersal rates, which are necessarily scale specific. A way forward could involve a hierarchical approach of space, distinguishing different types of dispersal movements (see Fontanillas et al. 2004 for an empirical example and Ravigné et al. 2006 for a theoretical example).

Introducing spatial heterogeneity in the landscape, or any other type of temporal autocorrelation in habitat quality, has repeatedly modified predictions of homogeneous models by facilitating either the coexistence of different dispersal strategies (Doebeli & Ruxton 1997, Mathias et al. 2001, Parvinen 2002) or the evolution of conditional dispersal (Doligez et al. 2003, McPeek & Holt 1992). Despite the prevalence of conditional dispersal in nature, early dispersal evolution models have mainly considered dispersal strategies with a pure genetic determinism. Theoretical studies of conditional dispersal strategies, however, have much increased in frequency in recent years.

Game theory: in the context of population genetics, theory seeking approximations for the long-term evolution of traits, when frequency dependence is expected

Convergence stable strategy: a phenotype toward which the population evolves by successive allelic substitution

Evolutionarily stable strategy: a phenotype characterizing a population such that any rare mutant with deviant phenotype is counterselected

Inclusive fitness: effects of a deviant phenotype on the fitness of individuals (*a*) expressing this phenotype, (*b*) when the deviant phenotype is expressed by others, weighted by a measure of genetic similarity between interacting individuals

Relatedness: a function of probabilities of genetic identity that measures the increased probability of recent coalescence between some pair of genes relative to another

Coalescence: time in the past when two particular gene copies of the present population had their most recent common ancestor

***Rm* fitness:** the overall production of successful mutant emigrants from a patch, from initial colonization by a single mutant to the extinction of the mutant lineage in that patch

5. HOW DO WE MODEL SELECTION ON DISPERSAL?

Because dispersal affects both the spatial distribution of genetic diversity and population dynamics, it alters the selective environment for different genotypes. Selection on genotypes differing in their dispersal propensity is thus generally frequency dependent. In the absence of precise knowledge about genetic variation in dispersal kernels, short-term quantitative genetic predictions about evolution rates are entirely lacking. Instead, models have aimed at predicting which mean dispersal phenotypes or coalition of different phenotypes would dominate in the long term. Game theory, therefore, has been and still is the preferred approach to investigate dispersal evolution patterns. Models have sought to identify convergence stable and evolutionarily stable dispersal strategies (see Geritz et al. 1998). Both stability criteria necessitate computing the fate of a mutant allele conferring a deviant dispersal phenotype when confronted with a resident allele.

Given the complexity of the ecological scenarios envisioned in dispersal evolution models (involving interactions between related individuals, spatial structure, and various sources of stochasticity), researchers have largely discussed the relevant analytical measure of fitness and its most useful approximations. Different measures have been developed to capture the long-term evolutionary consequences of the nonrandom spatial arrangement of population numbers and genetic diversity. They all have shown that selection on deviant dispersal strategies depends on (*a*) the expression of modified dispersal by mutant individuals, but also on (*b*) the statistical association between the phenotype of a mutant and the phenotype of its neighbors, as well as on (*c*) how such neighborhood might modify the local demography (see Rousset & Ronce 2004; Le Galliard et al. 2005). I now briefly review which are those measures, their assumptions, and to which situations they have been most successfully applied.

In patchy populations with either global or limited dispersal, direct fitness methods (Taylor & Frank 1996) have been used to derive inclusive fitness measures (Hamilton 1964), which are functions of relatedness coefficients between different pairs of individuals at various spatial distances (e.g., Frank 1986, Gandon & Rousset 1999, Irwin & Taylor 2000, Taylor 1988). Note that relatedness coefficients used in kin-selection models of dispersal evolution are not fixed parameters but dynamically emerge from localized ecological interactions between individuals and the process of genetic coalescence in a spatially structured population. In particular, they jointly evolve with dispersal. Convergence stability measures derived from inclusive fitness arguments can be used to compute the fixation probability of a deviant mutant classically considered by population genetics (Rousset 2006).

In metapopulations with infinite size and global dispersal, Metz & Gyllenberg (2001) have proposed the *Rm* fitness measure, which has the elegant property of being the spatial equivalent of the lifetime reproductive success *R0* in class-structured populations (for applications, see, e.g., Crowley & McLetchie 2002, Gyllenberg et al. 2002, Parvinen 2002, Parvinen et al. 2003). Metz & Gyllenberg (2001) also provided efficient numerical recipes to compute *Rm* fitness in various scenarios, which explains in part its success. Ajar (2003) has shown how the *Rm* fitness measure (Metz & Gyllenberg 2001), and its derivatives used to compute convergence and evolutionary stability relate to inclusive fitness concepts (Hamilton 1964).

At the other extreme, in lattice models with very localized dispersal, investigators have used pair approximation methods (van Baalen & Rand 1998) to derive spatial invasion fitness from the dynamics in the frequency of simple spatial configurations, such as neighboring pairs of sites harboring either one or two individuals with the same or different alleles (see Harada 1999, Ferrière & Le Galliard 2001, Le Galliard et al. 2005). The accuracy of approximations used to close the system of equations used in such models, however, has been variable (van Baalen & Rand 1998). The structural form of selection measures for dispersal derived from pair approximation methods bears close resemblance to inclusive fitness measures, including parameters that could be interpreted as relatedness coefficients (see Ferrière & Le Galliard 2001). Although feedbacks between demography and evolution had been at the core of pair approximation developments, they have been incorporated into inclusive fitness approaches only recently, with still few successful applications (Rousset & Ronce 2004).

The rarity of the deviant strategy is often invoked to derive approximations for fitness measures. Yet the above-mentioned approximations rely more exactly on the assumption of small phenotypic differences between the competing genotypes and therefore weak selection (Rousset 2006). More precisely, under weak selection, approximations for convergence stability require computing only the first-order effects of selection, which was shown to be independent of the allelic frequencies for both limited and global dispersal when the number of sites in the metapopulation is large (Rousset 2006). Weak selection also justifies the computation of relatedness coefficients, assuming neutrality at the dispersal modifying locus in this case. Conversely, second-order effects of selection, which determine evolutionary stability, are frequency dependent and require computing the effect of selection on genetic similarity measures (Ajar 2003).

