Beyond classical metapopulations: trade-offs and information use in dispersal ecology

Differentielle Energieallokation und informierte Emigration: Eine Erweiterung des Metapopulationskonzeptes

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Würzburg, 4th January, 2013

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Summary

All animal and plant species must disperse in order to survive. Although this fact may seem trivial, and the importance of the dispersal process is generally accepted, the eco-evolutionary forces influencing dispersal, and the underlying movement elements, are far from being comprehensively understood.

Beginning in the 1950s scientists became aware of the central role of dispersal behaviour and landscape connectivity for population viability and species diversity. Subsequently, dispersal has mainly been studied in the context of metapopulations. This has allowed researchers to take into account the landscape level, e.g. for determining conservation measures. However, a majority of theses studies classically did not include dispersal evolution. Yet, it is well known that dispersal is subject to evolution and that this process may occur (very) rapidly, i.e. over short ecological time-scales. Studies that do take dispersal evolution into account, mostly focus on eco-evolutionary forces arising at the level of populations — intra-specific competition or Allee effects, for example — and at the level of landscapes — e.g. connectivity, patch area and fragmentation. Yet, relevant ecological and evolutionary forces can emerge at all levels of biological complexity, from genes and individuals to populations, communities and landscapes.

Here, I focus on eco-evolutionary forces arising at the gene- and especially at the individual level. Combining individual-based modelling and empirical field work, I explicitly analyse the influence of mobility trade-offs and information use for dispersal decisions — i.e. individual level factors — during the three phases of dispersal — emigration, transfer and immigration. I additionally take into account gene level factors such as ploidy, sexual reproduction (recombination) and dominance.

Mobility-fertility trade-offs may shape evolutionarily stable dispersal strategies and lead to the coexistence of two or more dispersal strategies, i.e. polymorphisms and polyphenisms. This holds true for both dispersal distances (chapter 3) and emigration rates (chapter 4). In sessile organisms — such as trees or corals — maternal investment, i.e. transgenerational trade-offs between maternal fertility and propagule dispersiveness, can be the cause of bimodal and fat-tailed dispersal kernels. However, the coexistence of two or more dispersal strategies may be critically dependent on gene level factors, such as ploidy or dominance (chapter 4).

Passively dispersing individuals may realize such multimodal dispersal kernels by mixing different dispersal vectors. Active choice of these vectors allows to optimize the kernel. As most animals have evolved some kind of memory and sensory apparatus — chemical, acoustic or optical sensors — it is obvious that these capacities should be used for dispersal decisions. Chapter 5 explores the use of chemical cues for vector choice in passively dispersed animals. I find that the neotropical phoretic flower mites *Spadiseius calyptrogynae* non-randomly mix different dispersal vectors, i.e. one short- and one long-distance disperser, in order to achieve fat-tailed dispersal kernels. Such kernels allow an optimal exploitation of patchily distributed habitats. In addition, this strategy increases the probability of successful immigration as the short-distance dispersal vectors show directed dispersal towards suitable habitats. Results from individual-based simulations support and explain my empirical findings.

The use of memory and sensory apparatus in dispersal is also the main topic of chapter 6 which strives to bridge the gap between dispersal and movement ecology. In this part of my thesis I develop a model of non-random, memory-based animal movement strategies. Extending the movement ecology paradigm of Nathan et al. (2008a) I postulate that four elements may be relevant for the emergence of efficient movement strategies: perception, memory, inference and anticipation. Movement strategies including these four elements optimize search efficiency at two scales: within patches and between patches. This leads to a significantly increased search efficiency over a comparable area restricted search strategy.

These four chapters are completed by a general analysis of metapopulation dynamics (chapter 2). I find that although the metapopulation concept is very popular in theoretical ecology, classical metapopulations can be predicted to be rare in nature, as suggested by lacking empirical evidence. This is especially the case when gene level factors, such as ploidy and sex, are taken into account.

In summary, my work analyses the effects of ecological and evolutionary forces arising at the gene- and individual level on the evolution of dispersal and movement strategies. I highlight the importance of including these limiting factors, mechanisms and processes and show how they impact the evolution of dispersal in spatially structured populations. All chapters demonstrate that these forces may have dramatic effects on resulting ecological and evolutionary dynamics. If we intend to understand animal and plant dispersal or movement, it is crucial to include eco-evolutionary forces emerging at all levels of complexity, from genes to communities and landscapes. This endeavour is certainly not purely academic. Particularly nowadays, with rapidly changing landscape structures and anticipated drastic shifts of climatic zones due to global change, dispersal is a factor that cannot be overestimated.

Zusammenfassung

Alle Tier- und Pflanzenarten müssen sich ausbreiten, um ihr Überleben zu sichern. Diese Feststellung mag trivial erscheinen und es wird inzwischen allgemein anerkannt, dass Ausbreitungsverhalten von großer Relevanz ist. Trotzdem sind wir weit davon entfernt, die öko-evolutionären Kräfte zu verstehen, die Ausbreitungsverhalten und zu Grunde liegende Bewegungsstrategien determinieren.

Erst in den 50er Jahren des 20. Jahrhunderts begannen Ökologen die zentrale Rolle von Ausbreitungsverhalten und Konnektivität für die langfristige Überlebensfähigkeit von Populationen sowie für die Entstehung und Aufrechterhaltung von Artenvielfalt zu begreifen. Bis heute wurde Ausbreitungsverhalten vor allem im Kontext von Metapopulationen analysiert. So konnte, über die Untersuchung der Dynamik von lokalen Populationen hinaus, die Landschaftsebene mit einbezogen werden, um beispielsweise effiziente Naturschutzmaßnahmen abzuleiten. Die Evolution von Ausbreitungsverhalten wurde in diesen Studien allerdings traditionellerweise nicht berücksichtigt. Inzwischen ist jedoch zweifelsfrei erwiesen, dass Ausbreitungsverhalten sehr schnell evolvieren kann, wodurch dieser Prozess bereits auf kurzen ökologischen Zeitskalen von Bedeutung ist. Untersuchungen zur Evolution von Ausbreitungsverhalten berücksichtigen aber meist nur öko-evolutionäre Kräfte die auf der Populations- und Landschaftsebene entstehen, wie etwa intra-spezifische Konkurrenz oder Allee Effekte beziehungsweise Konnektivität, Habitatgröße und Fragmentierungsgrad. Es ist jedoch einleuchtend, dass ökologische und evolutionäre Kräfte auf allen Ebenen biologischer Komplexität, von Genen und Individuen über Populationen und Artengemeinschaften bis hin zu Landschaften, entstehen können.

In dieser Arbeit möchte ich die Bedeutung von öko-evolutionären Kräften, die speziell auf der individuellen und genetischen Ebene begründet sind, näher beleuchten. Ich verbinde einen individuen-basierten Modellierungsansatz mit empirischer Feldforschung, um den Einfluss von differentieller Energieallokation ("life-history trade-offs") und Informationsnutzung für Ausbreitungsentscheidungen während der drei Ausbreitungsphasen — Emigration, Transition und Immigration — zu untersuchen. Zusätzlich berücksichtige ich genetische Mechanismen und Rahmenbedigungen wie Ploidie, sexuelle Reproduktion (Rekombination) und Dominanz.

Differentielle Allokation von Energie für Ausbreitungsverhalten und Reproduktion kann evolutionär stabile Ausbreitungsstrategien entscheidend beeinflussen und zur stabilen Koexistenz zweier oder mehrerer Strategien führen, also Polymorphismen und Polyphenismen bedingen. Dies gilt sowohl für Ausbreitungsdistanzen (Kapitel 3) als auch für Ausbreitungsraten (Kapitel 4). In sessilen Organismen, wie beispielsweise Bäumen oder Korallen, kann mütterliche Investition in die Ausbreitungsfähigkeit von Propagulen zu Bimodalität und zu einer Häufung von besonders langen Ausbreitungsdistanzen ("fat

tail") in der evolutionär stabilen Häufigkeitsverteilung der Ausbreitungsdistanzen ("dispersal kernel") führen. Die stabile Koexistenz zweier oder mehrerer Ausbreitungsstrategien kann jedoch sehr stark von genetischen Faktoren, wie Ploidie oder Dominanz, abhängen.

Arten, die sich aufgrund zu geringer Mobilität nicht selbst aktiv ausbreiten können, werden solch bimodale Häufigkeitsverteilungen von Ausbreitungsdistanzen, z.B. durch eine gezielte Mischstrategie mit zwei Vektoren, realisieren. Eine aktive Auswahl der entsprechenden Vektoren ermöglicht es, die resultierende Verteilung der Ausbreitungsdistanzen zu optimieren. Da die meisten Tiere über eine Form von Gedächtnis und sensorischem Apparat verfügen — um chemische, akustische oder optische Reize aufzunehmen und zu verarbeiten — ist es naheliegend, dass diese Fähigkeiten auch für Ausbreitungsentscheidungen genutzt werden. In Kapitel 5 untersuche ich die Nutzung chemischer Signale für die Auswahl von Ausbreitungsvektoren bei Tieren mit passiver Ausbreitung. Ich zeige, dass die neotropischen, phoretischen Blütenmilben der Art *Spadiseius calyptrogynae* gezielt zwei Ausbreitungsvektoren nutzen — einen Vektor, der v.a. kurze Strecken, und einen, der besonders lange Strecken zurücklegt — und damit, wie oben beschrieben, eine Häufung von großen Werten in der Häufigkeitsverteilung der Ausbreitungdistanzen ("fat-tailed dispersal kernel") erzielen. Solche Strategien sind optimal an die Ausbreitung in fragmentierten Habitaten angepasst. Zusätzlich erhöhen diese Blütenmilben durch ihre Vektorwahl die Wahrscheinlichkeit, sich erfolgreich auszubreiten, da einer der beiden Vektoren bevorzugt die Futterpflanze der Milben, also geeignetes Habitat, anfliegt. Diese empirische Studie wird durch eine individuen-basierte Simulation des Systems vervollständigt, deren Ergebnisse die empirischen Befunde erklären und deren Interpretation bestätigen.

Die Nutzung von Gedächtnis und sensorischen Kapazitäten steht auch in Kapitel 6 im Vordergrund. In diesem Teil meiner Arbeit entwickle ich ein individuen-basiertes Modell für Bewegungs- und Suchstrategien, das, im Gegensatz zu den meisten Modellen in diesem Bereich, nicht auf Diffusionsprozessen ("random walks") sondern auf der Nutzung von mentalen und sensorischen Kapazitäten basiert. Ziel ist es, ein mechanistisches Bewegungsmodell im Sinne von Nathan und Kollegen (2008a) zu schaffen und dadurch Ausbreitungs- und Bewegungsökologie zu vereinen. Ich postuliere, dass vier Elemente für die Emergenz von effizienten Bewegungs- und Suchstrategien von zentraler Bedeutung sind: Wahrnehmung, Erinnerung, Inferenz und Antizipation. Suchstrategien, die diese vier Elemente berücksichtigen, sind im Vergleich zu analogen Modellen, die auf Diffusionsprozessen basieren, besonders effizient, da sie ihre Sucheffizienz auf zwei Skalen, nämlich innerhalb und außerhalb von Ressourcenansammlungen, optimieren.

Diese vier Kapitel werden durch eine allgemeine Analyse von Metapopulationsdynamiken in Kapitel 2 ergänzt. Hier zeige ich, dass, obwohl sich das Metapopulationskonzept in der theoretischen Ökologie großer Beliebtheit erfreut, klassische Metapopulationsdynamiken in natürlichen Systemen selten zu erwarten sind. Damit bestätigen sich Hinweise empirischer Studien, die seit Längerem berichten, dass klassische Metapopulationen wenig häufig aufzutreten scheinen. Klassische Metapopulationsdynamiken entstehen auch in Modellen besonders selten, wenn diese evolutionäre Faktoren, die auf der Genebene begründet sind, wie Ploidie und Rekombination, berücksichtigen.

In der vorliegenden Arbeit analysiere ich die Effekte von ökologischen und evolutionären Kräften, die auf der Gen- und Individuenebene entstehen und evolutionär stabile Ausbreitungs- und Suchstrategien bestimmen. Ich hebe die zentrale Bedeutung dieser Rahmenbedigungen, Mechanismen und Prozesse hervor und zeige, wie sie die Evolution von Ausbreitungsstrategien in räumlich strukturierten Populationen maßgeblich beeinflussen. Aus meiner Arbeit wird unmittelbar ersichtlich, dass die Berücksichtigung öko-evolutionärer Kräfte auf allen Ebenen, von Genen bis hin zu Artengemeinschaften und Landschaften, von zentraler Bedeutung ist, wenn wir Ausbreitungsstrategien von Tieren und Pflanzen verstehen wollen. Dieses Ziel ist über den rein akademischen Bereich hinaus, z.B. auch für den Naturschutz, von großer Relevanz, denn besonders heutzutage, in Anbetracht schneller, anthropogener Veränderungen von Landschaftsstrukturen und des globalen Klimawandels ist die Fähigkeit zur Ausbreitung essentiell.

