

The evolutionary ecology of dispersal

Dispersal is a life-history trait that has profound consequences for populations. Viewed from an ecological perspective, dispersal influences the dynamics and persistence of populations, the distribution and abundance of species, and community structure. From an evolutionary perspective, dispersal determines the level of gene flow between populations and affects processes such as local adaptation, speciation and the evolution of life-history traits. In fact, it is difficult to imagine any ecological or evolutionary problem that would not be affected by dispersal.

The various consequences of dispersal are extensively discussed in the ecological and evolutionary literature (the *Science Citation Index* gave more than 1000 occurrences of 'dispersal' in the abstract or title of papers for the year 1997 alone). Surprisingly, however, the question of why particular dispersal strategies evolve has received much less attention. Part of the problem is that many of the mechanisms proposed to affect the evolution of dispersal (Box 1) are notoriously difficult to test in the field. There exists a serious gap between theory and data, and consequently our understanding of why particular organisms disperse in specific ways is still limited. A recent workshop in Finland provided an opportunity to survey the state of the field.

The workshop – Evolution of Dispersal – took place in October last year at the Tvärminne Zoological Station of the University of Helsinki (financed by the Finnish Academy of Sciences through the Spatial Ecology Program in the Division of Population Biology). The organizers, Liselotte Sundström and Mikko Heino (both at the Division of Population Biology, Helsinki University) brought together an impressive array of researchers with diverse backgrounds and diverse approaches to the evolution of dispersal.

Adaptive dynamics of dispersal strategies

To understand present states and potential changes in dispersal traits, we have to evaluate the selective pressures that underly their evolution. These pressures arise from interactions between individuals of the dispersing population and their environment. Because dispersal often occurs in spatially heterogeneous environments, the resulting population dynamics and ecological feedbacks tend to be intricate.

It is difficult to incorporate such complicated feedbacks between an evolving population and its ecological environment into models of population genetics. Consequently, models of evolutionary game theory have been used, but these tend to oversimplify strategies and feedbacks by relying on payoff matrices. An alternative approach for studying the evolution of dispersal uses adaptive dynamics¹⁻³, where selective pressures and resulting adaptive changes are derived from population dynamics (Box 2).

Mats Gyllenberg (University of Turku, Finland) and Hans Metz (Leiden University, The Netherlands) presented a technique for predicting invasibility of metapopulations. For the first time, their method has allowed the initial growth rate of rare mutants in resident metapopulations to be obtained analytically. Ulf Dieckmann demonstrated how correlation dynamics (where spatially extended populations are described not only by densities of individuals, but also by densities of pairs of individuals) can provide insights into tradeoffs between competitive and dispersal abilities.

From methods to mechanisms

One new development facilitated by adaptive-dynamics theory is the inclusion of population dynamics into evolutionary models. Stefan Geritz (University of Turku) discussed how the evolutionary dynamics of dispersal rates in metapopulations are affected by the existence of multiple demographic attractors. Michael Doebeli (University of Basel, Switzerland) showed that complex population dynamics could lead to an 'evolutionary cycling' of dispersal rates: out-of-phase fluctuations

select for increasing dispersal rates until dispersal synchronizes the dynamics. If costly, dispersal is then selected against until the dynamics are again asynchronous so that the cycle can repeat itself. Other adaptive-dynamics models for studying the effects of spatial and temporal heterogeneities (both internally generated and externally imposed) on the evolution of dispersal rates were presented by Kalle Parvinen (University of Turku) and Andrea Mathias (Eötvös University, Budapest, Hungary).

Findings from these different models all point towards a common conclusion: in spatially structured populations, interactions between ecological and evolutionary dynamics can lead to polymorphisms in dispersal rates through repeated 'evolutionary branching'.