The majority of dispersal evolution models have assumed either clonal reproduction or a haploid life cycle with a single locus determining dispersal ability (however, see Ravigné et al. 2006, Roze & Rousset 2005, Taylor 1988 for diploid models with sexual reproduction and codominance between alleles affecting dispersal). Multilocus models in which a dispersal modifier locus recombines with another locus affecting fitness (Balkau & Feldman 1973, Wiener & Feldman 1993) had interesting developments recently. These recent models (Billiard & Lenormand 2005, Roze & Rousset 2005) take into account both the statistical associations between different loci in the same individual (due to selection, migration, and limited recombination) and their interaction with genetic associations between different individuals (due to genetic coalescence in finite populations). In particular, such models showed how measures of relatedness at dispersal modifier loci were affected by indirect selection at linked loci (see Sections 7 and 9).

6. DOES DISPERSAL ALLOW ESCAPE FROM COMPETITION?

Kin competition: competition among individuals bearing the same allele

Competition is at the core of many theoretical and empirical studies of dispersal (Lambin et al. 2001). Yet one must distinguish the effects of competition with conspecifics in general from those of competition with relatives. Investigators recognized early on that escaping conspecific competition is a major potential benefit of dispersal [e.g., the first model of dispersal evolution (van Valen 1971)]. In landscapes with variable density through space, dispersal by simple diffusion results in a net flow of individuals from highly populated to less crowded regions. If patterns of spatial variation in density do not match perfectly those in resource availability (Hastings 1983), this confers a selective advantage to genotypes with increased dispersal tendency, as they are more likely to exploit patches of abundant resources with few competitors. In particular, this is the case at the invasion front in expanding populations (see predictions in Travis & Dytham 2002). In extant metapopulation models with both a very large number of sites and very large numbers of individuals per site, escape from overcrowding is the only cause for dispersal evolution (Gyllenberg et al. 2002, Levin et al. 1984, Mathias et al. 2001, Olivieri et al. 1995). Stochastic demographic dynamics generate the conditions for such partially independent temporal variation in density at different sites. Local catastrophic extinctions are an extreme form of such variability. Chaotic population dynamics or asynchronous cycles among sites due to strong density dependence have the same effect (Doebeli & Ruxton 1997, Parvinen 1999). Dispersal strategies conditional on population density in the natal patch were predicted to be more efficient than fixed dispersal strategies at exploiting such heterogeneity (Jánosi & Scheuring 1997, Levin et al. 1984, Metz & Gyllenberg 2001, Poethke & Hovestadt 2002), in agreement with the abundant empirical evidence for density-dependent dispersal (see also Clobert et al. 2004, Ims & Hjermann 2001). It is, however, not always obvious from empirical data that dispersal indeed allows escape from overcrowding. Dispersal agent behavior, directed dispersal, and habitat selection may indeed often result in postdispersal aggregation of high density, as observed, for instance, in *Trilium grandiflorum* (Kalisz et al. 1999).

Even if it did not decrease conspecific aggregation, seed dispersal in *T. grandiflorum* still resulted in decreased relatedness among competing seedlings (Kalisz et al. 1999). Escaping sibling competition could provide ecological benefits for a dispersed individual, such as escaping specialized pests (for a theoretical treatment, see Muller-Landau et al. 2003) or competing with individuals with different ecological niches (e.g., Cheplick & Kane 2004). Yet theory (Hamilton & May 1977) has shown early on that such ecological benefits are not a necessary requirement for dispersal to evolve as a kin-competition avoidance strategy in stable habitats [later generalized by Frank (1986)]. Dispersal evolution can then be understood as an altruistic behavior, providing no direct ecological benefit to the dispersed individual, but alleviating competition for its kin. Spatial genetic aggregation generates spatial variation in postdispersal juvenile density, and highly dispersive genotypes benefit from relaxed competitive conditions, not through the emigrating individuals, but through the progeny that is not dispersed. When the intensity of kin competition varies owing to some heterogeneity in the population, dispersal strategies conditional on cues reflecting such heterogeneity, such as habitat carrying capacity (Leturque & Rousset 2002), maternal age (Ronce et al. 2000a), or family size (Kisdi 2004), have been predicted to evolve. The efficiency of dispersal as a strategy of kin-competition avoidance, however, may be reduced when the dispersal movements of related individuals are strongly correlated [see, e.g., the blue morphs of side-blotched lizards (Sinervo & Clobert 2003)], as when whole sibling families are dispersed in the same fruit.

Heterosis: higher fitness of progeny born to parents originating from different populations than from the same population

Distinguishing between the relative effects of kin competition and demographic stochasticity on the evolution of dispersal is often not obvious. This is especially the case in models in which small finite local population sizes generate both strong local genetic relatedness and random variation in population characteristics (Cadet et al. 2003, Heino & Hanski 2001, Le Galliard et al. 2005, Parvinen et al. 2003). Theoretical frameworks allowing the sequential neglect of one or the other type of effects (see, for instance, Ronce et al. 2000a) can help disentangle the respective role of different evolutionary mechanisms. Interactions between kin selection and demographic stochasticity can also lead to counterintuitive emergent properties, such as the evolution of increasing dispersal rates with increasing dispersal cost (Comins et al. 1980, Gandon & Michalakis 1999, Heino & Hanski 2001; see further discussion of such a result in Ronce & Olivieri 2004).

A final reason to escape the maternal environment in species with overlapping generations is to escape competition with parents. Increasing adult life span selects for increasing juvenile mobility in models allowing for empty sites to be colonized (Olivieri et al. 1995). Variation in adult survival rates due to senescence also selects for juvenile dispersal conditional on maternal age, as observed in the common lizard (Ronce et al. 1998). More generally, manipulations of maternal condition or presence suggest that escape from maternal competition is a major determinant of female progeny dispersal in that species (e.g., Le Galliard et al. 2003, Massot et al. 2002).

7. IS DISPERSAL AN INBREEDING AVOIDANCE STRATEGY?

Experimental removal of parents of one sex in high-density populations of white-footed mice causes a delay in the dispersal of the opposite sex progeny (Wolff 1992). More generally, sex-specific dispersal rates in animals and pollen dispersal in plants have often been interpreted as mechanisms for inbreeding avoidance, even though alternative explanations involving kin-competition avoidance (see, e.g., Ravigné et al. 2006 for a model of pollen-dispersal evolution) can also explain the same patterns. Recent theoretical work has helped clarify these issues. Heterosis favoring dispersal is most commonly thought to be the result of the uneven distribution of deleterious recessive alleles among populations and the masking of such alleles in interpopulation crosses. Heterosis thus is expected in metapopulations with strong genetic structure, in which kin competition is also intense (for theory, see Glémin et al. 2003, Whitlock et al. 2000; for an empirical example, see Willi & Fischer 2005). Kin-competition and inbreeding avoidance then cannot be perceived as alternative causes of dispersal evolution (Gandon 1999, Perrin & Goudet 2001). Whereas heterosis favors divergence in sex-specific dispersal rates, kin competition tends to have a stabilizing effect (Gandon

1999, Perrin & Mazalov 2000). Evolution of female preference for immigrant or related males, which further affects the evolution of male dispersal, depends on the balance between heterosis and kin selection (Lehmann & Perrin 2003). Complex interactions affect the evolution of dispersal under the joint influence of heterosis and kin competition, as the former increases the effective migration rate, decreasing relatedness and weakening the incentive effects of kin competition on dispersal (Gandon 1999, Roze & Rousset 2005).