1

Introduction

Contents

Movement and dispersal are central aspects of the life-histories of all living beings on earth. Seasonal migrations in birds, bats or butterflies, for example, have received considerable attention both scientifically (e.g. reviewed in Dingle 1996) and from society at large. Movement can be observed at all scales in all taxa: from short range foraging activities in animals, taxis in protozoans and tropisms in plants to animal migrations stretching over multiple continents or long-distance seed dispersal of sessile organisms such as trees. Movement may seem a trivial phenomenon to such highly mobile individuals as we human beings are. However, I hope that my work will help to convince the sceptical reader of the contrary.

I will here mainly focus on dispersal, which is defined as “movement leading to spatial gene flow” (Clobert et al. 2012) and therefore ignore other movement phenomena such as seasonal migrations, since the ecological and evolutionary implications differ. Examples for dispersal with subsequent gene flow are oviposition flights in female butterflies, ballooning in spiders, natal dispersal of territorial animals, pollen dispersal or movements of seeds away from a mother tree.

1.1 Why study dispersal?

Dispersal has a profound impact on the eco-evolutionary dynamics of the biosphere. It is a key factor influencing diversity patterns and community assembly (Chave et al. 2002; Nathan 2006) and is the driving force behind biological invasions, which might become more and more frequent in a globally changing world. A prime example of the latter phenomenon is the cane toad *Bufo marinus* with the ecological and evolutionary implications for the cane toad itself and the invaded landscapes with their biota (Caswell et al. 2003; Phillips 2009).

Currently, many species ranges are under pressure through global climate change, and range shifts with subsequent shifts in (meta-)population dynamics are increasingly documented (Altermatt et al. 2008; Thomas 2010). Under such conditions good dispersers may be at a decisive advantage over non-mobile individuals or species because of their ability to track suitable climatic conditions (Kubisch et al. in press a) and to cope with anthropogenic changes such as habitat loss and fragmentation (Dewhirst and Lutscher 2009).

Understanding the causes and consequences of dispersal is therefore of great importance for basic and applied research. Especially in the context of ongoing global climate change, this knowledge is crucial for the development of sensible conservation policies.

1.2 Population dynamics

More fundamentally, dispersal is the answer to the question why we and all other biota still exist. Local population dynamics are the result of births and deaths. Population growth can be described as a Markov process which, loosely speaking, means that the future of a system can be predicted by its present state. In terms of population growth: if a population has a certain size (N_t) in the present time step (t), its size in the next time step (t+1) can be either N_t+1 or N_t−1, given sufficiently short time steps. This does not require any knowledge about the past of the system. This concept and its application to population dynamics is depicted in figure 1.1. From the graph one can easily see that the state $N_t = 0$ is a special state. It is an attractor, because any population that reaches this state is fixed as births cannot occur in an extinct population. As a consequence, every local population that shows some stochastic fluctuations in population size is bound to go extinct in the long run. Of course, this process may be very slow, and depends on population size.

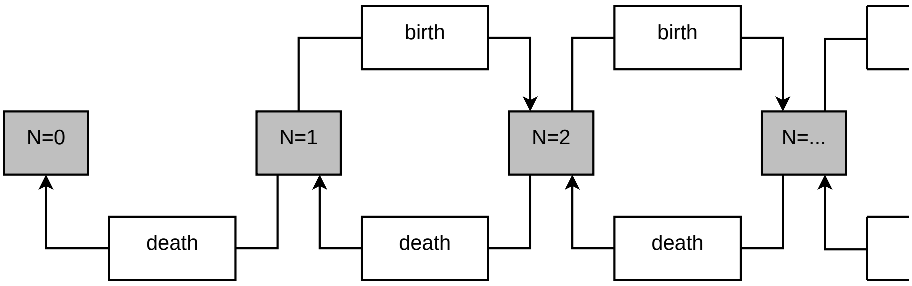

Figure 1.1: Population dynamics in a single isolated patch modelled as a Markov process. At the level of local populations two processes influence population growth: births and deaths. The state of a population is defined by its size (N). Only births and deaths may change this state. Being a Markov process the state of the population in the next time step ($N_t + 1$) is uniquely defined by the population's present state (N_t). It is immediately clear that the state $N_t = 0$ is a special state and an attractor. Death may lead to $N_t = 0$, i.e. the extinction of the local population. Yet, once this state has been reached, births cannot occur and therefore, the long-term fate of any local population is extinction.

Evidently, extinctions of local populations and even of entire communities do occur and have been well studied, for example, in the aftermath of volcanic eruptions, e.g. of the Krakatau in 1883 (e.g. Whittaker et al. 1989) or of Mount St. Helens in 1980 (e.g. Wood and del Moral 1987). It is also clear that extinctions may be followed by colonizations. As a consequence, population dynamics are determined by a total of four processes: besides births and deaths, one has to take into account immigration and emigration as shown in figure 1.2 A. Furthermore, the spatial scale of interest moves upwards and has to include multiple local populations that are connected by dispersal, i.e. "populations of populations" (Levins 1969) and their spatial structure.

Note that global extinctions may still occur. Once all populations are extinct ($n = 0$) no colonizations can happen. Thus $n = 0$ is an attractor similar to $N = 0$ for single populations (figure 1.2 B). The dynamics of whole spatially structured populations which are defined e.g. by occupancy, i.e. the number of occupied local populations (n), are again analogous to those of single populations (figure 1.2).

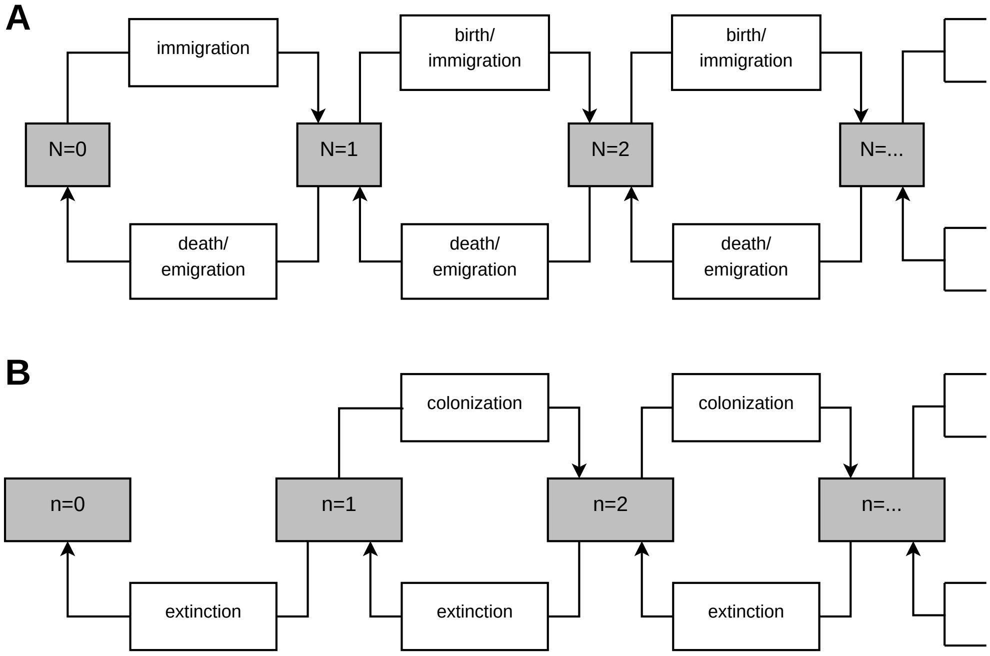

Figure 1.2: Population dynamics modelled as a Markov process including spatial structure. (A) If local populations are connected to each other by dispersal four processes influence population growth: births, deaths, emigration and immigration and the population size $N = 0$ is no longer an attractor.
Scaling up to the level of the whole spatially structured population (B) one may model the dynamics of such SSPs in analogy to single local populations (see figure 1.1). The number of occupied patches (n) is influenced by colonizations and extinctions, which correspond to birth and death events. Here again, $n = 0$, i.e. all patches are extinct, is an attractor.

1.3 Spatially structured populations

It was only in the 1950s that a growing number of ecologists started to realize that space matters. The beginning of this paradigm shift may be traced back to Andrewartha and Birch (1954). Among others, these authors recognized that local populations show turnover due to extinctions and recolonizations. A few years later Curtis (1956) already discusses the consequences of habitat loss and fragmentation.

Similar ideas led MacArthur and Wilson (1967) to the development of their seminal “Theory of Island Biogeography”. This work explores how immigration and extinctions influence species richness on oceanic islands, introduces the species-area relationship and specifies processes that are responsible for the assembly of biological communities. The "Theory of Island Biogeography" also represents the coming of age of ecology as a natural science, the transition from Natural History to theory based research (see Losos and Ricklefs 2010, for an excellent and detailed discussion of MacArthur and Wilson's book).

In the early 1970s, Levins (1969, 1970) introduced the idea of the metapopulation, i.e. a "population of populations" to ecology. This concept, which was further developed and refined by Ilkka Hanski (e.g. Hanski 1999; Hanski et al. 2004), is of great relevance for both basic and applied research. It provides a framework for the study of spatially structured populations and is highly relevant to conservation biology, since it focuses on the interplay between extinctions and colonizations (figure 1.2 B). Note that the metapopulation concept will be discussed at length in Chapter 2 (p. 15).

Besides the "classical metapopulation" envisaged by Levins, other spatially structured populations (SSPs) can be described depending on connectivity, i.e. the level of dispersal between local populations (patches), and the distribution of patch sizes (see figure 1.3 for a rough classification). A set of isolated habitat patches may be termed a "decreasing non-equilibrium metapopulation", since without dispersal there is no colonization (see figure 1.2) and the long-term fate of this system is global extinction as outlined above. Classical metapopulation dynamics are defined, among other measures, by high levels of turnover, i.e. extinctions and recolonizations, and intermediate occupancy, i.e. a certain amount of non-occupied patches which can be recolonized (e.g. Hanski et al. 1995). The local population dynamics are not synchronized, which is a key feature of classical metapopulations, and allows the recolonization of extinct patches. This requires enough connectivity for a significant number of successful dispersal events, but not too much, which would lead to such high levels of dispersal that the local population dynamics become tightly linked and all patches are always occupied ("patchy metapopulation"). Such tightly linked population dynamics may also occur through synchronous variation in environmental factors.

Introducing different patch sizes does not *per se* invalidate this classification, as long as all patches are at least principally prone to extinction. The probability of extinction due to demographic stochasticity decreases with population size. If a spatially structured population includes patches with population sizes that are orders of magnitudes larger than the others, such systems are called "mainland-island metapopulations". Note that this differentiation is not purely conceptual or academic. The resulting eco-evolutionary dynamics may be completely different depending on the type of metapopulation (Poethke et al. 2011).

As chapter 2 (p. 15) is a detailed discussion of this topic, I won't elaborate on it any

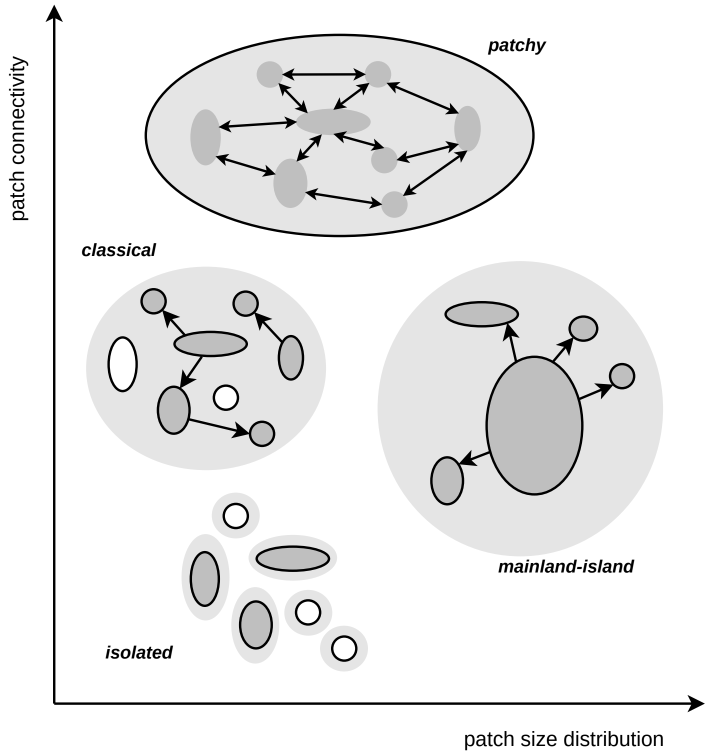

Figure 1.3: Spatially structured populations (SSPs). Systems of local habitat patches which may support animal or plant populations can be classified depending on connectivity and on the distribution of patch sizes. The classical metapopulation is a special case of spatially structured populations in general. Classical metapopulations are characterized by some degree of dispersal, yet not too much in order to allow for turnover and intermediate occupancy. Isolated patches are non-equilibrium systems since they are determined to go extinct (see text and figure 1.1). Most SSPs will be patchy, i.e. show high levels of dispersal or be of mainland-island type where the dynamics of the system are governed by the large mainland population which is so large that it has a vanishing extinction probability. Dark grey areas indicate local populations, black boundaries their limits. Light grey areas show the spatial extent of the SSP (after Harrison and Taylor 1997).

further here. Note that classical metapopulations, although very popular in theoretical ecology, are only rarely found in nature (e.g. Baguette 2004; Driscoll et al. 2010). Chapter 2 (p. 15) explores this disconnection and explains why classical metapopulation can indeed be predicted to occur only under very specific conditions. The occupancy patterns and levels of turnover that define classical metapopulations do not emerge readily and indicate that such populations are highly prone to extinction or represent populations from range margins. Most spatially structured populations can probably be classified as patchy or as mainland-island systems.

