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The Evolutionary Ecology of Dispersal

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IIASA STUDIES IN ADAPTIVE DYNAMICS   NO. 31

The Adaptive Dynamics Network at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems.

Focusing on these long-term implications of adaptive processes in systems of limited growth, the Adaptive Dynamics Network brings together scientists and institutions from around the world with IIASA acting as the central node.

Scientific progress within the network is reported in the IIASA Studies in Adaptive Dynamics series.

THE ADAPTIVE DYNAMICS NETWORK

The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physicochemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

Two examples illustrate this assertion. Although Darwin's publication of "The Origin of Species" sparked off the whole evolutionary revolution, oddly enough, the population genetic framework underlying the modern synthesis holds no clues to speciation events. A second illustration is the more recently appreciated issue of jump increases in biological complexity that result from the aggregation of individuals into mutualistic wholes.

These and many more problems possess a common source: the interactions of individuals are bound to change the environments these individuals live in. By closing the feedback loop in the evolutionary explanation, a new mathematical theory of the evolution of complex adaptive systems arises. It is this general theoretical option that lies at the core of the emerging field of adaptive dynamics. In consequence a major promise of adaptive dynamics studies is to elucidate the long-term effects of the interactions between ecological and evolutionary processes.

A commitment to interfacing the theory with empirical applications is necessary both for validation and for management problems. For example, empirical evidence indicates that to control pests and diseases or to achieve sustainable harvesting of renewable resources evolutionary deliberation is already crucial on the time scale of two decades.

The Adaptive Dynamics Network has as its primary objective the development of mathematical tools for the analysis of adaptive systems inside and outside the biological realm.

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The Evolutionary Ecology of Dispersal

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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 (a search in 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. Consequently, there exists a serious gap between theory and data, and 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 1998 at the Tvärminne Zoological Station of the University of Helsinki and was 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 ecologists, evolutionary biologists and mathematicians with diverse backgrounds and diverse approaches, both empirical and theoretical, 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 are underlying their evolution. These pressures arise from interactions between individuals of the dispersing population and from those with the remainder of their environment. Since dispersal often occurs in (or sometimes brings about) spatially heterogeneous environments, resulting population dynamics and ecological feedbacks tend to be intricate. Whilst models of population genetics and of quantitative genetics have difficulties in incorporating such complicated feedbacks between an evolving population and its ecological environment, models of evolutionary game theory often have to oversimplify strategies and feedbacks by relying on payoff matrices. An alternative approach for studying the evolution of dispersal is offered by adaptive dynamics[1-3], where selective pressures and resulting adaptive changes are derived from their population dynamical origin (Box 2).

Mats Gyllenberg (University of Turku, Finland) and Hans Metz (Leiden University, the Netherlands) presented a technique for predicting invasibility into metapopulations: their method for the first time allows obtaining analytically the initial growth rate of rare mutants in resident metapopulations. Ulf Dieckmann (IIASA Laxenburg, Austria) demonstrated how correlation dynamics (where spatially extended populations are described not only by densities of individuals but also by those of pairs of individuals) can provide insights into trade-offs 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, Finland) 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 can 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 dynamics are again asynchronous, so that the cycle can repeat itself. Other adaptive dynamical 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, Finland) 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 may 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 non-autocorrelated temporal fluctuations. Francois Rousset (University of Montpellier, France) and Nicolas Perrin (Lausanne, Switzerland) demonstrated the importance of kin selection for the evolution of dispersal; the effects of social structure were investigated by Pekka Pamilo (Uppsala University, Sweden) in his study of dispersal in ants.

The evolution of dispersal has consequences for other life-history traits, which in turn can affect dispersal rates. Eva Kisdi (University of Turku, Finland) analyzed 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, i.e. in an evolutionarily stable dimorphism of two phenotypes each of which is a specialist for only one habitat. Differences between habitats and the magnitude of temporal fluctuations, however, have a strong effect on evolutionary outcomes.

Three speakers explicitly aimed at identifying 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 -

although problems in following dispersers made quantitative fitness estimates very difficult.

Habitat fragmentation may lead to a decrease in dispersal rates, as 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 (see below), this process has implications for conservation biology. Chris Thomas (University of Leeds, UK) presented data from a number of 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 theoretical models suggest to influence the evolution of dispersal may act together even within the same population. As 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) in discussing his findings on acorn woodpeckers. 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 may 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 a problem not faced by Bruno Baur (University of Basel, Switzerland) 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, Switzerland) demonstrated difficulties in delineating local populations of aphids. David Jenkins (University of Illinois, USA) discussed empirical data taken from paddling pools 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.

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

Dispersal and metapopulation viability

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

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

Régis Ferrière (ENS Paris, France) 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 may obstruct a dispersal trait's evolutionary path towards more viable rescue states. From within such an ‘adaptive trap’, gradual evolution of dispersal can no longer prevent population extinction.

The value of workshops such as this is that they allow a diverse assemblage of people to meet, and to exchange viewpoints. 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 to the workshop suggested that new techniques, for example 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[5].

Box 1: The evolution of dispersal: Mechanisms

In the last 30 years, a number of 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[6]. Johnson and Gains[7] review models published until about 1989.

Habitat extinction risks[8,9] (‘unstable habitats’) Risks of local extinction are the most intuitive reason for an evolution of dispersal and thus have been tested repeatedly in the field, using, for example, wing-dimorphic insects[10].

Competition among kin[11] 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[12,13] 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 are chaotic population dynamics[14].

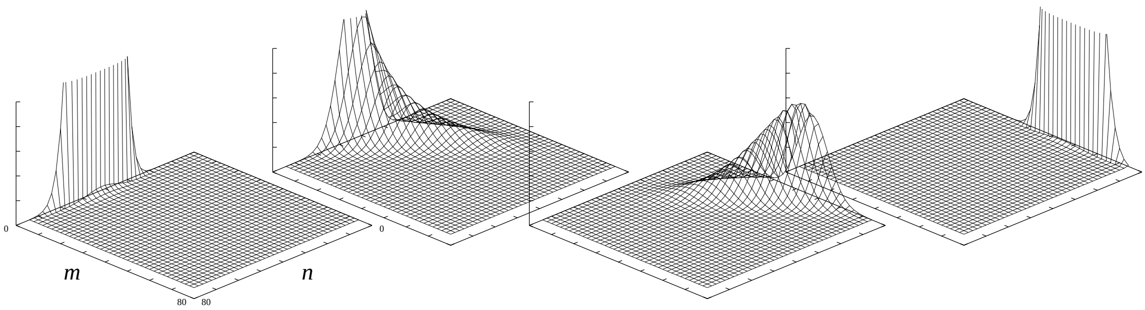
Costs of dispersal[11] If dispersal is costly (due to, for example, mortality risks during travelling or investments into dispersal morphology), optimal dispersal rates are decreased.

Inbreeding[15] Costs of inbreeding can also select for dispersal, 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 among and 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'[6]. The theory of adaptive dynamics[1-3] allows us to predict the resulting evolutionary change in continuous adaptive traits such as dispersal rates. Also contingent dispersal strategies can be investigated, like 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. While initially mutant strategists are few and far between, 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.

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