Until recently, however, dispersal evolution models did not account for the full spectrum of interactions between kin competition and heterosis because the latter parameter was considered to be fixed (Motro 1991) or to be a simple mathematical function of the probability of coancestry among individuals in the same patch (Gandon 1999, Perrin & Mazalov 2000). Investigators have shown that heterosis varies with the average effect of mutations, their dominance and rate of occurrence, but also with the intensity of gene flow among local populations and their size (Glémin et al. 2003, Whitlock et al. 2000). Roze & Rousset's (2005) multilocus analytical model allows the quantification of direct selective effects on a dispersal modifier locus owing to kin competition and indirect selection through its association with deleterious alleles at loci contributing to heterosis. Their model predicts that heterosis increases the selected dispersal rate by an order of magnitude in some situations, but also that increasing heterosis can select unexpectedly for decreased dispersal. Simulations have cast doubts about the quantitative importance of heterosis for the evolution of dispersal when the total metapopulation size is small, as heterosis then vanishes rapidly when higher dispersal evolves (Guillaume & Perrin 2006, Ravigné et al. 2006).

8. IS DISPERSAL AN ADAPTATION TO EPHEMERAL HABITATS?

Increased rates of patch destruction in artificial metapopulations of *C. elegans* resulted in the increasing frequency of more dispersive mutants (Friedenberg 2003). Habitat persistence correlates negatively with intraspecific variation in macroptery in several species of insects (Denno et al. 1996). There are two distinct theoretical reasons why dispersal may provide adaptation to ephemeral habitats, which are not always distinguished clearly in the literature. First, dispersal allows tracking patches of favorable habitat and escape from deteriorating local conditions. Local disturbances generate patches with underexploited resources, allowing dispersers to escape from overcrowding (see Section 6). Predictable habitat deterioration through time (due to overexploitation, ecological succession, or any factor generating favorable patches of habitat with a finite life span) creates additional selection pressures favoring dispersal because less dispersive genotypes tend to be more frequent in older patches of habitat of lesser quality (Olivieri et al. 1995). Again, conditional dispersal and habitat selection should provide a strong advantage in variable environments, as long as habitat deterioration can be accurately predicted from some ecological cues [e.g., see the models by Doligez et al. (2003) and Ronce et al. (2005)]. Low conspecific density, for instance, can then convey different types of information about habitat quality, reflecting either low competition for resources or deteriorating ecological conditions such as with root voles for which emigration rates increase with decreasing density (Ims & Andreassen 2000; see a more general discussion in Clobert et al. 2004).

The second argument frequently invoked is that dispersal acts as a bet-hedging strategy in temporally variable environments. By spreading their progeny more evenly among different sites, genotypes with a higher dispersal ability better sample habitat variation within a generation, thus reducing the generation-to-generation variance in their mean performance. Venable & Brown (1988) clearly showed that such an argument does not hold in models in which the number of occupied sites is assumed to be infinite. Indeed, stochastic variance in mean performance between generations then vanishes for all genotypes. In models with a finite number of patches, demographic stochasticity, and density dependence (Doebeli & Ruxton 1997, Kisdi 2002, Parvinen 1999), the respective roles of bet hedging and escape from crowding in shaping the evolution of dispersal have never been quantified clearly.

The relationship between habitat instability and the dispersal propensity of organisms might also not be as straightforward as originally thought. Complex relationships between dispersal and the frequency of local extinction emerge because of feedbacks between population dynamics and evolution (see a review in Ronce & Olivieri 2004). Indeed, more frequent disturbance can result in slower population growth and less incentive to disperse to escape overcrowding (Ronce et al. 2000b), whereas changes in dispersal may also affect the probability of local extinction (Poethke et al. 2003).

9. HOW COSTLY IS DISPERSAL?

Dispersal is a risky behavior. First, mortality may be increased during the vagrancy stage of dispersal owing, for instance, to the transient use of nonoptimal habitat and increased predation risk, such as observed in dispersing root voles (Ims & Andreassen 2000). Estimations of mortality during dispersal from mark-recapture data, such as with the virtual migration model (Hanski et al. 2000), have shown a large amount of variation depending on both species traits and landscape characteristics (Matter 2006, Schtickzelle et al. 2006).

Dispersal is also risky when habitat selection during the settlement stage is constrained or limited, leading to frequent immigration into nonfavorable habitat. A large fraction of wind-dispersed pollen, for instance, never ends up on the stigma of a receptive flower of the same species. Nonephemeral patterns of spatial heterogeneity in habitat quality thus tend to select against passive dispersal (Hastings 1983, McPeek & Holt 1992). In particular, mismatch between postdispersal environment and phenotypes having developed in some other environment could contribute to immigrant inadequacy [but see also examples of dispersal based on phenotype matching (e.g., Cote & Clobert 2007)]. Local adaptation emerges when different alleles have different effects on fitness in different environments. It has been extensively documented in the field (Lenormand 2002) and indirectly selects against dispersal because immigrant individuals are less likely to carry locally favored alleles [see theoretical predictions by Wiener & Feldman (1993)]. The strength of such indirect selection, however, varies with dispersal itself, which attenuates genetic differences among sites and weakens local adaptation (Billiard & Lenormand 2005). Both theory (Gandon et al. 1996) and data (e.g., Morgan et al. 2005), however, have shown that higher dispersal may provide an evolutionary advantage to either host or pathogens engaged in a coevolutionary arms race, increasing the probability of local adaptation. How such an arms race affects the evolution of dispersal has not been explored.