In summary, extinctions and colonizations are SSP level processes analogous to births and deaths in local populations. While extinctions are driven by population dynamics, colonizations are the result of dispersal. This again highlights the importance of dispersal which is responsible for the long-term viability of spatially structured populations.

1.4 Dispersal is a three-step process

If one takes a closer look at dispersal, it is clear that colonization is not identical with dispersal. Three more or less distinct dispersal phases can be differentiated (see e.g. Ronce 2007): emigration, a transition or roaming phase and immigration or settlement (figure 1.4). Emigration and immigration influence population dynamics as described in figure 1.2 by respectively reducing or increasing population size (figure 1.4, arrows 1 and 2). Due to emigration and deaths populations may go extinct (figure 1.2 A and figure 1.4, arrow 3). Immigration is responsible for colonization events (figure 1.4, arrow 4) and may also reduce the occurrence of extinctions through rescue effects (Brown and Kodric-Brown 1977), i.e. influx of individuals that prevent a population from going extinct. This influences SSP dynamics which are defined by turnover rates and occupancy (figure 1.2 B and figure 1.4, arrows 5 and 6; see also chapter 2, p. 15). The transition phase acts as a numerical filter between emigration and immigration and additionally determines the spatial movement component of dispersal (see also Chapter 6, p. 95). Figure 1.4 depicts these selected ecological processes but does not take into account the evolution of dispersal and the forces that may influence these processes and the resulting dynamics.

1.5 Eco-evolutionary dynamics of dispersal

Although already MacArthur and Wilson (1967) dedicate a whole chapter of their book to evolutionary changes and although Dobzhansky (1973) knew that “nothing in biology makes sense except in the light of evolution”, evolutionary processes are often ignored in ecological studies. This is due to the traditional distinction between short term ecological effects and long term evolutionary change (see also Pigliucci 2007).

Today we know that evolution can occur rapidly (Stockwell et al. 2003; Carroll et al. 2007). As a consequence, the distinction between ecological and evolutionary time scales is mostly artificial and superfluous. It is interesting to note that the notion of evolutionary changes occurring over just a few generations may have been familiar even to Darwin (discussed in Pigliucci and Müller 2010, an excellent volume on the Extended Modern Synthesis). In his “Origin of species” Darwin depicts a tree of life that shows speciation events occurring in just 1000 generations (Darwin 1859, p. 91).

Dispersal has been demonstrated to be heritable, to show significant variation and to be highly relevant to fitness (e.g. Saastamoinen 2007, 2008). These three prerequisites

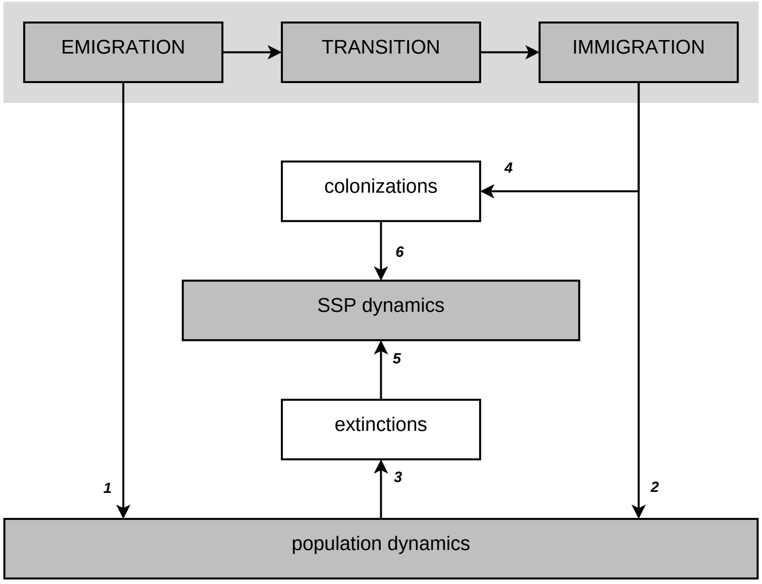

Figure 1.4: Dispersal and the dynamics of spatially structured populations (SSPs). Dispersal is a three step process comprising emigration, transition and immigration. Emigration and immigration directly influence population dynamics (arrows 1 and 2). Deaths, emigration and demographic stochasticity may lead to local extinctions (arrow 3), while immigration is responsible for colonization of empty patches (arrow 4), preventing extinctions by the rescue effect or simply increasing population size (arrow 2). Extinctions and colonizations of local populations influence the dynamics of the entire SSP (turnover and occupancy; arrows 5 and 6).

have to be fulfilled for evolution to act and therefore dispersal is subject to evolution (e.g. reviewed in Bowler and Benton 2005; Ronce 2007; Clobert et al. 2012). Dispersal evolution may be fast and therefore highly relevant for conservation strategies (see e.g. Poethke et al. 2011, and below). In order to gain a well-grounded understanding of the dynamics of SSPs it is therefore not sufficient to study the demographic consequences of dispersal but also its evolutionary causes and even the interactions between ecological and evolutionary processes. Unfortunately, this is not the rule.

Ignoring the evolutionary component may have fatal consequences, as e.g. Poethke et al. (2011) could show. Conservation strategies that rely on the metapopulation framework mostly do not take evolutionary responses into account. Yet, dispersal strategies will evolve as landscapes change. It is irrelevant whether landscapes change naturally, are managed by human beings or suffer from anthropogenic influences such as habitat destruction and fragmentation. This may even lead to the unexpected extinctions of managed populations through evolutionary suicide (Rankin and López-Sepulcre 2005), i.e. evolutionary adaptations that decrease the population's viability.

Note that most theoretical and empirical research on the evolution of dispersal focuses exclusively on emigration and ignores transition and immigration (Bowler and Benton 2005). I take all three phases of dispersal into account, e.g. in chapter 5 (p. 71); chapter 3 (p. 39) analyses the evolution of dispersal distance, i.e. addresses the transition phase and chapter 6 (p. 95) is an explicit treatment of animal movement.

1.6 A hierarchical concept of dispersal evolution

The eco-evolutionary dynamics of dispersal are influenced by internal and external conditions or limiting factors, mechanisms, processes and interactions that may be assigned to five hierarchical levels: genes, individuals, populations, communities and landscapes (figure 1.5; see also Kubisch et al. in prep. for a discussion of these ecological and evolutionary forces in the context of range border formation). Please note that this categorization may sometimes be redundant and some mechanisms or processes can emerge from multiple levels. I do not claim that either figure 1.5 or the following paragraphs are a comprehensive review of the relevant literature. The scheme only intends to highlight major ecological and evolutionary forces and especially those relevant for a better understanding of my work.

Although this categorization has not been taken into account previously, the eco-evolutionary forces arising from some of these levels are well known. The effects of ecological and evolutionary forces emerging from the landscape and the population level have been traditionally and extensively studied in dispersal ecology (see Bowler and Benton 2005; Ronce 2007).

1.6.1 The landscape level

Connectivity, habitat fragmentation, patch area and patch size distributions as well as spatio-temporal variance in carrying capacity are the traditional focus of dispersal and metapopulation ecology and have therefore been very well studied (for reviews see Bowler and Benton 2005; Ronce 2007; Clobert et al. 2012). Although metapopulation ecology mainly concentrates on emigration and immigration, these external, mostly abiotic conditions in general act on the transition phase of dispersal. Fragmentation and the resulting reduction of connectivity are numerical filters and responsible for dispersal mortality (for a recent review on the costs of dispersal see Bonte et al. 2012). These ecological factors are at the same time evolutionary forces as they feed back on emigration propensities: increased fragmentation implies higher mortality rates during transition which selects against emigration. Spatial and temporal variance in habitat conditions directly influences birth and death rates and therefore acts on population dynamics. The influence of the landscape level is modelled and discussed in detail in

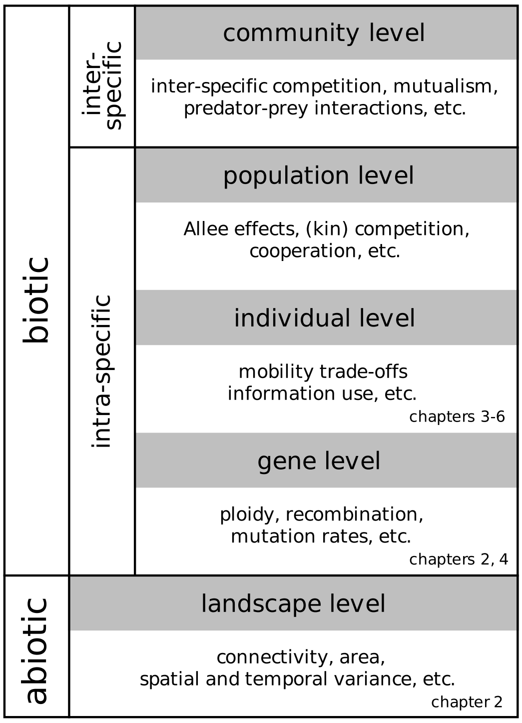

Figure 1.5: A hierarchical concept of dispersal evolution in spatially structured populations (SSPs). Eco-evolutionary forces that influence dispersal arise from five hierarchical levels: genes, individuals, populations, landscapes and communities. Note that this scheme only intends to highlight major limiting factors, mechanism or processes and especially those relevant for a better understanding of my work and therefore does not claim to be comprehensive. The focus of my work is on gene and individual level eco-evolutionary forces, specifically on trade-offs and information use.

chapter 2 (p. 15) and will therefore not be addressed extensively here. All chapters take this level into account to some extent.

1.6.2 The population level

Local competition influences population dynamics directly and leads to limited population growth, i.e. density regulation (for a review see Henle et al. 2004). The strength and quality of this interaction may reach from contest to scramble competition (exponent β in the logistic growth function; Hassell et al. 1976). In general, competition is a major driving force for dispersal evolution. It makes the colonization of empty patches attractive in the first place. Especially kin competition may lead to dispersal even if the costs (reviewed by Bonte et al. 2012) are extremely high (Hamilton and May 1977), because dispersers always have indirect fitness benefits by increased reproduction of relatives in their natal patch.

Besides this negative density-dependent effect at high population densities, at low population densities one may observe positive density-dependent growth, i.e. Allee effects. These are due to a range of phenomena, including sociality, mate limitation or environmental conditions, and in general impede population growth at low densities (reviewed in Courchamp et al. 2008). Allee effects reduce colonization rates and directly influence local population dynamics which may cause local extinctions. This in turn will lead to more empty patches and to an evolutionary reduction of emigration rates (Travis and Dytham 2002) or to “pulsed” emigration (Kubisch et al. 2011) in order to overcome the Allee effect during invasions.

Cooperation may not only cause Allee effects but can also deeply influence population dynamics at high densities. More specifically cooperative foraging and subsequent resource sharing is a risk-sensitive foraging strategy (see e.g. Poethke and Liebig 2008) and may lead to “supersaturation” (Dickinson and Hatchwell 2004), i.e. an increase in carrying capacity (Fronhofer et al. 2011b, in prep. a).

Population level mechanisms are not the focus of my work, yet Allee effects and kin competition are important evolutionary forces that influence dispersal evolution and, as a consequence, I do take these forces into account. Chapter 2 (p. 15) for example highlights the effect of the mate-finding Allee effect which decreases colonization rates as pointed out above. Kin competition is responsible for the evolution of heavily fat-tailed dispersal kernels (chapter 3, p. 39) and influences vector choice in phoretic flower mites (chapter 5, p. 71).

1.6.3 The community level

Dispersal ecology mostly ignores the community level. Nevertheless, communities are shaped by dispersal (see above) and inter-specific interactions in turn act as eco-evolutionary forces and influence dispersal. As my work does not take into account this level of complexity, I will not elaborate on it in detail here. Competition may decrease colonization probabilities (Case et al. 2005) and lead to stable ranges (Kubisch et al. in press a). Mutualistic interactions have been shown to reduce emigration (Mack 2012) because interaction partners have to track each other. Predator-prey interactions may lead to the evolution of predator-induced dispersal (e.g. Poethke et al. 2010). Host-parasite interactions may result in the evolution of diversity in hosts (e.g. Chaianunporn and Hovestadt 2011). Merging dispersal and community ecology is certainly one of the challenges of the next years and maybe even decades.

