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Meeting report

Organisms on the move: ecology and evolution of dispersal

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The symposium and workshop ‘Organisms on the move: ecology and evolution of dispersal’, held in Ghent (Belgium), 14–18 September 2009, brought together a wide range of researchers using empirical and modelling approaches to examine the dispersal process. This meeting provided an opportunity to assess how much cross-fertilization there has been between empiricists and theoreticians, to present novel insights on dispersal patterns in plants, animals and micro-organisms and to measure the progress made in examining the causes and consequences of dispersal.

Keywords: dispersal; condition dependent; costs; information; movement ecology

1. INTRODUCTION

Dispersal is the process that ultimately causes gene flow through space or time. In the context of landscape fragmentation and global climate change, understanding how, where and why organisms move among local populations and to new areas is of utmost importance. To function over ecological and evolutionary time scales, populations facing such environmental changes need to be provided with functionally connected networks of habitats, and the success of these networks is reliant on the species having sufficient dispersal ability to track suitable habitats. Besides this crucial role in population dynamics, dispersal also plays a central role in the evolution of populations and species. Indeed, dispersal drives the spatial and temporal redistribution of genotypes, a process that is inseparable from the evolution of life-history traits (Ronce 2007).

The biology of dispersal is thus a fundament for many areas of ecology and evolutionary biology (Clobert *et al.* 2001; Bullock *et al.* 2002; Bowler & Benton 2005; Kokko & Lopez-Sepulcre 2006). As a consequence, dispersal has attracted the attention of a growing number of researchers, resulting in a large amount of papers and meetings devoted solely to the ecology and evolution of dispersal. After having first

regarded the phenomenology of dispersal, researchers gradually considered a more mechanistic approach to dispersal. This approach stimulated the dissection of dispersal into its three constitutive steps: emigration, transfer and settlement, as previously proposed by Lidicker & Stenseth (1992). This mechanistic approach encouraged major advances in our understanding of dispersal (e.g. Van Dyck & Baguette 2005; Baguette & Van Dyck 2007).

The symposium ‘Organisms on the move: ecology and evolution of dispersal’ was co-organized by Dries Bonte and Hans Van Dyck and sponsored by the Flemish Fund for Scientific Research. This was the fourth meeting of an informal and open group of researchers, which first met in 2005 at the joint initiative of Silke Hein, Thomas Hovestadt, Hans-Joachim Poethke and Hans Van Dyck, and aimed to invite and encourage theoreticians and empiricists to work together more closely. It was this emphasis on using a more integrated approach that ensured the success of this workshop. After this seminal impulse, the group regularly met at workshops and conferences. This fourth meeting provided an opportunity to assess how much integration has been achieved between empiricists and theoreticians, to present novel insights on dispersal patterns in plants, animals and micro-organisms, and to measure the progress made in examining the causes and consequences of dispersal. Here we summarize the most recent advances in dispersal research presented and discussed at this meeting.

2. DISPERSAL FRAMEWORK: THE ROLE OF INFORMATION

In his introductory talk, Thomas Hovestadt presented a ‘movement framework’ originating from discussions in the dispersal workshop in Paris, 2007. According to this framework, decisions about direction and speed of movement are based on the information available to an individual. Information is used to update more or less complex ‘prior’ internal representations of the location of fitness-relevant environmental attributes to ‘posterior’ expectations. Posteriors may be built from multiple levels of information, such as resource distribution, mating opportunities, predation risk or competition. They can be based on personal experience, cultural experience, or experience accumulated by natural selection into the genome. These layers are continuously updated according to the current internal state of the individual, and then assimilated into the individual’s actual needs. Thus, at any moment, the weighted integration of the different layers results in an overall posterior reflecting the current fitness expectations across space. Movements should always be directed towards peaks of this current spatial fitness map. The statistical attributes of movement paths like distribution of step lengths and turning angles thus reflect the series of those external and internal events that made individuals change their movement.

This new framework highlights the potential importance of information during dispersal processes, which was confirmed by several empirical studies at this meeting. Jean Clobert experimentally demonstrated that dispersing common lizards ‘carry’ information about their dispersal status (philopatric or disperser),

the density at their natal site, conditions during dispersal and even the distance they have moved. Using microcosms, Nicolas Schtickzelle showed that even simple organisms such as protists use direct (own population, surrounding population) and indirect information sources (immigrants) during dispersal.

3. DISPERSAL AT THE LEVEL OF INDIVIDUALS

After being long ignored, it is now recognized that interindividual differences in dispersal are important. In her meta-analysis, Virginie Stevens showed that dispersal ability of butterflies varied as much within species as among species. Another example also showed that within-species variation in butterfly flight morphology can vary greatly along a latitudinal cline and across landscape types (Sofie Vandewoestijne). This emphasizes the importance of considering the causes and consequences of such interindividual variation.

Erik Matthysen highlighted the importance of personality types and showed that in great tits, fast explorers moved further away than slow explorers in response to the removal of a food source; however, the tits' personality was not correlated with spatial behaviour before food was removed, suggesting that this trait is a way to 'cope' when challenged by a decrease in food availability, rather than just a baseline behaviour. This suggests that dispersal behaviour could differ according to the personality of the tits.