Dispersal may also result in a loss of social status when joining a new group of individuals, involving an exposure to xenophobic behaviors (O'Riain & Jarvis 1997) or a loss of cooperation with related individuals (see a review in Lambin et al. 2001). Perrin & Goudet (2001) showed theoretically that kin cooperation in groups of philopatric females, as observed in many mammals, could counteract kin-competition effects and lead to the evolution of greater sex bias in dispersal. Evolution of dispersal and cooperative behaviors, however, is not always antagonistic, as shown by models of the joint evolution of altruism and mobility (Le Galliard et al. 2005). In the side-blotched lizards, blue morphs actively cooperate, and their nonrandom dispersal movements result in their postdispersal spatial aggregation (Sinervo & Clobert 2003).

Finally, increased mobility may trade off for other life-history traits. Smaller seed size might increase dispersal distance but compromises the survival and competitive ability of seedlings after germination. Flight-fecundity trade-offs, and their physiological basis, have been studied to a great extent in wing dimorphic insects (for a review, see Roff & Fairbarn 2001). In particular, in *Gryllus firmus*, individuals from genetic lineages characterized by a higher macroptery proportion are less fecund, independent from their individual dispersal morph (Roff & Fairbarn 2001). Dispersing individuals, however, may exhibit different sets of life-history traits while achieving the same lifetime reproductive success (see review in Bélichon et al. 1996).

The measurement of dispersal costs is plagued with numerous methodological difficulties and pitfalls in interpretation (for a review, see Bélichon et al. 1996, Clobert et al. 2004). Difficulties in measuring dispersal costs also emerge from the fact that selection may act to reduce such costs (see empirical evidence in Schtickzelle et al. 2006). Dispersing individuals are generally not a random subset of the population and have behavioral, physiological, and morphological attributes to reduce mortality during dispersal and increase settlement success in new patches of habitat (see, e.g., Gundersen et al. 2002). More generally, we lack an efficient framework to combine information about mortality during dispersal, genetic correlations between dispersal propensity and life-history traits, and phenotypic differences between dispersing and philopatric individuals to relate such estimates to parameters describing the cost of dispersal in evolutionary models.

Dispersal cost is indeed a salient feature of dispersal evolution models (see, e.g., Ravigné et al. 2006). In most models, the simplest interpretation of this parameter corresponds to a measure of increased mortality of dispersers during vagrancy or settlement. Its relationship to landscape characteristics is rarely explicit (see, however, Travis & Dytham 1999, Heino & Hanski 2001, Hovestadt et al. 2001), and it is generally not assumed to evolve. Models of joint evolution of local adaptation and dispersal (Billiard & Lenormand 2005, Kisdi 2002) provide an exception to this rule and have led to original predictions. Billiard & Lenormand (2005) found that, for the same set of parameters, evolution could lead to either very high or very low dispersal depending on initial mobility, owing to positive feedbacks in the joint evolution of dispersal and dispersal cost. The cost of dispersal in their model indeed depends tightly on the linkage disequilibrium between loci controlling dispersal propensity and local adaptation. As linkage disequilibrium peaks at intermediate dispersal, this can result in disruptive selection on dispersal.

10. IS LONG-DISTANCE DISPERSAL A CONSEQUENCE OF SELECTION FOR SHORT-DISTANCE DISPERSAL?

We may generally question the fact that different parts of the kernel (for instance, long- and short-distance dispersal) evolve independently. If the same traits enhance the probability of short- and long-distance journeys, occasional long-distance dispersal might be interpreted as a side effect of selection for short-distance movement. Conversely, traits enhancing dispersal may be selected for essentially because they allow long-distance movement, and the large fraction of individuals dispersing at short distance, as in seed or pollen dispersal, may simply be failures to do so. However, there are increasing suggestions that short- and long-distance dispersal events rely on different mechanisms (Higgins et al. 2003) or are accomplished by different types of individuals.

Despite the number of theoretical studies focusing on dispersal evolution, the evolution of dispersal distance rather than dispersal rate has been examined theoretically only recently. Some of these studies (Ezoe 1998, Murrell et al. 2002) have constrained the dispersal kernel to belong to a fixed (Gaussian or exponential) unique distribution. The evolution of short- and long-distance dispersal is completely linked under such assumptions. Two recent models have addressed the question of the evolution of the dispersal kernel's shape in a simple ecological context, without any constraints on the dispersal-distance distribution (Hovestadt et al. 2001, Rousset & Gandon 2002). In both models, dispersal evolves as a strategy for kin-competition avoidance, and dispersal costs vary with distance dispersed. Fat-tailed dispersal kernels deviating from the Gaussian and exponential distribution evolved readily, which suggests that kin competition alone can select for long-distance dispersal. What happens when several selective forces (such as kin-competition avoidance and recolonization of empty space) acting at different spatial scales affect the evolution of dispersal kernels has not been investigated. Clarifying those issues implies a better understanding of the mechanisms and specific traits affecting the dispersal kernel's shape and its different parts (see Donohue et al. 2005), as well as incorporating such constraints into evolutionary models to quantify the intensity of selection acting in different parts of the dispersal kernel.

11. CONCLUSIONS

Both theory and empirical studies have shown that searching for a unique cause for dispersal evolution is misleading (Ronce et al. 2001). Researchers have also claimed that using a single term, dispersal, to describe movements with different spatial scales and different ultimate or proximate motivations is equally misleading (Bowler & Benton 2005). However, I feel that different evolutionary explanations always will be entangled to some extent in promoting dispersal in any realistic situation. A better understanding of their interactions represents the exciting challenge of future theoretical and experimental studies of dispersal.

Theory about dispersal evolution has taught us much more than just the selective pressures acting on a particular life-history trait. It has motivated the study of whole life-history syndromes through the joint evolution of dispersal with dormancy (Venable & Brown 1988; see review in Olivieri 2001), reproductive effort (Crowley & McLetchie 2002, Ronce et al. 2000c), senescence (Dytham & Travis 2006), ecological specialization (Billiard & Lenormand 2005, Kisdi 2002), altruism (Le Galliard et al. 2005), kin recognition (Lehmann & Perrin 2003), sex ratio (Leturque & Rousset 2004), and mating strategies (Ravigné et al. 2006).

From a technical point of view, problems posed by dispersal evolution have stimulated many methodological advances. They have helped clarify theoretical approaches of evolution in the presence of multiple levels of selection and the concepts of inclusive fitness. They have drawn attention to the role of spatial interactions on selective processes. They have stimulated more careful thinking about the effect of genetic drift in life-history evolution. They have forced us to study the many complex feedbacks between population dynamics and evolution. Finally, they have allowed the integration of complex parts of evolutionary theory, such as that of neutral population differentiation, game theory, mutation load, and life-history evolution. Recent multilocus models of dispersal evolution (Billiard & Lenormand 2005, Roze & Rousset 2005), for instance, have contributed to a better conceptual unification in the treatment of genetic associations between and within individuals in a spatial context. Transferring these methodological advances to the study of other phenotypic traits and taking into account the spatial dimension in their evolution are now timely (Ronce & Olivieri 2004).