1.7 The focus of my work

The focus of my work is on the gene and individual level. I analyse internal conditions such as ploidy or genetic linkage, dominance (gene level), mating preferences and trade-offs but also information use (individual level) and their effect on the eco-evolutionary dynamics of dispersal. I will now shortly discuss these levels as depicted in figure 1.5 and point out the contributions of each of the following chapters.

1.7.1 The gene level: ploidy, recombination, linkage and dominance

Of course, the study of allele frequencies and the influence of evolutionary processes on the distribution of alleles is traditionally the domain of population genetics (Hartl and Clark 2007). Therefore it is not surprising that the gene level is mostly being ignored in dispersal ecology. Yet, this fact is quite disturbing, especially in individual-based evolutionary simulation models, since these often include (implicit) assumptions about ploidy or mutation rates, for example.

A majority of models in dispersal ecology simply assume clonal reproduction (e.g. Doebeli and Ruxton 1997; Mathias et al. 2001; Bonte et al. 2010). The importance of sex, diploidy, linkage and the relation between geno- and phenotype is very rarely taken into account and studied explicitly. Chapters 2 (p. 15) and 4 (p. 57) include an analysis of factors emerging from the gene level and their effects on SSP dynamics and individual dispersal strategies respectively. I could show that the assumption of clonal reproduction compared to sexual, diploid systems considerably affects SSP dynamics in terms of occupancy, turnover and spatial genetic structure (chapter 2, p. 15). Furthermore, diploidy and linkage may completely alter evolutionary stable dispersal strategies: chapter 4 (p. 57) shows how these gene level factors may lead to or destroy the stable coexistence of multiple dispersal strategies.

1.7.2 The individual level: mobility trade-offs

Individual level mechanisms are the main focus of my work (Chapters 3–6) and I explore the influence of mobility trade-offs and of information use. Trade-offs emerge because individuals generally have only a limited amount of resources that can be allocated to different fitness relevant traits and behaviours. This implies that an increase in one fitness component will lead to the reduction of another (see e.g. Roff and Fairbairn 2007). Mobility-fertility trade-offs mainly act on the transition phase of dispersal (figure 1.4) by increasing dispersal ability and therefore reducing dispersal costs (reviewed in Bonte et al. 2012). This leads to an evolutionary feedback and may modify evolutionarily stable dispersal distances (chapter 3, p. 39) and emigration rates (chapter 4,

p. 57) fundamentally. Trade-offs have been studied in wing-dimorphic insects and were found to be responsible for the evolution of distinct dispersal morphs (e.g. Roff 1994). In chapter 3 (p. 39), I analyse the evolution of dispersal distances in sessile organisms, such as trees or corals. In order to derive the evolutionarily stable distribution of dispersal distances, i.e. the dispersal kernel, I do not a priori define a specific kernel shape, as usually done, but model the evolution of a function-valued trait (Dieckmann et al. 2006). The emerging evolutionarily stable dispersal kernel is heavily fat-tailed. Maternal investment, i.e. a trade-off between maternal fecundity and the dispersal ability of propagules (seeds), leads to a bimodal distribution of dispersal distances with long-distance dispersers and non-dispersive individuals. Chapter 4 (p. 57) explores the influence of such trade-offs in actively dispersing animals and finds analogous patterns.

1.7.3 The individual level: information use

Information use is relevant to all three phases of dispersal (figure 1.4) and has the potential to modify ecological and evolutionary dynamics. Density-dependent emigration, for example, has been studied in detail and could be shown to increase dispersal efficiency and reduce extinction risk by reducing emigration rates (e.g. Poethke and Hovestadt 2002; Hovestadt et al. 2010). Information use during transition and for immigration may feed back and select for or against emigration depending on transition and immigration success.

I analyse information use in two different contexts: chapter 5 (p. 71) presents empirical and modelling results for the use of chemical information for emigration and immigration in neotropical phoretic flower mites. I find evidence for rare long-distance dispersal events and fat-tailed dispersal kernels that result from "kernel mixing", i.e. the use of different vectors for short- and long-distance dispersal. Information use for emigration, i.e. vector choice, leads to directed dispersal due to vector behaviour. These findings are supported by modelling results and can be applied to other passively dispersed animals but also to zoochorous seed dispersal.

Chapter 6 (p. 95) analyses information use for foraging movements and takes a closer look at the movement strategies responsible for successful transition. In contrast to most research in this area I do not use the random walk framework (Codling et al. 2008) to model animal movement but develop a novel, mechanistic model of animal movement that includes intelligent information use (see also Nathan et al. 2008a). I show that such an informed strategy may detect resources considerably more efficiently than a comparable area restricted search.

In summary, chapters 3–6 represent the core of my work. These four chapters are supplemented by a general discussion of metapopulation ecology in chapter 2 (p. 15).

2

Why are metapopulations so rare?[1]

Contents

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[1] This chapter is published as: Fronhofer, E.A., Kubisch, A., Hilker, F.M., Hovestadt, T. and Poethke, H.J. (2012) Why are metapopulations so rare? Ecology 93: 1967–1978. Recommended by the Faculty of 1000.

Abstract

Roughly forty years after its introduction, the metapopulation concept is central to population ecology. The notion that local populations and their dynamics may be coupled by dispersal is without any doubt of great importance for our understanding of population-level processes.

A metapopulation describes a set of subpopulations linked by (rare) dispersal events in a dynamic equilibrium of extinctions and recolonizations. In the large body of literature that has accumulated the term “metapopulation” is often used in a very broad sense — most of the time simply implying spatial heterogeneity. A number of reviews have recently addressed this problem and have pointed out that, despite the large and still growing popularity of the metapopulation concept, there are only very few empirical examples that conform with the strict classical metapopulation (CM) definition.

In order to understand this discrepancy between theory and observation, we use an individual-based modelling approach which allows us to pinpoint the environmental conditions and the life-history attributes required for the emergence of a CM structure. We find that CM dynamics are restricted to a specific parameter range at the border between spatially structured but completely occupied and globally extinct populations. Considering general life-history attributes our simulations suggest that CMs are more likely to occur in arthropod species than in (large) vertebrates.

Since the specific type of spatial population structure determines conservation concepts, our findings have important implications for conservation biology. Our model suggests that most spatially structured populations are panmictic, patchy or of mainland-island type which makes efforts spent on increasing connectivity (e.g. corridors) questionable. If one does observe a true CM structure this means that the focal metapopulation is on the brink of extinction and that drastic conservation measures are needed.

2.1 Introduction

The number of scientific articles, edited volumes, and books on metapopulation biology has steadily increased over the last decades which indicates a large and persistent interest in this topic (Hanski and Gaggiotti 2004b). A search of the keyword "metapopulation" in the database "ISI Web of Knowledge" reveals over 13,000 papers since the 1980s. Since the mid 2000s a steady number of about 400 articles related to metapopulation biology is published very year.

This interest is not purely academic. A central topic in metapopulation biology is the study of extinctions and recolonizations. Therefore, it is of no surprise that the metapopulation concept has frequently been applied in conservation biology (see e.g. Alvarez-Buylla et al. 1996; Hanski et al. 1996; Kuussaari et al. 2009). Yet, in a large number of publications, the term "metapopulation" is loosely defined and used in an unspecific way. It appears problematic to use a concept that originates from theoretical work in applied research fields such as conservation biology without being stringent about definitions (Elmhagen and Angerbjörn 2001).

The term "metapopulation" was coined by Richard Levins in the early 1970s. With his studies on optimal pest control (Levins 1969) and on between-population selection (Levins 1970), he introduced the idea of a "population of populations". Note that similar ideas were applied by MacArthur and Wilson (1967) to develop their theory of island biogeography (Hanski 2010). Even earlier descriptions of spatial population structure and fragmentation can be found in Andrewartha and Birch (1954) and Curtis (1956). In general, a metapopulation describes a set of subpopulations linked by (rare) dispersal events in a dynamic equilibrium of extinctions and recolonizations (Hanksi and Gilpin 1991; Hanski 1999). Yet, not all spatially structured populations (SSP) are classical metapopulations (CM) *sensu stricto*. In contrast to mainland-island systems (Harrison 1991) a CM is thought to have subpopulations of roughly similar size. These subpopulations should be coupled by just enough migration to avoid complete isolation on the one hand, but not too much migration on the other hand which would lead to a single panmictic population. Of course, CMs built of identical patches in terms of population size and mainland-island systems are only two extreme examples of SSPs. Yet, note that the resulting (evolutionary) dynamics may be completely different (e.g. Poethke et al. 2011).

Following Hanski et al. (1995) four conditions have to be fulfilled by a CM: (1) each discrete habitat patch must be able to support a breeding population; (2) in contrast to mainland-island metapopulations, any subpopulation must be prone to extinction; (3) recolonization has to be possible; (4) subpopulation dynamics are asynchronous in order to avoid the extinction of the entire metapopulation. Following this definition, CMs can be clearly distinguished from other SSPs like mainland-island, source-sink, patchy and non-equilibrium metapopulations (Harrison 1991). Mainland-island metapopulations imply that some habitat patches are orders of magnitude larger than others. Usually large mainland populations serve as source populations from which the smaller populations may be recolonized (Morrison 1998). Note that in contrast to source-sink systems (Pulliam 1988) habitat quality is assumed to be similar in all patches. True sink populations are characterized by a significantly reduced fitness of the focal species that would not allow the persistence of the populations on its own (for an example see Gaona et al. 1998). A patchy population can be thought of as a set of habitat patches linked by such high levels of dispersal that local extinctions are prevented (by a rescue effect) and no genetic structure can be found (for an example see Sweanor et al. 2000) — such a population is panmictic. Finally, non-equilibrium metapopulations may be declining or expanding with respectively more or less frequent extinctions than recolonizations.

Evidence of proper CMs in the field remains scarce. In general, recent reviews find only few examples for CMs (Elmhagen and Angerbjörn 2001; Baguette 2004; Driscoll 2007, but see Hanski (2004)). Most of these examples come from range margins. It has even been suggested that the observed turnover has nothing to do with classical metapopulation dynamics (Baguette 2004, but see Hanski (2004)): marginal populations often have higher extinction than colonization rates but are sustained by migrants from core areas (Holt and Keitt 2000; Holt et al. 2005).

The most prominent metapopulation is certainly the Glanville fritillary *Melitaea cinxia* (Hanski et al. 1994), which has inspired a large number of researchers. However, it appears to be the only unequivocal example. Other populations that have been invoked as CMs remain controversial, e.g. the cranberry fritillary *Boloria aquilonaris* (Mousson et al. 1999) — which shows a declining non-equilibrium structure in one landscape and an occupancy of nearly 100% in an other (discussed in Baguette 2004) — or the American pika *Ochotona princeps* (Peacock and Smith 1997; Smith and Gilpin 1997; Moilanen et al. 1998) — where the occupancy pattern employed to identify the focal population as a metapopulation could be reproduced in simulations using a completely different mechanism (spatially correlated extinctions, see Clinchy et al. 2002).

Hence, true CMs seem to be rare in nature (Harrison and Hastings 1996; Harrison and Taylor 1997; Driscoll 2008; Driscoll et al. 2010), a fact that should lead to reflections about the relevance of the metapopulation concept, especially in such applied areas as conservation biology. Note that similar empirical results — indicating that metapopulations are rare — also exist for plant species (Quintana-Ascencio and Menges 1996).

Here, we provide a possible explanation for this discrepancy between theory and nature. We use an individual based modelling approach, which allows us to pinpoint the environmental conditions and the life-history attributes required for the emergence of a CM structure. Following the CM definition laid out above (Hanski et al. 1995) and by many others (e.g. Reich and Grimm 1996; Grimm et al. 2003; Baguette 2004; Hanski 1999; Driscoll 2007) it is clear that indices like turnover (e.g. the relative frequency of extinction and re-colonization events), patch occupancy, and the genetic divergence of sub-populations (e.g. the fixation index F_{ST}) should allow to distinguish CMs from other types of SSPs. Qualitatively this can be quite easily done. However, since CMs are a general concept an exact quantitative definition of such indices is not possible. Specific values are very difficult to assign and will always depend on the ecological system of interest. Nevertheless, we propose some very broad and conservative criteria based on a number of relevant publications.

(1) Since local population dynamics are asynchronous a metapopulation can be seen as a network of occupied and empty patches (e.g. Baguette 2004). As a consequence, occupancy should clearly be below 100%. It is often found to be below 90%. Studies using occupancy as an index for CM structure found occupancies to lie roughly between 5 and 85% (among many others Hanski et al. 1994; Pajunen and Pajunen 2003; Baguette 2004; Risk et al. 2011).