Another important factor is interindividual variation in the costs associated with dispersal, as dispersing individuals face increased energy expenditure, potentially higher predation risks and the risk of not finding a suitable area to settle. These costs can obviously have important repercussions for the evolution of dispersal, and this was intensively discussed during the workshop that followed the symposium. Dispersal costs have been very little investigated so far (as demonstrated by a review of the literature, Aurélie Coulon). However, one noticeable characteristic of this symposium was the relatively high number of talks covering this topic. Debora Arlt investigated search costs in the northern wheatear. Marjo Saastamoinen and Melanie Gibbs examined the costs of flight on reproductive output in butterflies. Gibbs showed the potential for flight-induced changes in egg provisioning to have cross-generational consequences for offspring. Saastamoinen showed that the cost of flight is condition dependent: alterations in phenotype induced by stressful conditions during the larval stage helped females to buffer against stressful forced flight.

4. DISPERSAL AND POPULATION DYNAMICS

A number of presentations examined how environmental factors may influence individual dispersal decisions, and how these individual decisions can affect population dynamics. Tim Benton demonstrated that by experimentally manipulating mites in microcosms, it was possible to investigate the factors determining individual movement decisions and to assess population consequences. Benton showed that movement decisions are often condition dependent,

and that condition may reduce mortality costs during dispersal. Benton also showed how the effects of dispersal on population dynamics are sometimes counterintuitive, e.g. reducing synchrony and population size.

In animals, both empirical and theoretical studies have successfully demonstrated how dispersal influences the long-term persistence of a metapopulation, as local extinctions need to be compensated via recolonizations. James Bullock illustrated how the metapopulation theory may not always be applicable to plant populations, as even in populations with a high turnover, the seedbank may have a greater role in recolonizations than dispersal. Bullock highlighted the need for comparative research at multiple taxonomic levels to improve our general understanding of the processes and implications of dispersal on population dynamics and survival.

Studies involving biological interactions such as bird-mediated seed dispersal showed the potential impact of these complex and often context-dependent processes on ecosystems (Valerie Lehouck). Future research investigating species interactions during dispersal may have important implications for conservation and habitat management.

5. DISPERSAL EVOLUTION

Theoretical models provide a powerful tool to study the evolution of dispersal. However, as Justin Travis pointed out, although the three-step framework of dispersal was already proposed in 1992 (Lidicker & Stenseth 1992), most work exploring dispersal evolution still focuses only on the first step (emigration). In general, theoretical work exploring the actual process by which individuals move between patches is lacking. Using a continuous space population model, Travis explored how the evolution of a random walk depends on the cost of dispersal, patch density and emigration rate, and emphasized that models like this are required to make long-term predictions of population dynamics in fragmented landscapes. The inclusion of patch quality and condition-dependent costs of dispersal in event-based models can greatly affect global population size and the evolution of dispersal distance (Calvin Dytham). The importance of addressing condition-dependent dispersal and interindividual variation in dispersal costs was a common conclusion throughout the meeting. Selection on individual variation in dispersal does not necessarily promote dispersal rules that make populations use space in an optimal way. This may lead to tension between individual and population-level benefits and greatly affect the evolution of dispersal (Hanna Kokko).

6. PERSPECTIVES

The general consensus at this meeting was that a more integrative approach to studying dispersal is imperative: (i) for a detailed examination of the costs and benefits associated with each of the three steps of dispersal, and (ii) to gain a better understanding of how interactions between dispersal and other life-history

traits may contribute to variation in dispersal across individuals, populations and species. The new framework presented by Hovestadt proposed to incorporate the concept of information-driven decision rules (Dall *et al.* 2005) to examine how individuals use information from their environment to assess the costs and benefits associated with dispersal, and to mitigate such costs. This would improve our ability to predict how dispersal patterns will alter in response to changing ecological conditions.

Another common conclusion of the meeting was the need to address condition-dependent movement decisions and interindividual variation in dispersal costs. Further discussions at the workshop concluded that we need to specifically design experimental studies integrated with modelling approaches to better understand the way in which various costs of dispersal—incurred at the three steps of dispersal—interact with each other to shape the evolution of dispersal-related traits.

In his recent review on dispersal modelling, Hawkes (2009) highlighted the fact that models addressing how heritable changes in dispersal propensity can impact population dynamics were currently missing from the literature. Modelling work presented at this meeting will go some way towards filling this gap. Furthermore, these theoretical models continue to move the field forward by incorporating interindividual variation and each of the three steps of dispersal. Another review revealed a general lack of integration across research fields studying dispersal (Holyoak *et al.* 2008). This dispersal meeting clearly highlighted how interchange between empiricists and theoreticians can be mutually productive and beneficial and as such, we strongly encourage further cross-fertilization in the future.

Although this meeting successfully addressed various recent advances in the study of dispersal, we feel that some important topics were still under-represented. In her review, Coulon showed that the influence of landscape configuration on dispersal has been under-investigated, but rather encouragingly, the development of new technologies has stimulated more research into this area (also see Nathan *et al.* 2008). In addition, few of the studies presented investigated the relationship between landscape structure, dispersal and population genetics. We are confident, however, that recent advances in landscape genetics should help disentangle how landscape configuration can influence the evolution of dispersal. Another research angle that was under-represented at this meeting is the role that developmental/phenotypic plasticity and, in particular, transgenerational plasticity (i.e. maternal effects) may play in generating variability in dispersal propensity both within and across populations (e.g. Duckworth 2009).

This meeting brought together researchers studying a wide range of taxa, from viruses through micro-organisms and plants to animals, presenting work on a wide range of topics including conservation biology, epidemiology, climate change biology, landscape ecology and evolutionary ecology. In general, these

researchers shared a common goal: to understand how dispersal patterns are, and will continue to be, affected by rapidly changing ecological conditions. The framework proposed by Hovestadt should provide a much needed step towards achieving this goal. Through increased collaboration and integration across fields, it should be possible to provide timely and accurate data to improve our understanding of this linchpin process in the functioning and evolution of natural populations.

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