Such exciting conceptual and methodological challenges probably explain in part the abundant theoretical production on dispersal evolution. There are, however, two downsides to this prolific theoretical development. First, the increasing ecological complexity incorporated in analytical dispersal evolution models has often implied relying on the numerical evaluation of complex mathematical terms (Rousset & Ronce 2004) with diminishing insight into the exact evolutionary mechanisms at stake in the models, making the contribution of such models more similar to that of simulations. This is particularly the case in models with complex demographical dynamics. A pessimistic view would consider that we have reached the limit of what we can extract from these types of models. An optimistic perspective is that we need to put even greater efforts into thinking about the relevant parameters that we should compute to better test ideas about the selective forces explaining evolutionary patterns. The relative ease with which large spatially explicit individual-based simulations can be run currently (Travis & French 2000) should not make us forget that the contribution of such simulations to the understanding of evolutionary mechanisms is always increased by a careful comparison to analytical predictions.

The second downside is that the production of empirical results specifically testing model predictions has comparatively lagged behind (Ronce et al. 2001). This resulted in part because of the difficulty of measuring dispersal in nature, but the lack of dialogue between theory and experiments in this field of research has more complex causes. The very difficulty of the modeling exercises of dispersal evolution, and probably the excitement about methodology, has long distracted theoreticians from empirical evidence, such as the predominance of conditional dispersal, the complex shapes of dispersal kernels, the dynamical nature of dispersal costs, and the simultaneous action of several selective forces. Evolution of the reaction norms of dispersal to various environmental factors has received more theoretical interest recently, as well as the interaction between kin competition, heterosis, stochastic demographic dynamics, or local adaptation. We, however, still lack a general theory for the ontogeny of dispersal that would allow an understanding of the complex interactions between different ultimate causes for dispersal, between different environment effects at different stages of the life history (Ronce et al. 2001), and how such interactions shape the whole dispersal kernel (Ronce et al. 2001; see Section 10). The focus on long-term evolutionary equilibrium has also prevented theory from saying much about transient patterns and the rates of dispersal evolution following ongoing changes, such as climate warming or habitat fragmentation. It is, however, with the latter type of evidence that empiricists are currently confronted. Designing different types of models aiming at describing short-term patterns of evolution, both grounded on empirical estimates of heritability for dispersal characteristics and incorporating the complex demographic and genetic feedbacks revealed by previous theory, might represent a new theoretical challenge.

Refined measurements of dispersal variation in nature (Schtickzelle et al. 2006) and the identification of candidate genes affecting this behavior (Haag et al. 2005) should lead to better empirical insights into dispersal evolution. Given the multiple selective forces and feedbacks affecting dispersal, descriptive approaches, however, may tell us little about the evolutionary mechanisms at stake. Manipulative approaches are unfortunately seldom used in the study of dispersal and have mainly explored its plasticity. Proximate causes for dispersal, however, might not inform us about the ultimate causes having shaped the evolution of its reaction norm. Further development of experiments of the artificial evolution of dispersal with short-lived organisms (Friedenberg 2003), aiming at testing theoretical predictions, is therefore encouraged.

SUMMARY POINTS

1. Expression of dispersal behavior is sensitive to many aspects of the environment in the broad sense (including individual condition, social context, and abiotic factors). Differences among genotypes in their dispersal properties also depend on the environmental context.
2. Some model assumptions preclude the study of particular forces acting on dispersal evolution. This allows the disentanglement of selective pressures but spreads confusion when it is not clearly acknowledged.
3. The consequences of inbreeding depression for the evolution of dispersal cannot be understood without taking into account its complex interactions with kin competition.

4. Distinct consequences of dispersal may be advantageous in ephemeral habitats but feedbacks between population dynamics and the evolution of dispersal make the relationship between dispersal and local extinction frequency highly nonlinear.
5. Potential costs of dispersal are multiple, yet empirical evidence is ambiguous. Both data and theory suggest that these costs can evolve.
6. Theory about dispersal evolution has given us the opportunity to much refine our understanding of evolution in spatially structured systems.

FUTURE ISSUES

1. We need more information about both the heritability of dispersal kernels and the heritability of dispersal reaction norms to environmental cues.
2. We need models to focus on the evolution of the distribution of dispersal distances to better understand how the different evolutionary forces shape such distribution and to better relate theoretical predictions to data.
3. We need to better understand empirically and model theoretically the ontogeny of dispersal to predict the evolution of environmental effects on dispersal.
4. We need to produce short-term predictions about evolutionary changes in dispersal in the context of global change.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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LITERATURE CITED

Ajar E. 2003. Analysis of disruptive selection in subdivided populations. *BMC Evol. Biol.* 3:22

Balkau BJ, Feldman MW. 1973. Selection for migration modification. *Genetics* 74:171–74

Barton NH. 2001. The evolutionary consequences of gene flow and local adaptation: future approaches. See Clobert et al. 2001, pp. 329–40

Bélichon S, Clobert J, Massot M. 1996. Are there differences in fitness components between philopatric and dispersing individuals? *Acta Oecol.* 17:503–17

Billiard S, Lenormand T. 2005. Evolution of migration under kin selection and local adaptation. *Evolution* 59:13–23

Bolker BM, Pacala SW. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *Am. Nat.* 153:575–602

Boudjemadi K, Lecomte J, Clobert J. 1999. Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. *J. Anim. Ecol.* 68:1207–24

Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* 80:205–25

Brown JH, Kodric-Brown A. 1977. Turnover rates in insular biogeography: effect of migration on extinction. *Ecology* 58:445–49

Bullock JM, Kenward RE, Hails RS, eds. 2002. *Dispersal Ecology*. Oxford, UK: Blackwell

Cadet C, Ferrière R, Metz JAJ, van Baalen M. 2003. The evolution of dispersal under demographic stochasticity. *Am. Nat.* 162:427–41

Cheplick GP, Kane KH. 2004. Genetic relatedness and competition in *Triplasis purpurea* (Poaceae): resource partitioning or kin selection? *Int. J. Plant Sci.* 165:623–30

Clobert J, Danchin E, Dhondt AA, Nichols JD, eds. 2001. *Dispersal*. New York: Oxford Univ. Press

A complete synthesis of the evolutionary ecology of dispersal, with a large emphasis on dispersal plasticity.