(2) Since CMs are characterized by a dynamic equilibrium of extinction and recolonization processes, turnover has to be significant (e.g. Hanski et al. 2004). This could be interpreted as over 5%. Analyses of CMs yielded turnover values approximately between 10 and 40% (among many others Hanski et al. 1994, 2004; Risk et al. 2011).

Besides these demographic measures CM structure can be assessed using population genetics. Such genetic measures are often used to analyse whether dispersal events are too rare or too common for a CM (see Driscoll 2007, and literature cited therein). (3) A simple measure of genetic structure is Wright's fixation index F_{ST}, the standardized genetic variance among populations (Hastings and Harrison 1994; Pannell and Charlesworth 2000). The fixation index should have intermediate values since CMs are not panmictic populations (if there is no genetic structure F_{ST} is zero), nevertheless subpopulations are thought to be linked by (rare) dispersal events (for complete isolation F_{ST} is one). F_{ST} mostly takes values over 0.1. The observed values scatter roughly between 0.1 and 0.7 (among many others Kankare et al. 2005; Walser and Haag 2012). Note that Wright (1951) states that populations become substantially differentiated for $F_{ST} > 0.25$ (for a review see Pannell and Charlesworth 2000).

We thus adopt the following conservative criteria to define a metapopulation: occupancy should be below 90% ($O \leq 0.9$), turnover should be at least 5% ($T \geq 0.05$) and $F_{ST} \geq 0.1$. With these rules of thumb in mind we will analyse the conditions under which CMs may occur. Previous studies have investigated links between individual-based models and various metapopulation models (e.g. Keeling 2002; Ovaskainen and

Hanski 2004; Hilker et al. 2006), but there is a lack of relating individual behaviour directly to the typical metapopulation measures identified above.

It transpires that CMs satisfying these three criteria only emerge in a well defined window of plausible individual behaviour. We investigate and discuss the mechanisms responsible for this observation and conclude that only particular life-history traits allow the emergence of CMs. These traits are most probably found in arthropod species.

2.2 The Model

2.2.1 Landscape

We use an individual-based model of an SSP of individuals with non-overlapping generations, a modelling approach that has been commonly used, see e.g. Travis and Dytham (1999); Poethke and Hovestadt (2002); Kubisch et al. (2010); Fronhofer et al. (2011a). Importantly, the model can account for demographic and environmental stochasticity as well as for environmentally driven extinctions. As Poethke et al. (2007) point out, individual-based models include the effects of kin competition by default. The simulated world consists of discrete habitat patches with a large number of subpopulations ($n = 100$) as is usually assumed for CMs (Hanski 1999, 2004; Driscoll 2007). Each patch is characterized by a carrying capacity, which is fixed to $K = 50$ as a standard. This value ensures that subpopulations may suffer extinction and is in the range of plausible subpopulation size values observed in the field (Hanski et al. 1995). The effect of varying K is analysed in the appendix (see figure 2.6). It will be indicated explicitly when we deviate from this standard value.

2.2.2 Individuals

Each individual carries different attributes which may evolve, i.e. one locus coding for emigration propensity (this will be described in more detail below), and a neutral locus that is used for the calculation of the fixation index F_{ST} (see below).

Since the genetic system is known to influence simulation outcomes, especially in the context of metapopulations (see e.g. Parvinen and Metz 2008; Fronhofer et al. 2011a), we compare results for two different genetic systems. The system with haploid individuals, which are assumed to reproduce parthenogenetically, will be termed “females only”. Note that this is a common assumption in theoretical and simulation models (see below for a more detailed discussion). This scenario resembles sexual systems with mating before dispersal, which is very often found in arthropods. In addition to this, we run simulations with sexual reproduction and model female and male individuals which mate and produce offspring after dispersal. Note that in order to be able to

compare the results of both scenarios the carrying capacity in the “females only” case is half as large as in the sexual case, i.e. $K' = 25$ as a standard.
Any offspring inherits all alleles from the parent in the “females only” simulations or one randomly chosen allele per locus from each of its parents in the sexual scenarios. Alleles may mutate with a fixed probability ($m = 10^{-4}$). When a mutation occurs at the dispersal locus, a random number drawn from a Gaussian distribution with mean 0 and standard deviation $\Delta m = 0.2$ is added to the actual value. For the (neutral) discrete locus, a random integer number is drawn from the interval $[1, 100]$. Dispersal alleles are initialized following a uniform distribution between 0 and 1, and the neutral alleles are initialized with random integers drawn from the interval between 1 and 100.
In summary, we use a genetic algorithm (GA) to calculate evolutionarily stable (ES) emigration rates. This method was pioneered by Fraser (1957) and is widely used in ecological modelling (for a review on individual-based models in ecology and evolution see DeAngelis and Mooij 2005). Evolutionary stable dispersal strategies have been analysed and discussed at length elsewhere (for reviews see Bowler and Benton 2005; Ronce 2007) and are not the focus of this article. Our approach guarantees that the emigration rate is optimal for any given combination of parameters (results are shown in the Appendix: Figure 2.9).

Local population dynamics

Local population dynamics follow the logistic growth model for discrete generations provided by Hassell (1975). Newborn individuals survive to maturity with a certain probability $s_{i,t}$:

$$s_{i,t} = \frac{1}{(1 + a \cdot N_{i,t})^{\beta}}, \tag{2.1}$$

where $a = \frac{\lambda^{\beta^{-1}}-1}{K_i}$ and $N_{i,t}$ represents the population size in patch i at time t and K the carrying capacity of that patch. a is known as the susceptibility to crowding. λ represents the mean number of offspring per generation (rate of population increase) and is set to $\lambda = 2$ as a standard. This value is quite representative for a large number of species ranging from arthropods (Hassell et al. 1976, e.g.) to mammals (e.g. Ericsson et al. 2001). Characteristically, arthropods show a higher variation in breeding success than mammals which is represented by the parameter σ (see below). The effect of varying λ is analysed in the appendix (see figure 2.7). The parameter β determines the strength of density regulation. The effect of varying β is analysed in the appendix (see figure 2.8). Note that $\beta = 1$ indicates contest competition, values over 1 scramble-like competition and values under 1 undercompensation, i.e. weak density regulation (Hassell 1975).

In the “females only” simulations, each individual gives birth to Λ offspring during the reproduction period. In the sexual simulations, each female mates with one randomly chosen male from the same patch (if no males are present, reproduction is not possible) and gives birth to 2Λ offspring, so that the per capita growth rate is the same compared to the “females only” simulations. Λ itself is drawn from a Poisson distribution with patch- and time-specific mean $\overline{\lambda_{i,t}}$. The value for the latter is drawn for each patch and generation from a lognormal distribution with mean λ and standard deviation σ. The parameter σ reflects uncorrelated environmental stochasticity, i.e. environmentally caused fluctuations in offspring number. The resulting demographic stochasticity may lead to population turnover.

Turnover may also result from externally induced extinctions that are independent of population size such as floods, volcanic eruptions, or epidemics. In the simulations incorporating such external extinction risks, at the end of each generation every population in a patch goes extinct with a probability ϵ, independently of the actual population size.

2.2.3 Dispersal

After maturation, individuals emigrate with a certain (density-independent) probability d. We have tested the robustness of our model by implementing density-dependent dispersal as in Poethke and Hovestadt (2002). This did not change our results qualitatively (results see Appendix figure 2.5; compare to figure 2.1). Note that the dispersal trait may evolve as outlined above. In the “females only” simulations, the emigration probability is directly coded by the single allele. For sexual reproduction the emigration probability is simply calculated as the arithmetic mean of an individual’s two dispersal alleles $a_{d,1}$ and $a_{d,2}$:

$$d = \frac{a_{d,1} + a_{d,2}}{2}. \tag{2.2}$$

Any emigrating individual suffers a certain dispersal mortality μ that sums up all costs that can be involved in dispersal (for a review see Bonte et al. 2012), including fertility loss through investment in dispersal ability and predation during movement (see e.g. Zera and Mole 1994; Cody and Overton 1996). Dispersal mortality or costs (μ) can also be interpreted as the degree of fragmentation of a landscape (see e.g. Kubisch et al. 2011).

If the emigrant survives, its destination patch is chosen randomly from all patches (excluding its natal one). This corresponds to global dispersal. We tested the influence of an alternative dispersal mode, i.e. nearest neighbour dispersal, and found that our results do not change (results not shown).

2.2.4 Calculation of the fixation index F_{ST}

As mentioned above, besides the dispersal alleles, each individual carries one (in the sexual system two) marker allele(s) at a neutral locus, i.e. there is no selection acting on this locus. This allows us to measure genetic distance (differentiation) between the populations by calculating Wright's fixation index F_{ST} (Wright 1950, 1951). For all alleles j within a population i, we determine the frequencies $p_{i,j}$ (i.e. their occurrence in population i divided by the total number of alleles in the population) and then calculate the average expected within-patch heterozygosity H_S (assuming random mating) over all populations as follows:

$$H_S = \frac{1}{n} \sum_{i=1}^{n} \left(1 - \sum_{j=1}^{n_j} p_{i,j}^2 \right) \tag{2.3}$$

with n being the total number of patches and n_j being the total number of integer alleles.

The expected total heterozygosity for the whole metapopulation H_T is calculated by determining the allele frequencies $\overline{p_j}$ over all populations (i.e. their number of occurrence in the whole metapopulation divided by the total number of alleles): $H_T = 1 - \sum_{j=1}^{n_j} \overline{p_j^2}$. Finally, we calculate the fixation index as

$$F_{ST} = \frac{H_T - H_S}{H_T}. \tag{2.4}$$

In summary, F_{ST} is the "correlation of randomly chosen alleles within the same subpopulation relative to the entire population" as Holsinger and Weir (2009) put it in their review of genetics in SSPs. Thus, this measure represents the variation of allele frequencies among populations. If F_{ST} is zero no variation could be observed and, as a consequence, the population is panmictic. If $F_{ST} = 1$ there is no resemblance among individuals from different populations, i.e. no gene flow (dispersal) occurred and the populations are completely isolated.

2.2.5 Calculation of turnover rates and occupancy

To determine the turnover rate ($T_{\Delta t}$) between two generations we quantify the number of patch extinctions ($n_{extinct,\Delta t}$) and colonizations ($n_{colonized,\Delta t}$) from one generation to the next and divide the number of these events by the total number of patches:

$$T_{\Delta t} = \frac{n_{extinct,\Delta t} + n_{colonized,\Delta t}}{n}. \tag{2.5}$$

The census is conducted after the dispersal period and thus accounts for rescue effects. Occupancy (O) is calculated as the relative number of occupied patches.

2.2.6 Simulation experiments and scenarios

Our standard scenario (A) assumes asexual reproduction ("females only" scenario), equal patch sizes ($K' = 25$) and no externally induced patch extinctions ($\epsilon = 0$). See table 2.1 for more information on parameter values. In alternative scenarios respectively one of these assumptions is modified and the effect analysed: scenario (B) introduces sexual reproduction ($K = 50$ to keep the results comparable with scenario A), scenario (C) includes externally induced patch extinctions and scenario (D) variable patch sizes. Simulation time is set to 5,000 generations. This period of time is more than sufficient for the system to reach a state of (quasi-)equilibrium. Note that a steady state is usually reached within 2,000 generations. The analysis is conducted over the last 500 generations. The values for F_{ST} and turnover given are arithmetic means over that period.

As outlined above we analyse the influence of relaxing our strict assumption of equal patch sizes. In the scenario with varying carrying capacities the values for individual patches (K_i) are drawn from a uniform distribution between [5...45]. In the mainland-island scenario the size of one habitat patch is set to $K_{mainland} = 10,000$, while the other 99 habitat patches have a carrying capacity of $K_{island} = 10$.

2.3 Results

In all simulation experiments turnover rates (T) and the genetic structure of populations (fixation F_{ST}) increase with increasing cost of dispersal (μ), i.e. increasing habitat fragmentation. Note that, conversely, the fraction of occupied patches decreases with increasing dispersal costs (occupancy O).

The results of our simulations show that in the "females only" case (figure 2.1 a–c) relevant turnover rates only arise for specific values of dispersal costs. For lower dispersal costs ($\mu < 0.5$) there is hardly any turnover and occupancy approaches 100%, whereas higher dispersal costs result in evolutionary suicide (Rankin and López-Sepulcre 2005; Dieckmann and Metz 2006) of the metapopulation, i.e. dispersal evolves to values too low to balance demographic extinctions with sufficient recolonization rates (see figure 2.9 for results of evolved emigration rates).

The influence of environmental stochasticity is also depicted in figure 2.1. In general, more variable environments lead to a higher risk of global extinctions as well as to a reduced occupancy (figure 2.1 a) and to more turnover (figure 2.1 b).