Olof Leimar, Ulf Norberg (both at Stockholm University, Sweden) and Graeme Ruxton (University of Glasgow, UK) used lattice models to investigate causal mechanisms for the evolution of dispersal. Justin Travis (Imperial College, Silwood Park, UK) and Calvin Dytham (University of York, UK) explored the effects of habitat heterogeneity by using random fractals to create spatial and temporal fluctuations in carrying capacities of habitats. If spatial fluctuations were autocorrelated (red noise), greater dispersal rates evolved than when the fluctuations were not autocorrelated (white noise). Autocorrelated temporal fluctuations caused lower dispersal rates to evolve than nonautocorrelated temporal fluctuations. Francois Rousset (University of Montpellier, France) and Nicolas Perrin (University of Lausanne, Switzerland) demonstrated the importance of kin selection for the evolution of dispersal, and Pekka Pamilo (Uppsala University, Sweden) discussed his investigations of the effects of social structure on dispersal in ants.

Box 1. How does dispersal evolve?

In the past 30 years, several mechanisms have been identified that influence the evolution of dispersal strategies. Mathematical models designed to investigate the evolution of dispersal usually assume that local populations occur in discrete habitats, and that in each generation a certain fraction of individuals disperses from natal habitats. Most models are based on game theory and seek to delineate evolutionarily stable strategies^{5,6}.

Habitat extinction risks^{7,8} ('unstable habitats'): risks of local extinction are the most intuitive reason for why dispersal evolved and thus have been tested repeatedly in the field, using, for example, wing-dimorphic insects⁹.

Competition among kin¹⁰: dispersal is selected for if it reduces competition between close relatives, even in the absence of other dispersal-promoting factors, such as unstable habitats.

Temporal and spatial variability in habitat quality^{11,12}: in general, spatial variability selects against and temporal variability selects for dispersal. If habitats fluctuate both spatially and temporally, the optimal dispersal rate depends on how fluctuations are correlated. A possible source of variability is chaotic population dynamics¹³.

Costs of dispersal¹⁰: if dispersal is costly (e.g. because of mortality risks during travelling or investments into dispersal morphology), optimal dispersal rates are decreased.

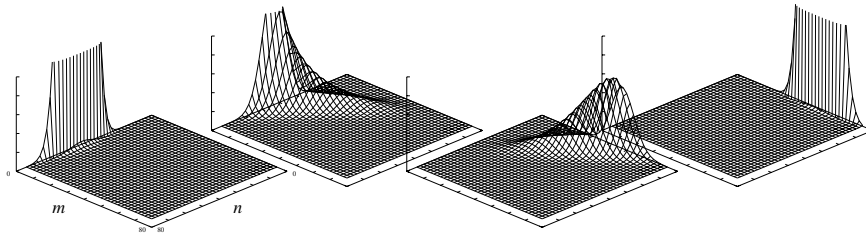
Inbreeding¹⁴: costs of inbreeding can also select for dispersal, and is independent of competition between related individuals.

Box 2. Evolutionary invasion analysis

To assess which dispersal strategies are favored by natural selection, the potential of invasion by mutant (or immigrant) strategies into populations of resident dispersal strategists can be investigated. Such evolutionary invasion analyses are best based on the population dynamics between mutant and resident individuals. If the initial growth rate of a rare mutant within a given resident population is positive, the mutant can invade and typically replace the former resident.

Repeated substitutions of this kind can take populations to a dispersal strategy (or to a polymorphism thereof) that is 'unbeatable' or 'evolutionarily stable'⁵. The theory of adaptive dynamics¹⁻³ allows us to predict the resulting evolutionary change in continuous adaptive traits such as dispersal rates. Also, contingent dispersal strategies can be investigated, such as probabilities of dispersing from or into subpopulations of given densities, or dispersal rates that are dependent on age.

How a model metapopulation is invaded by a new dispersal strategy is shown by the sequence of illustrations below. Each graph depicts the frequency distribution of patches inhabited by n resident and m mutant individuals. Within-patch dynamics are individual-based and logistic, and the rate of dispersal between patches is adaptive. Initially mutant strategists are few and far between, but they eventually take over the entire population.