Clobert J, Ims RA, Rousset F. 2004. Causes, mechanisms and consequences of dispersal. In *Ecology, Genetics and Evolution of Metapopulations*, ed. I Hanski, O Gaggiotti, pp. 307–35. Amsterdam: Academic

Cody ML, Overton JM. 1996. Short-term evolution of reduced dispersal in island plant populations. *J. Ecol.* 84:53–61

Colas B, Olivieri I, Riba M. 1997. *Centaurea corymbosa*, a cliff dwelling species tottering on the brink of extinction: a demographic and genetic study. *Proc. Natl. Acad. Sci. USA* 94:3471–76

Comins HN. 1982. Evolutionarily stable strategies for localized dispersal in two dimensions. *J. Theor. Biol.* 94:579–606

Comins HN, Hamilton WD, May RM. 1980. Evolutionary stable dispersal strategies. *J. Theor. Biol.* 82:205–30

Cote J, Clobert J. 2007. Social personalities influence natal dispersal in a lizard. *Proc. R. Soc. London Ser. B Biol. Sci.* 274:383–90

Crowley PH, McLetchie DN. 2002. Trade-offs and spatial life-history strategies in classical metapopulations. *Am. Nat.* 159:190–208

Denno RF, Hawthorne DJ, Thorne BL, Gratton C. 2001. Reduced flight capability in British Virgin Island populations of a wing-dimorphic insect: the role of habitat isolation, persistence, and structure. *Ecol. Entomol.* 26:25–36

Denno RF, Roderick GK, Peterson MA, Huberty AF, Döbel HG, et al. 1996. Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecol. Monogr.* 66:389–408

Dingle H. 1996. *Migration: The Biology of Life on the Move*. New York: Oxford Univ. Press

Doebeli M, Ruxton GD. 1997. Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. *Evolution* 51:1730–41

Doligez B, Cadet C, Danchin E, Boulinier T. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Anim. Behav.* 66:973–88

Doligez B, Danchin E, Clobert J. 2002. Public information and breeding habitat selection in a wild bird population. *Science* 297:1168–70

Donohue K. 1999. Seed dispersal as a maternally influenced character: mechanistic basis of maternal effects and selection on maternal characters in an annual plant. *Am. Nat.* 154:674–89

Donohue K, Polisetty CR, Wender NJ. 2005. Genetic basis and consequences of niche construction: plasticity-induced genetic constraints on the evolution of seed dispersal in *Arabidopsis thaliana*. *Am. Nat.* 165:537–50

First attempt to measure heritability and genetic correlations of dispersal kernels' characteristics.

Dytham C, Travis JMJ. 2006. Evolving dispersal and age at death. *Oikos* 113:530–38

Ezoe H. 1998. Optimal dispersal range and seed size in a stable environment. *J. Theor. Biol.* 190:287–93

Ferrière R, Le Galliard JF. 2001. Invasion fitness and adaptive dynamics in spatial population models. See Clobert at al. 2001, pp. 57–79

Fontanillas P, Petit E, Perrin N. 2004. Estimating sex-specific dispersal rates with autosomal markers in hierarchically structured populations. *Evolution* 58:886–94

Frank SA. 1986. Dispersal polymorphism in subdivided populations. *J. Theor. Biol.* 122:303–9

Fréville H, Colas B, Riba M, Caswell H, Mignot A, et al. 2004. Spatial and temporal demographic variability in the endemic plant species *Centaurea corymbosa* (Asteraceae). *Ecology* 85:694–703

Friedenberg NA. 2003. Experimental evolution of dispersal in spatiotemporally variable microcosms. *Ecol. Lett.* 6:953–59

Investigates the evolution of dispersal in the lab, using *C. elegans* in artificial landscapes.

Gandon S. 1999. Kin competition, the cost of inbreeding and the evolution of dispersal. *J. Theor. Biol.* 200:345–64

Gandon S, Capowiez Y, Dubois Y, Michalakis Y, Olivieri I. 1996. Local adaptation and gene-for-gene coevolution in a metapopulation model. *Proc. R. Soc. London Ser. B Biol. Sci.* 263:1003–9

Gandon S, Michalakis Y. 1999. Evolutionary stable dispersal rate in a metapopulation with extinctions and kin competition. *J. Theor. Biol.* 3:275–90

Gandon S, Rousset F. 1999. Evolution of stepping-stone dispersal rates. *Proc. R. Soc. London Ser. B Biol. Sci.* 266:2507–13

Geritz SAH, Kisdi E, Meszena G, Metz JAJ. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* 12:35–57

Glémin S, Ronfort J, Bataillon T. 2003. Patterns of inbreeding depression and architecture of the load in subdivided populations. *Genetics* 165:2193–212

Guillaume F, Perrin N. 2006. Joint evolution of dispersal and inbreeding load. *Genetics* 173:497–509

Gundersen G, Andreassen HP, Ims RA. 2002. Individual and population level determinants of immigration success on local habitat patches: an experimental approach. *Ecol. Lett.* 5:294–301

Gyllenberg M, Parvinen K, Dieckmann U. 2002. Evolutionary suicide and evolution of dispersal in structured metapopulations. *J. Math. Biol.* 45:79–105

Haag CR, Saastamoinen M, Marden JH, Hanski I. 2005. A candidate locus for variation in dispersal rate in a butterfly metapopulation. *Proc. R. Soc. London Ser. B Biol. Sci.* 272:2449–56

Hamilton WD. 1964. The genetical evolution of social behaviour, I. *J. Theor. Biol.* 7:1–16

Hamilton WD, May RM. 1977. Dispersal in stable habitats. *Nature* 269:578–81

Hanski I, Alho J, Moilanen A. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* 81:239–51

Hanski I, Eralahti C, Kankare M, Ovaskainen O, Siren H. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecol. Lett.* 7:958–66

Harada Y. 1999. Short- vs. long-range disperser: the evolutionarily stable allocation in a lattice-structured habitat. *J. Theor. Biol.* 201:171–87

Hastings A. 1983. Can spatial variation alone lead to selection for dispersal? *Theor. Popul. Biol.* 24:244–51

Heino M, Hanski I. 2001. Evolution of migration rate in a spatially realistic metapopulation model. *Am. Nat.* 157:495–511

Higgins K, Lynch M. 2001. Metapopulation extinction caused by mutation accumulation. *Proc. Natl. Acad. Sci. USA* 98:2928–33

Higgins SI, Nathan R, Cain ML. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* 84:1945–56