Thus, we find a clearly defined range of values of dispersal costs and environmental stochasticity that lead to a system behaviour which agrees with the demographic CM criteria. The clear reaction of occupancy and turnover is not reflected in the genetic

Table 2.1: Important model parameters, their meaning and the values used for different scenarios. Scenario A ("females only") implies mating before dispersal which is very often found in arthropods. Sexual reproduction (equal sex-ratio) is introduced for scenario B. In order to keep the results comparable with scenario A K was set to 50. This scenario includes mating after dispersal which is often found in vertebrates. Scenario C analyses the influence of externally induced extinctions and scenario D relaxes our assumption of equal patch sizes (see text).

parameter	**meaning**	**scenario**				**parameter space explored**
		A	**B**	**C**	**D**	
		Fig. 1 a–c	*Fig. 1 d–f*	*Fig. 2*	*Fig. 3*	*Appendix: Fig. 2.6–2.8*
K	carrying capacity	25	50	25	[5..45] {10,10000}	12.5, 25, 50, 75, 100
σ	environmental stochasticity	[0..2]	[0..2]	0	[0..2]	[0..2]
ϵ	patch extinction probability	0	0	[0..0.25]	0	[0..0.5]
λ	fertility	2				1.1, 1.2, 1.3, 1.4, 1.5, 2, 3, 4
β	density regulation	1				0.5, 1, 2
μ	dispersal costs	[0..1]				[0..1]

structure of the metapopulation (figure 2.1 c). The pattern of F_{ST} is dominated by the effect of fragmentation (μ): F_{ST} continuously increases with increasing dispersal costs until it reaches a critical limit for dispersal costs above which the metapopulation cannot persist. Note that a clear spatial structure ($F_{ST} > 0.1$; Hartl and Clark (2007)) can be seen already in SSPs without any turnover and full occupancy. The influence of σ on genetic structure is less pronounced (figure 2.1 c).

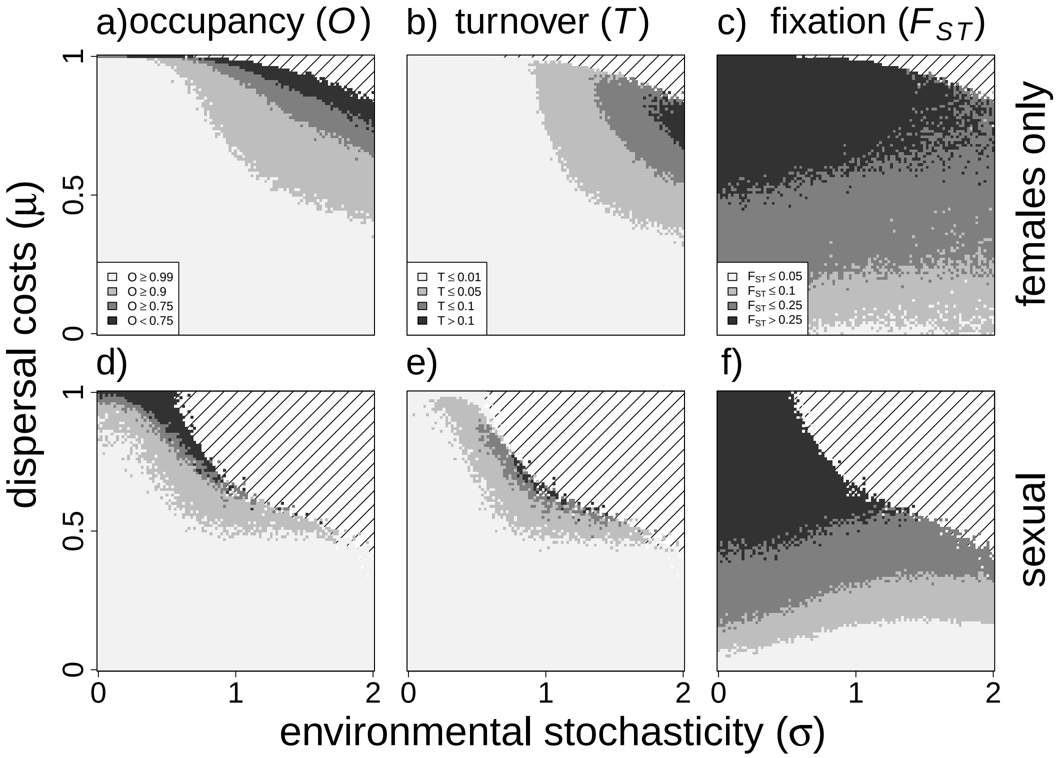

Figure 2.1: Influence of dispersal costs (μ), environmental fluctuations (σ) and reproduction mode ("females only" vs. sexual) on occupancy (O; panels a and d), turnover (T; panels b and e), and genetic structure (F_{ST}; panels c and f) for asexually (top row; panels a–c) and sexually reproducing populations (bottom row; panels d–f). Hatched areas indicate extinct populations. Constant parameters: $\lambda = 2$; $K' = 25$ (panles a–c); $K = 50$ (panels d–f); $\epsilon = 0$.

2.3.1 Sexual reproduction

The introduction of sexual reproduction does not lead to qualitative changes in comparison to the "females only" case (figure 2.1 d–f). Yet, importantly, with sexually reproducing individuals, the fraction of parameter space leading to global extinction is increased, and the transition zone with intermediate occupancy and substantial turnover is considerably reduced (figure 2.1). Particularly for strong environmental fluctuations

($\sigma > 1.5$) or high dispersal costs ($\mu > 0.7$) the transition zone becomes very narrow. Genetic structure (F_{ST}; figure 2.1 f) is less sensitive to the mode of reproduction. Taking all parameter ranges together, the overlap of the above presented CM criteria for sexual systems is very small. This is well depicted by the turnover rates (figure 2.1 e).

2.3.2 Externally driven patch extinctions

In many metapopulation models local patch extinctions are assumed to be independent of patch- and population-size (see discussion). Such externally driven extinctions may be the result of environmental catastrophes or may be induced by the immigration of efficient predators.

Figure 2.2 shows the influence of such externally driven patch extinctions (ϵ) on SSP structure. They increase the risk of global extinction (hatched areas in figure 2.2). Even for rather small extinction probabilities (ϵ) the metapopulation will go extinct if dispersal costs (μ) surpass a critical level. Occupancy is significantly reduced (figure 2.2 a) and turnover rates (figure 2.2 b) are considerably increased. F_{ST} values (figure 2.2 c) indicate that completely isolated populations are rare. This is due to strong selection for dispersal (not shown).

In our model of discrete generations (with strict synchronization of reproduction, dispersal and extinction events), the measurement of turnover rate critically depends on the exact moment of data collection. If turnover is evaluated immediately after externally induced patch extinctions, the turnover rate is trivially at least equal to the extinction rate. However, due to high emigration rates a great fraction of the empty patches will be immediately recolonized (rescue effect). To account for this rescue effect, we have evaluated turnover rates after dispersal.

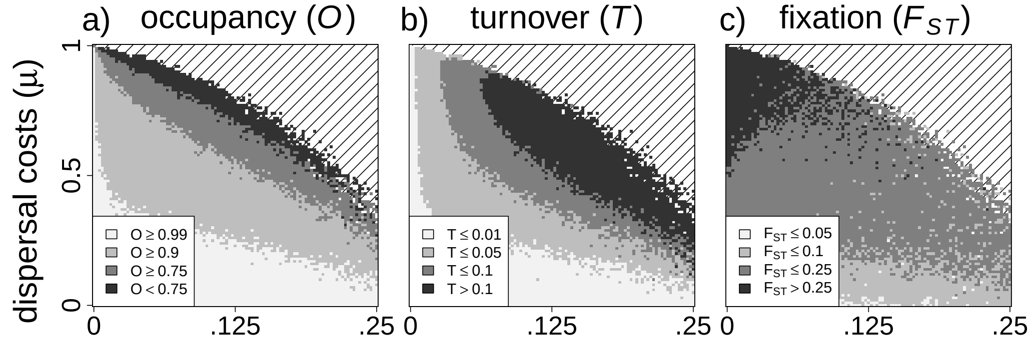

Figure 2.2: Influence of dispersal costs (μ) and the frequency of externally induced extinctions (ϵ) on occupancy (O, panel a), turnover (T; panel b) and genetic structure (F_{ST}; panel c) for "females only" populations. Hatched areas indicate extinct populations. Constant parameters: $\lambda = 2$; $K' = 25$; $\sigma = 0$.

2.3.3 Variable patch sizes

In all simulation experiments presented up to this point, we have assumed an SSP of equally large patches ($K = const. = 50$). This is a rather restrictive and unrealistic assumption. If we assume habitat patches of different sizes (figure 2.3), we find that with increasingly variable carrying capacities the area of parameter space allowing intermediate occupancy (figure 2.3 a) and significant turnover becomes larger (figure 2.3 b). Note that the panmictic area ($F_{ST} < 0.05$) nearly disappears when patch sizes vary substantially (figure 2.3 c).

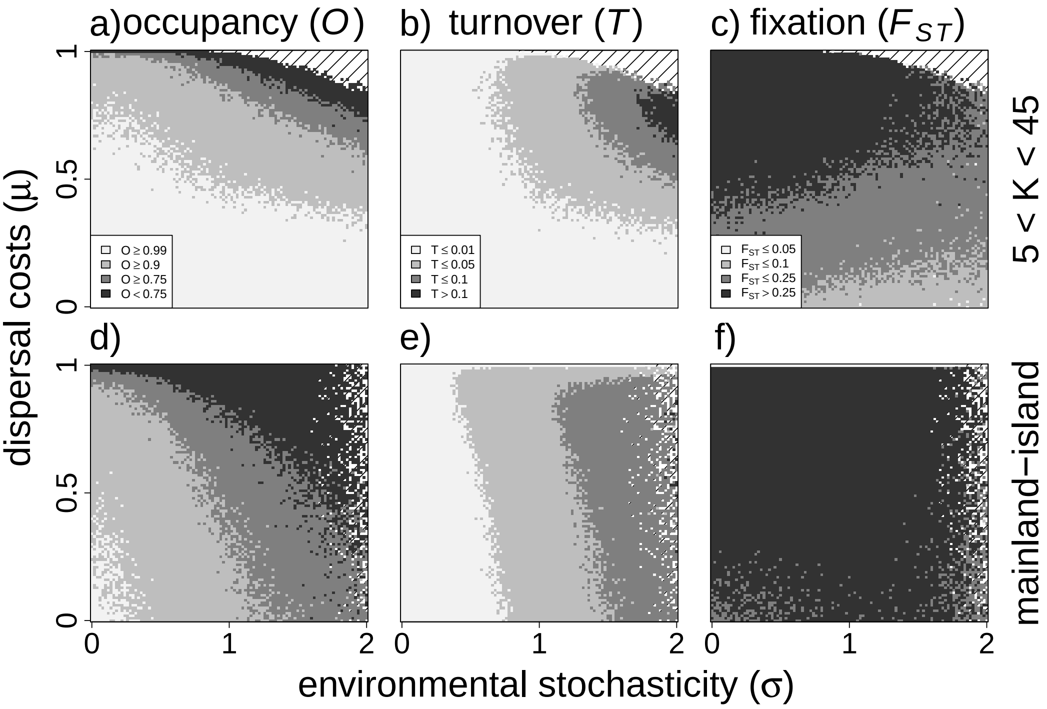

Figure 2.3: Influence of dispersal costs and environmental stochasticity on occupancy (O, panels a and d), turnover (T, panels b and e) and genetic structure (F_{ST}; panels c and f) for "females only" populations in an environment with varying carrying capacities. Upper panels (a–c): variable K between 5 and 45; lower panels (d–f): mainland-island scenario with one large patch at $K_{mainland} = 10,000$ and the other 99 patches at $K_{island} = 10$. Hatched areas indicate extinct populations. Constant parameters: $\lambda = 2$; $\epsilon = 0$.

Mainland-island populations are an extreme case of variability in patch size (figures 2.3 d–f). The SSP nearly never goes completely extinct since the mainland is far too large to be affected by demographic and environmental stochasticity. There are critical parameter combinations, however, where only very few of the small (island) patches are occupied (large values of μ). In this region of parameter space, the SSP tends to become highly genetically structured (figure 2.3 f; $F_{ST} > 0.25$) as its structure is determined by founder effects. Note that this is not the case in sexual systems since the mate-finding Allee effect lowers the rate of successful recolonization which leads to substantially lower F_{ST} values.