Using knowledge of population dynamics to predict success or failure of such invasions gives a theory for the evolution of dispersal that is firmly rooted in descriptions of ecological change.

(Online: Fig. 1)

The evolution of dispersal has consequences for other life-history traits, which in turn can affect dispersal rates. Éva Kisdi (University of Turku) analysed the joint evolution of dispersal and a trait determining survival in two different types of habitat with environmental stochasticity. In her adaptive-dynamics model, evolution often resulted in low dispersal rates and local adaptation (thus yielding an evolutionarily stable dimorphism of two phenotypes, each of which is a specialist for only one habitat). However, differences between habitats and the magnitude of temporal fluctuations have a strong effect on evolutionary outcomes.

Three speakers explicitly aimed to identify causes or consequences of dispersal in particular organisms. Janis Dickinson (University of California, Berkeley, USA) argued that differences between sexes in the relative success of philopatric versus dispersing individuals might be a reason for sex-biased dispersal in western bluebirds (*Sialia mexicana*) – although problems in following dispersers made quantitative fitness estimates very difficult.

Habitat fragmentation could lead to a decrease in dispersal rates, because genes associated with dispersal will be lost from isolated populations when individuals leave the habitats. Because the decrease in dispersal propensity can influence the persistence of a species in metapopulations, this process has implications for conservation biology. Chris Thomas (University of Leeds, UK) presented data from several butterfly species to suggest that the ability to disperse might indeed

be decreasing in isolated or fragmented populations.

Jean Clobert (University of Paris VI, France) argued that several of the factors that are suggested by theoretical models to influence the evolution of dispersal might act together, even within the same population. Because many factors lead to similar predictions, identifying their relative importance is a major goal that can only be achieved experimentally. A recurrent result of Clobert's studies on the common lizard (*Lacerta vivipara*) is that dispersal is condition-dependent – a fact largely ignored by current models.

Measuring dispersal

Some of the practical statistical problems of measuring dispersal in the field were outlined by Walt Koenig (University of California, Berkeley, USA) when discussing his findings on acorn woodpeckers (*Melanerpes formicivorus*). Koenig emphasized that if the scale over which dispersal is measured is smaller than the scale over which organisms actually move, then average dispersal distances can be grossly underestimated. This is a 'right censoring' problem, familiar to those analysing medical trials (where not all patients die or relapse before the end of the trial). Unfortunately, there was no clear shape in the dispersal pattern that would have allowed extrapolation of measurements to longer distances.

Individuals moving too far was not a problem faced by Bruno Baur (University of Basel) in his tracking of snails, which can move as far as 7 m per year. Indeed,

Baur suggested that catastrophes such as avalanches and floods after torrential rains were the major mechanism for long-range dispersal. Wolfgang Weisser (University of Basel) demonstrated difficulties in delineating local populations of aphids. David Jenkins (University of Illinois, USA) discussed empirical data taken from artificial ponds and argued that the movement of zooplankton between ponds is a much rarer and less predictable phenomenon than previously thought. Bruce Rannala (State University of New York, USA) assessed the utility of Wright's island model and used a Bayesian framework to develop methods for the estimation of past immigration, based on population genetical data.

By itself, the measurement of dispersal is merely a descriptive exercise. Linking measurements to mechanisms, Jens Roland (University of Alberta, USA) has estimated the effects of spatial pattern of woodland and meadow on dispersal behavior in *Parnassius* butterflies, which inhabit meadows that arise in gaps created by forest fires. Roland has shown that the intervening landscape between sampling sites had a predictable effect on the amount of movement between sites.

Dispersal and metapopulation viability

Are extinction risks for endangered species reduced by evolving dispersal strategies? In a process known as 'adaptive rescue'⁴, populations exposed to environmental threats can increase their viability through the evolution of critical life-history traits. However, what is beneficial to the population as a whole is not necessarily favored by individual selection. In a given ecological setting, the evolutionary stable rate of dispersal need not be identical to the rate that would optimize population persistence (Isabelle Olivieri, University of Montpellier). Also, the response of these two rates to changing ecological conditions can be qualitatively different. Coevolution of dispersal rate and reproductive effort might enhance metapopulation persistence in highly disturbed landscapes.