Hill JK, Thomas CD, Lewis OT. 1999. Flight morphology in fragmented populations of a rare British butterfly, *Hesperia comma*. *Biol. Conserv.* 87:277–83

Hovestadt T, Messner S, Poethke HJ. 2001. Evolution of reduced dispersal mortality and 'fat-tailed' dispersal kernels in autocorrelated landscapes. *Proc. R. Soc. London Ser. B Biol. Sci.* 268:385–91

Imbert E. 2001. Capitulum characters in a seed heteromorphic plant, *Crepis sancta* (Asteraceae): variance partitioning and inference for the evolution of dispersal rate. *Heredity* 86:78–86

Imbert E, Ronce O. 2001. Phenotypic plasticity for dispersal ability in the seed heteromorphic *Crepis sancta* (Asteraceae). *Oikos* 93:126–34

Ims RA, Andreassen HP. 2000. Spatial synchronization of vole population dynamics by predatory birds. *Nature* 408:194–96

Ims RA, Hjermann D. 2001. Condition dependent dispersal. In *Dispersal*, ed. J Clobert, E Danchin, A Dhondt, JD Nichols, pp. 203–16. New York: Oxford Univ. Press

Irwin AJ, Taylor PD. 2000. Evolution of dispersal in a stepping-stone population with overlapping generations. *Theor. Popul. Biol.* 58:321–28

First theoretical demonstration of the effect of kin selection on dispersal.

Jánosi IM, Scheuring I. 1997. On the evolution of density dependent dispersal in a spatially structured population model. *J. Theor. Biol.* 187:397–408

Kalisz S, Hanzawa FM, Tonsor SJ, Thiede DA, Voigt S. 1999. Ant-mediated seed dispersal alters pattern of relatedness in a population of *Trillium grandiflorum*. *Ecology* 80:2620–34

Kisdi E. 2002. Dispersal: risk spreading versus local adaptation. *Am. Nat.* 159:579–96

Kisdi E. 2004. Conditional dispersal under kin competition: extension of the Hamilton-May model to brood size-dependent dispersal. *Theor. Popul. Biol.* 66:369–80

Kokko H, Lopez-Sepulcre A. 2006. From individual dispersal to species ranges: perspectives for a changing world. *Science* 313:789–91

Lambin X, Aars J, Piertney SB. 2001. Interspecific competition, kin competition and kin facilitation: a review of empirical evidence. See Clobert et al. 2001, pp. 110–22

Le Galliard JF, Ferrière R, Clobert J. 2003. Mother-offspring interactions affect natal dispersal in a lizard. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 270:1163–69

Le Galliard JF, Ferrière R, Dieckmann U. 2005. Adaptive evolution of social traits: origin, trajectories, and correlations of altruism and mobility. *Am. Nat.* 165:206–24

Lehmann L, Perrin N. 2003. Inbreeding avoidance through kin recognition: Choosy females boost male dispersal. *Am. Nat.* 162:638–52

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7:601–13

Lenormand T. 2002. Gene flow and the limits to natural selection. *Trends Ecol. Evol.* 17:183–89

Leturque H, Rousset F. 2002. Dispersal, kin competition, and the ideal free distribution in a spatially heterogeneous population. *Theor. Popul. Biol.* 62:169–80

Leturque H, Rousset F. 2004. Intersexual competition as an explanation for sex-ratio and dispersal biases in polygynous species. *Evolution* 58:2398–408

Levin SA, Cohen D, Hastings A. 1984. Dispersal strategies in patchy environments. *Theor. Popul. Biol.* 26:165–91

Levin SA, Muller-Landau HC, Nathan R, Chave J. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. *Annu. Rev. Ecol. Evol. Syst.* 34:575–604

Massot M, Clobert J, Lorenzon P, Rossi J-M. 2002. Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. *J. Anim. Ecol.* 71:253–61

Mathias A, Kisdi E, Olivieri I. 2001. Divergent evolution of dispersal in a heterogeneous landscape. *Evolution* 55:246–59

Matter SF. 2006. Changes in landscape structure decrease mortality during migration. *Oecologia* 150:8–16

McPeek MA, Holt RD. 1992. The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* 140:1010–27

Metz JAJ, Gyllenberg M. 2001. How should we define fitness in structured metapopulation models? Including an application to the calculation of ES dispersal strategies. *Proc. R. Soc. London Ser. B Biol. Sci.* 268:499–508

First theoretical demonstration that conditional dispersal may much attenuate the cost of dispersal.

Molofsky J, Ferdy JB. 2005. Extinction dynamics in experimental metapopulations. *Proc. Natl. Acad. Sci. USA* 102:3726–31

Morgan AD, Gandon S, Buckling A. 2005. The effect of migration on local adaptation in a coevolving host-parasite system. *Nature* 437:253–56

Motro U. 1991. Avoiding inbreeding and sibling competition: the evolution of sexual dimorphism for dispersal. *Am. Nat.* 137:108–15

Muller-Landau HC, Levin SA, Keymer JE. 2003. Theoretical perspectives on evolution of long-distance dispersal and the example of specialized pests. *Ecology* 84:1957–67

Murrell DJ, Travis JMJ, Dytham C. 2002. The evolution of dispersal distance in spatially-structured populations. *Oikos* 97:229–36

O'Riain MJ, Jarvis JUM. 1997. Colony member recognition and xenophobia in the naked mole-rat. *Anim. Behav.* 53:487–98

Olivieri I. 2001. The evolution of seed heteromorphism in a metapopulation: interactions between dispersal and dormancy. In *Integrating Ecology and Evolution in a Spatial Context*, ed. J Silvertown, J Antonovics, pp. 245–68. Oxford, United Kingdom: Br. Ecol. Soc. & Blackwell Sci.

Olivieri I, Gouyon P-H. 1985. Seed dimorphism for dispersal: theory and implications. In *Structure and Functioning of Plant Populations*, ed. J Haeck, JW Woldendrop, pp. 77–90. Amsterdam: North-Holland Pub.