2.4 Discussion

Our simulations represent a systematic exploration of conditions that favour the emergence of significant turnover, which is the most critical attribute of classical metapopulation dynamics. We analyse two more measures often used to classify metapopulations: occupancy and genetic structure F_{ST}. The results of our simulation experiments clearly show that only specific environmental conditions and life-history attributes promote the emergence of CM dynamics as defined in the introduction. Figure 2.4 schematically illustrates this point and recapitulates our results. Note that our results are not strongly affected by the exact minimum values assumed for occupancy, turnover and F_{ST} (see introduction), since the transition zones are very abrupt (figures 2.1–2.3). In summary, it is not surprising that CMs are only rarely found in nature (Harrison and Taylor 1997; Elmhagen and Angerbjörn 2001; Baguette 2004; Driscoll 2007). Typical requirements for the emergence of CMs are reduced dispersal and a substantially variable environment. The general tendency of F_{ST} values observed above can be readily explained by

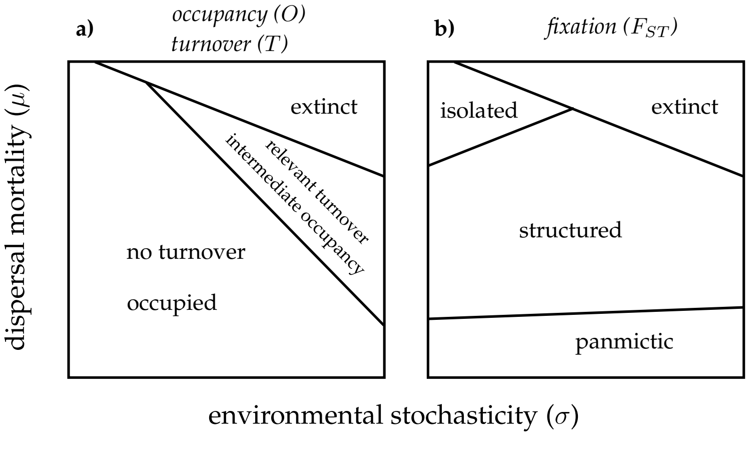

Figure 2.4: Schematic representation of the influence of dispersal mortality (μ) and environmental stochasticity (σ) on occupancy, turnover (O and T; panel a) and genetic structuring (F_{ST}; panel b). As becomes clear from our results occupancy and turnover react similarly to dispersal mortality and environmental stochasticity. CMs can only be found in a well defined band in parameter space which is characterized by intermediate occupancy, relevant turnover and spatial structure.

the influence of environmental fluctuations (σ) and dispersal costs (μ) on the evolving emigration rate (see Appendix figure 2.9). For a given value of dispersal costs, increasing environmental fluctuations lead to higher inter-patch variance of population size and consequently to increased emigration rates (Cadet et al. 2003; Poethke et al. 2007) which in turn result in reduced genetic spatial structure (smaller F_{ST}). If dispersal is costly (high dispersal costs μ), selection favours lower emigration tendencies, and, as a result, the genetic structure of the metapopulation is increased. Clearly, an interaction of both selective forces (high μ and σ) implies a high net loss of individuals from the metapopulation due to high dispersal mortality (at high dispersal rates). This ultimately leads to an increased global extinction risk. The parameters dispersal costs (μ) and environmental stochasticity (σ) can also be interpreted as proxies for colonization and (population size dependent) extinction probability, respectively. Higher values of dispersal costs lead to a lower colonization probability, because fewer individuals emigrate to begin with and more migrants die *en route*. Increasing the environmental stochasticity (σ) leads to more stochasticity in population size and consequently increases the rate of patch extinctions.

We have also tested the influence of further assumptions of dispersal behaviour: nearest neighbour dispersal (NND; not shown here) and density-dependent emigration (DDE; figure 2.5). Both factors have no qualitative influence on the results. However, DDE generally increases the persistence of metapopulations under high environmental fluctuations, i.e. the area with complete population extinction is reduced (compare figures 2.1 and 2.5).

Moreover, the influence of fertility (λ) and carrying capacity (K) has been tested thoroughly (see appendix, figures 2.6 and 2.7). Generally, varying carrying capacity and fertility only shifts the position of the transition zone in parameter space but does not lead to important qualitative changes. Clearly, larger values of fertility (λ) or carrying capacity (K) stabilize the system, so that turnover is reduced and ultimately tends towards zero. The same pattern is true for the strength of density regulation (β, figure 2.8).

Our analysis of the influence of the genetic system shows that a characteristic pattern of “females only” simulations is a highly reduced extinction risk of the metapopulation (figure 2.1). Although a “females only” scenario seems to be very artificial it may be seen as equivalent to sexual systems with mating before dispersal, i.e. where only fertilized females disperse, as in many insects. This explains the reduced extinction risk which is due to a higher colonization efficiency in comparison to sexual systems, because the latter implicitly includes a mate-finding Allee effect (Courchamp et al. 2008). Generally, mating before dispersal can be expected when migrants are likely to immigrate into empty habitat patches.

Externally induced extinctions increase the transition zone, i.e. the area in which CMs can be observed (figure 2.2). As mentioned above, the time of measurement is of great importance. If turnover is measured after extinctions take place, the results only reflect the external extinction rate, which is trivial. Yet, an important rescue effect (Brown and Kodric-Brown 1977; Hanski 1999) changes the results substantially. This is due to high emigration rates selected under externally driven extinctions (Comins et al. 1980; Ronce et al. 2000; Poethke et al. 2003). Regarding genetic structure (figure 2.2 b), the direct effect of external extinctions, which increases the transition zone, is nearly compensated by their effect on the evolving emigration propensity and the rescue effect.

Many metapopulation models assume asexual populations ("females only"; for a discussion see Rankin and Kokko 2007) and/or externally driven extinctions (Ronce and Olivieri 1997; Travis et al. 1999; Ronce et al. 2000; Keeling 2002; Bonte et al. 2010) or implicitly include these assumptions (e.g. the Levins model). These two factors are obvious mechanisms that introduce at least massive rescue effects and in the case of asexual reproduction also considerable turnover and thus CM dynamics.

We believe that the assumption that population extinctions occur completely independently of the state and size of local populations must be carefully justified and, therefore, not taken as a standard assumption. Clearly, external catastrophes like diseases, volcanic eruptions, or flooding may occur. Stelter et al. (1997), for example, examine a SSP of the grasshopper *Bryoderma tuberculata* which inhabits vegetation free gravel bars along rivers in the Alps. Here, catastrophic floods have a dual effect: on the one hand, of course, floods destroy local populations, yet on the other such extinctions counteract succession. This creates suitable habitat for the species (see also Thomas 1994). Yet, we think that for most species it is reasonable to assume that extinctions are related to the population's current state. This is reflected by our parameter for environmental fluctuations (σ; for an in-depth discussion see Poethke et al. 2003). In these scenarios population extinctions occur purely because of environmental and demographic stochasticity.

Introducing patch size variability leads to a large transition zone with significant turnover, intermediate occupancy, and a clear genetic spatial structure (figure 2.3). The increased probability of intrinsic local population extinction and ultimately global extinction can be explained by the fact that large differences in patch-size or quality may select against dispersal (Hastings 1983). This can even lead to a decrease in successful recolonizations, subsequently to reduced incidence, and ultimately to global extinction ("Metapopulation paradox"; see Poethke et al. 2011). In addition to this, if the SSP does not go extinct, panmictic areas disappear because metapopulation dynamics are defined by the few large patches. In the mainland-island scenario, complete extinction is very rare since the mainland is too large to be affected significantly. As outlined in the introduction, the mainland-island scenario is, strictly speaking, not a CM (Harrison and Taylor 1997; Driscoll 2007).

In our simulations we include a large variety of life-history strategies. These range from typically mammalian (e.g. mating after dispersal, only very limited effect of environmental stochasticity; see figure 2.1 d–f) to characteristic insect or arthropod life-histories (e.g. mating before dispersal, high impact of environmental stochasticity; see figure 2.1 a–c). In scenarios including life-history parameters typical for large mammals the parameter space showing CM dynamics is very restricted (see figure 2.1). This finding is supported by evidence from field data which indicates that mammalian populations do usually not exhibit CM dynamics (Elmhagen and Angerbjörn 2001; Olivier et al. 2009). In contrast to this, especially in "females only" scenarios typical for arthropod taxa, we have found significant areas in parameter space that do show CM dynamics. We therefore suggest that the CM concept is more applicable to arthropod species.

2.5 Conclusion

In our simulation model, CM dynamics can only be found under specific circumstances. For typical life-histories of large mammals our model indicates the occurrence of CMs in the strict sense only very rarely. In contrast, for stereotypic insect species we do find the emergence of CM dynamics.

Heterogeneity in habitat size is an important factor increasing turnover and thus facilitating the emergence of CM dynamics. As outlined in the introduction, variable patch sizes are not included in the original (Levins) CM definition. Of course, it is a matter of taste where to draw the separation line between moderate (realistic) variability and mainland-island systems. Nevertheless, our results show that considerable variability is needed to increase turnover noticeably.

The CM concept may be applicable to populations on the brink of extinction. A classical metapopulation structure will often occur as a transient state before extinction (see e.g. the parameter combinations indicating extinct population in our model). Such populations are typically of concern for conservation biologists. Here, time to extinction is an important issue because if the delay is long enough conservation measures may be successful. The question remains whether sensible conservation guidelines can be derived in such cases or whether populations conforming to the CM concept may already be too far down the path towards extinction (Kuussaari et al. 2009). Many management recommendations derived from metapopulation models appear applicable to spatially structured populations as well (see Hanski et al. 2004, for a number of examples). In general, however, it is important to be aware of the specificity of CMs, since the specific spatial structure of focal populations does influence conservation decisions (Guiney et al. 2010). For instance, efforts spent on increasing patch connectivity (e.g. by constructing corridors) may be wasted when the population is actually of a mainland-island type and the primary concern therefore should be the conservation of the mainland population. If a population is actually panmictic (patchy) rather than a CM, this would suggest to focus on different spatial scales and change the monitoring and sampling system. Wrong assumptions about spatial population structure may thus lead to unnecessary spending of resources that would be much better invested elsewhere and incorrect conservation concepts with potentially fatal consequences such as loss of biodiversity. We thus advise to be more careful when using the term “metapopulation”. Often, “spatially structured population” may be more appropriate.

2.6 Appendix

Analysis of the influence of density-dependent emigration, carrying capacity (K), fertility (λ) and competition strength (density regulation, β) on our results. In addition we show evolutionarily stable emigration rates depending on environmental stochasticity (σ), dispersal costs (μ), fertility (λ) and carrying capacity (K).

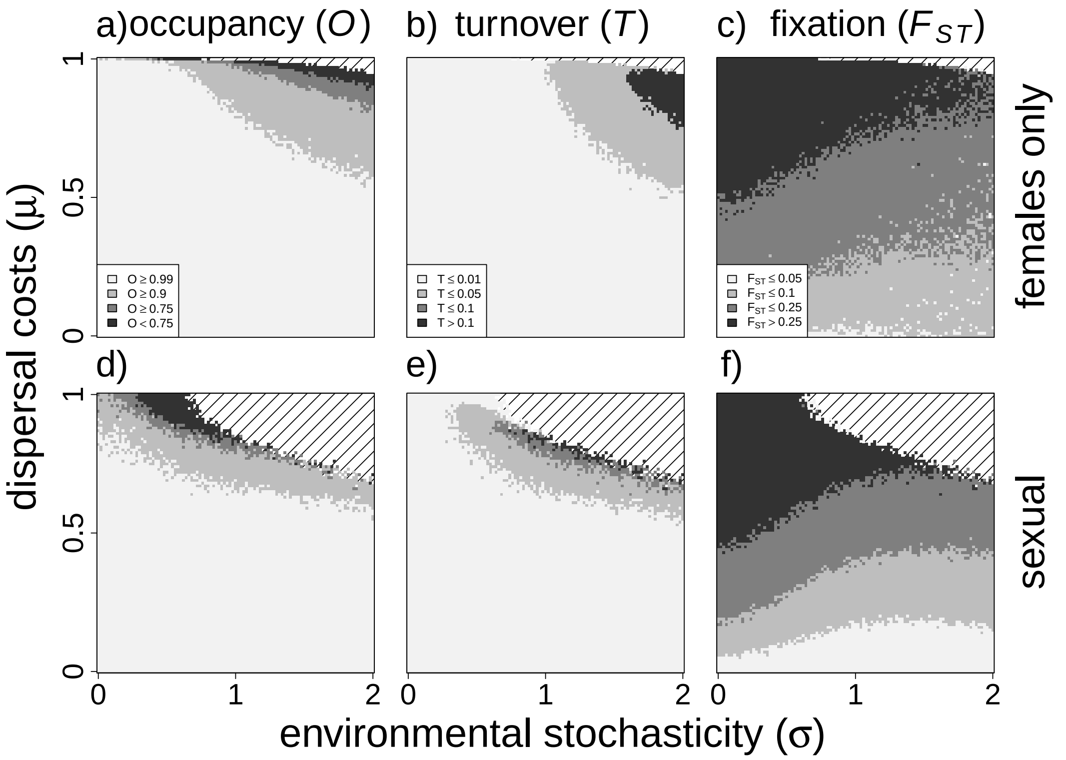

Figure 2.5: Influence of density dependent emigration (DDE), dispersal costs (μ), environmental stochasticity (σ) and reproduction mode ("females only" vs. sexual) on occupancy (O, panels a and d), turnover (T; panels b and e), and genetic structure (F_{ST}; panels c and f) for asexually (top row; panels a and b) and sexually reproducing populations (bottom row; panels c and d). Hatched areas indicate extinct populations. Constant parameters: $\lambda = 2$; $K' = 25$ (panles a, b and c); $K = 50$ (panels d, e and f); $\epsilon = 0$.