Pierre-Henri Gouyon (University Paris-Sud, France) illustrated (from empirical data and theoretical analyses) the importance of dispersal for the persistence of threatened plant metapopulations. Transitions between vegetation types, brought about by environmental change, can result in extinctions if adaptation of dispersal strategies cannot occur fast enough.

Régis Férière (Ecole Normale Supérieure, Paris) presented models of metapopulations that are driven to extinction by natural selection acting on dispersal rates. In contrast to adaptive rescue, such

populations actually undergo an 'adaptive suicide'. A degrading environment can obstruct the evolutionary path of a dispersal trait towards more viable rescue states. From within such an 'adaptive trap', gradual evolution of dispersal can no longer prevent population extinction.

In this workshop, the recent rise of adaptive dynamics theory was very apparent, with many speakers using this tool to explore different aspects of dispersal evolution. In the real world, however, detailed knowledge about dispersal in many organisms remains scarce. Some contributions suggested that new techniques, such as those from molecular biology, might help to overcome this shortage. It will remain a challenge to integrate the various approaches presented, so that more theoretical predictions can be tested in the field. A forthcoming symposium* in France will provide the next opportunity to see how close we are to finding a unifying approach in the study of dispersal.

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Cloning *Odysseus* and the seed of speciation

The origin of new species, although a core subject in evolutionary biology, continues to mystify. One hundred and sixty years ago, John Herschel referred to speciation as 'that mystery of mysteries', and Darwin echoed him¹. In 1922, William Bateson said, 'that... bit of the theory of evolution which is concerned with the origin and nature of species remains utterly mysterious'². Even as recently as 1974, Richard Lewontin stated that 'we know virtually nothing about the genetic changes that occur in species formation'³.

Lamenting our ignorance about speciation appears to be a habitual penance for evolutionary biologists. Although Lewontin might have been overly pessimistic at the time, it is certainly true that our understanding of the fine workings of speciation has progressed only slowly. Over the past two decades, studies of natural and experimental hybridization have given some information on the

numbers and locations of genes involved in reproductive isolation. But only now has a study appeared that dissects speciation genes with molecular precision⁴, rewarding us with unexpected insights.

Better insights are desperately needed because, since the years that the New Synthesis was conceived, many different speciation models have accumulated in the literature. Although nature is so multifarious that no single unified speciation theory can exist, this plethora of models has sometimes caused more confusion than might be necessary. Fortunately, researchers are beginning to recognize that some speciation models are more plausible than others⁵, and most are best viewed as extreme points in a landscape of speciation possibilities, largely determined by two forces: gene flow and selection.

One corner of the speciation landscape is occupied by sympatric speciation, where strong selection acts on populations to diversify despite considerable

gene flow. The theory of sympatric speciation has only just started to be taken seriously, and attempts to identify the 'speciation genes' are barely under way⁶. Progress has been faster on the other edge of the speciation landscape, where classic allopatric speciation sits. In the complete absence of gene flow, any amount of selection will make populations diverge genetically, which might result in pre- and/or postzygotic isolation. The type and intensity of selection, however, have been controversial⁵, but might be understood if the speciation genes responsible are identified.

But identifying them is difficult. In principle, a speciation gene could be any sort of gene, or even an extranuclear factor, such as the incompatibility-causing symbiont *Wolbachia*⁷. Moreover, they cannot be found by simply pinpointing the genes responsible for reproductive isolation, because many of their differences could have accumulated after speciation took place. So, the best way to go about the tracking down of speciation genes is by studying sibling species that have attained only partial reproductive incompatibility. In dioecious animals, this incompatibility usually follows Haldane's Rule: sterile hybrids belong to the heterogametic sex only⁸.