Olivieri I, Gouyon P-H. 1997. Evolution of migration rate and other traits: the metapopulation effect. In *Metapopulation Biology: Ecology, Genetics, and Evolution*, ed. I Hanski, ME Gilpin, pp. 293–323. San Diego: Academic

Olivieri I, Michalakis Y, Gouyon P-H. 1995. Metapopulation genetics and the evolution of dispersal. *Am. Nat.* 146:202–28

Parvinen K. 1999. Evolution of migration in a metapopulation. *Bull. Math. Biol.* 61:531–50

Parvinen K. 2002. Evolutionary branching of dispersal strategies in structured metapopulations. *J. Math. Biol.* 45:106–24

Parvinen K, Dieckmann U, Gyllenberg M, Metz JAJ. 2003. Evolution of dispersal in metapopulations with local density dependence and demographic stochasticity. *J. Evol. Biol.* 16:143–53

Pen I. 2000. Reproductive effort in viscous populations. *Evolution* 54:293–97

Peroni PA. 1994. Seed size and dispersal potential of *Acer rubrum* (Aceraceae) samaras produced by populations in early and late successional environments. *Am. J. Bot.* 81:1428–34

Perrin N, Goudet J. 2001. Inbreeding and dispersal. See Clobert et al. 2001, pp. 123–42

Perrin N, Mazalov V. 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *Am. Nat.* 155:116–27

Phillips BL, Brown GP, Webb JK, Shine R. 2006. Invasion and the evolution of speed in toads. *Nature* 439:803

Poethke HJ, Hovestadt T. 2002. Evolution of density-and-patch-size-dependent dispersal rates. *Proc. R. Soc. London Ser. B Biol. Sci.* 269:637–45

Poethke HJ, Hovestadt T, Mitesser O. 2003. Local extinction and the evolution of dispersal rates: causes and correlations. *Am. Nat.* 161:631–40

Ravigné V, Olivieri I, Gonzalez-Martinez SC, Rousset F. 2006. Selective interactions between short distance pollen and seed dispersal in self-compatible species. *Evolution* 60:2257–71

Roff DA. 1986. The evolution of wing dimorphism in insects. *Evolution* 40:1009–20

Roff DA. 1990. The evolution of flightlessness in insects. *Ecol. Monogr.* 60:389–421

Roff DA, Fairbarn DJ. 2001. The genetic basis of dispersal and migration and its consequences for the evolution of correlated traits. See Clobert et al. 2001, pp. 191–202

Ronce O, Brachet S, Olivieri I, Gouyon PH, Clobert J. 2005. Plastic changes in seed dispersal along ecological succession: theoretical predictions from an evolutionary model. *J. Ecol.* 93:431–40

Ronce O, Clobert J, Massot M. 1998. Natal dispersal and senescence. *Proc. Natl. Acad. Sci. USA* 95:600–5

Ronce O, Gandon S, Rousset F. 2000a. Kin selection and natal dispersal in an age-structured population. *Theor. Popul. Biol.* 58:143–59

Ronce O, Olivieri I. 2004. Life history evolution in metapopulations. In *Ecology, Genetics, and Evolution of Metapopulations*, ed. I Hanski, OE Gaggiotti, pp. 227–58. Amsterdam: Academic

Ronce O, Olivieri I, Clobert J, Danchin E. 2001. Perspectives on the study of dispersal evolution. See Clobert et al. 2001, pp. 341–57

Ronce O, Perret F, Olivieri I. 2000b. Evolutionarily stable dispersal rates do not always increase with local extinction rates. *Am. Nat.* 155:485–96

Ronce O, Perret F, Olivieri I. 2000c. Landscape dynamics and evolution of colonizer syndromes: interactions between reproductive effort and dispersal in a metapopulation. *Evol. Ecol.* 14:233–60

Rousset F. 2006. Separation of time scales, fixation probabilities and convergence to evolutionarily stable states under isolation by distance. *Theor. Popul. Biol.* 69:165–79

Rousset F, Gandon S. 2002. Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. *J. Evol. Biol.* 15:515–23

Analyzes how kin competition shapes the evolution of the whole dispersal kernel.

Rousset F, Ronce O. 2004. Inclusive fitness for traits affecting metapopulation demography. *Theor. Popul. Biol.* 65:127–41

Roze D, Rousset F. 2003. Selection and drift in subdivided populations: a straightforward method for deriving diffusion approximations and applications involving dominance, selfing and local extinctions. *Genetics* 165:2153–66

Roze D, Rousset F. 2005. Inbreeding depression and the evolution of dispersal rates: a multilocus model. *Am. Nat.* 166:708–21

Quantifies the interactions between direct and indirect selection on dispersal (see also Billiard & Lenormand 2005), and illustrates how kin selection operates in multilocus models.

Schtickzelle N, Mennechez G, Baguette M. 2006. Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology* 87:1057–65

Simmons AD, Thomas CD. 2004. Changes in dispersal during species' range expansions. *Am. Nat.* 164:378–95

Sinervo B, Clobert J. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science* 300:1949–51

Sorci G, Massot M, Clobert J. 1994. Maternal parasite load increase sprint speed and philopatry in female offspring of the common lizard. *Am. Nat.* 144:153–64

Tallmon DA, Luikart G, Waples RS. 2004. The alluring simplicity and complex reality of genetic rescue. *Trends Ecol. Evol.* 19:489–96

Taylor PD. 1988. An inclusive fitness model for dispersal of offspring. *J. Theor. Biol.* 130:363–78

Taylor PD, Frank SA. 1996. How to make a kin selection model. *J. Theor. Biol.* 180:27–37

Travis JMJ, Dytham C. 1999. Habitat persistence, habitat availability and the evolution of dispersal. *Proc. R. Soc. London Ser. B Biol. Sci.* 266:723–28

Travis JMJ, Dytham C. 2002. Dispersal evolution during invasions. *Evol. Ecol. Res.* 4:1119–29

Travis JMJ, French DR. 2000. Dispersal functions and spatial models: expanding our dispersal toolbox. *Ecol. Lett.* 3:163–65

van Baalen M, Rand DA. 1998. The unit of selection in viscous populations and the evolution of altruism. *J. Theor. Biol.* 193:631–48

van Valen L. 1971. Group selection and the evolution of dispersal. *Evolution* 25:591–98

Historically, the first model of dispersal evolution.

Venable DL, Brown JS. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* 131:360–84

Whitlock MC, Ingvarsson PK, Hatfield T. 2000. Local drift load and the heterosis of interconnected populations. *Heredity* 84:452–57

Wiener P, Feldman MW. 1993. The effects of the mating system on the evolution of migration in a spatially heterogeneous population. *Evol. Ecol.* 7:251–69

Willi Y, Fischer M. 2005. Genetic rescue in interconnected populations of small and large size of the self-incompatible *Ranunculus reptans*. *Heredity* 95:437–43

Wolff JO. 1992. Parents suppress reproduction and stimulate dispersal in opposite-sex juvenile white-footed mice. *Nature* 359:409–10

Wright S. 1969. *The Theory of Gene Frequencies*. Chicago: Univ. Chicago Press

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