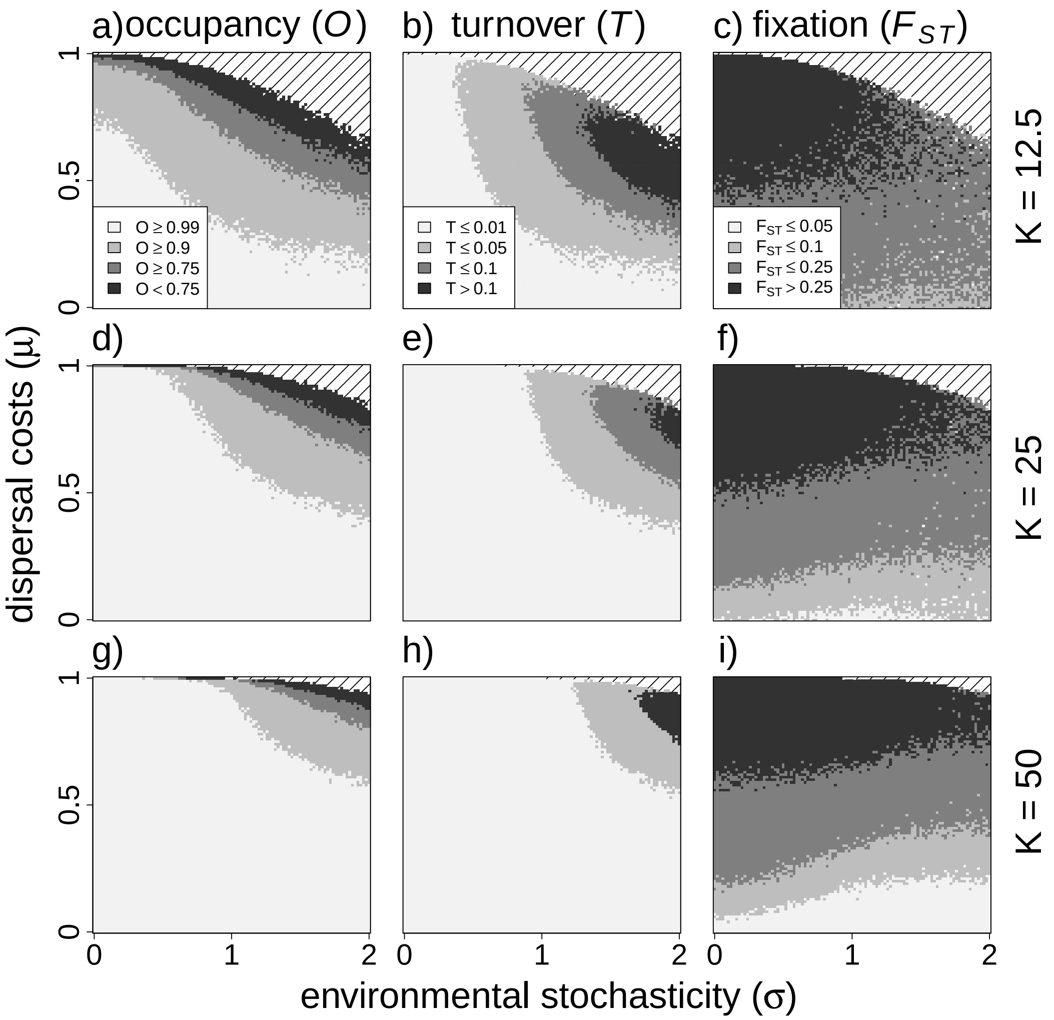

Figure 2.6: Influence of carrying capacity (K), dispersal costs (μ) and environmental stochasticity (σ) on occupancy (O, panels a, d and g), turnover (T, panels b, e and h) and genetic structure (F_{ST}; panels c, f and i) for asexually reproducing populations. Upper panels (a–c): $K = 12.5$; middle panels (d–f): $K = 25$ (standard case for comparison); lower panels (g–i): $K = 50$. Clearly, increasing carrying capacity reduces the transition zone relevant to CMs, shifts its position in parameter space, and reduces the occurrence of global extinctions. Hatched areas indicate extinct populations. Constant parameters: $\lambda = 2$; $\epsilon = 0$.

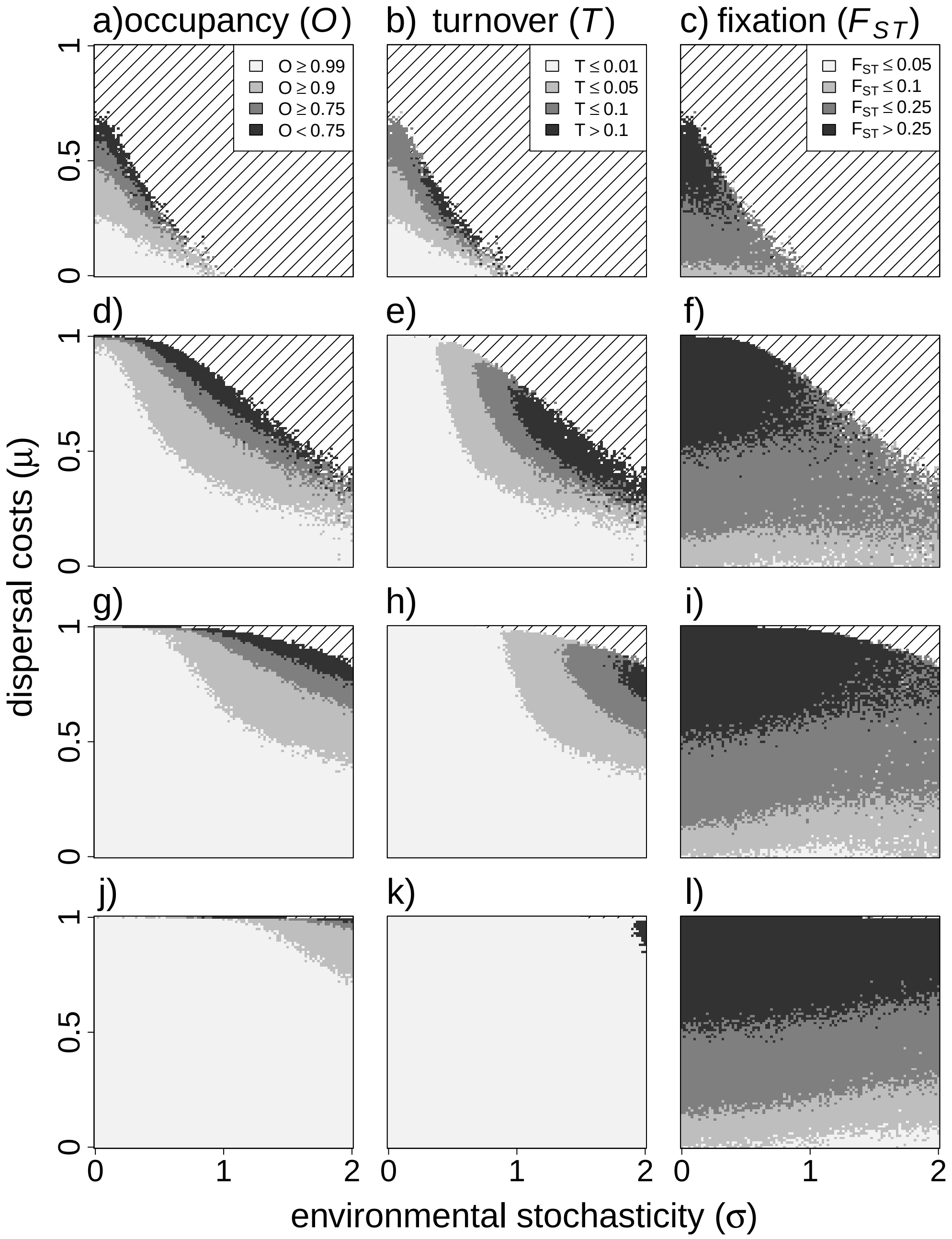

Figure 2.7: Influence of fertility (λ), dispersal costs (μ) and environmental stochasticity (σ) on occupancy (O, panels a, d, g and j), turnover (T, panels b, e, h and k) and genetic structure (F_{ST}; panels c, f, i and l) for asexually reproducing populations. Upper panels (a–c): $\lambda = 1.1$; upper middle panels (d–f): $\lambda = 1.5$, lower middle panels (g–i): $\lambda = 2$ (standard case for comparison); lower panels (j–l: $\lambda = 3$. Increasing fertility shifts the transition zone relevant to CMs in parameter space and reduces the occurrence of global extinctions. Hatched areas indicate extinct populations. Constant parameters: $K = 25$; $\epsilon = 0$.

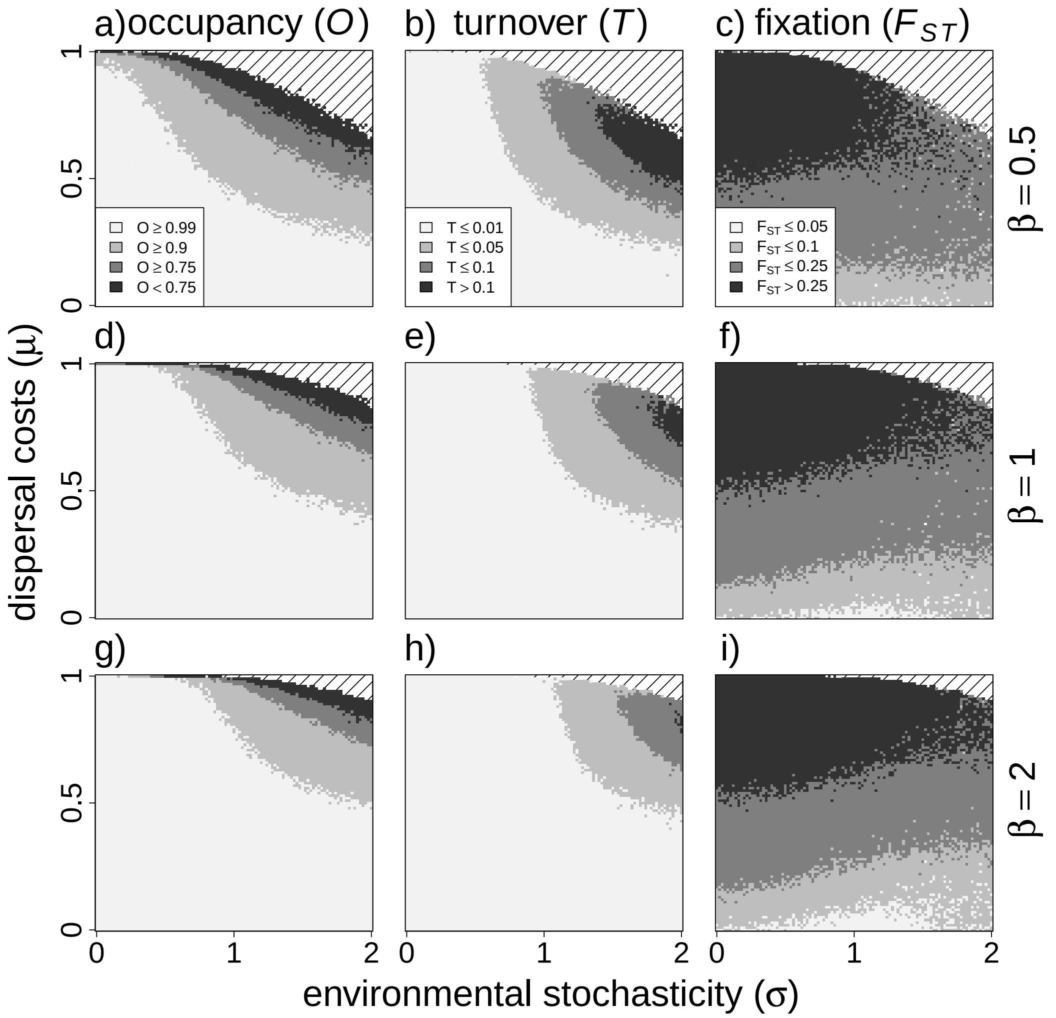

Figure 2.8: Influence of competition strength (β), dispersal costs (μ) and environmental stochasticity (σ) on occupancy (O, panels a, d and g), turnover (T, panels b, e and h) and genetic structure (F_{ST}; panels c, f and i) for asexually reproducing populations. Upper panels (a–c): $\beta = 0.5$; middle panels (d–f): $\beta = 1$ (standard case for comparison); lower panels (g–i): $\beta = 2$. Increasing competition strength shifts the transition zone relevant to CMs in parameter space and reduces the occurrence of global extinctions. Hatched areas indicate extinct populations. Constant parameters: $K = 25$; $\epsilon = 0$.

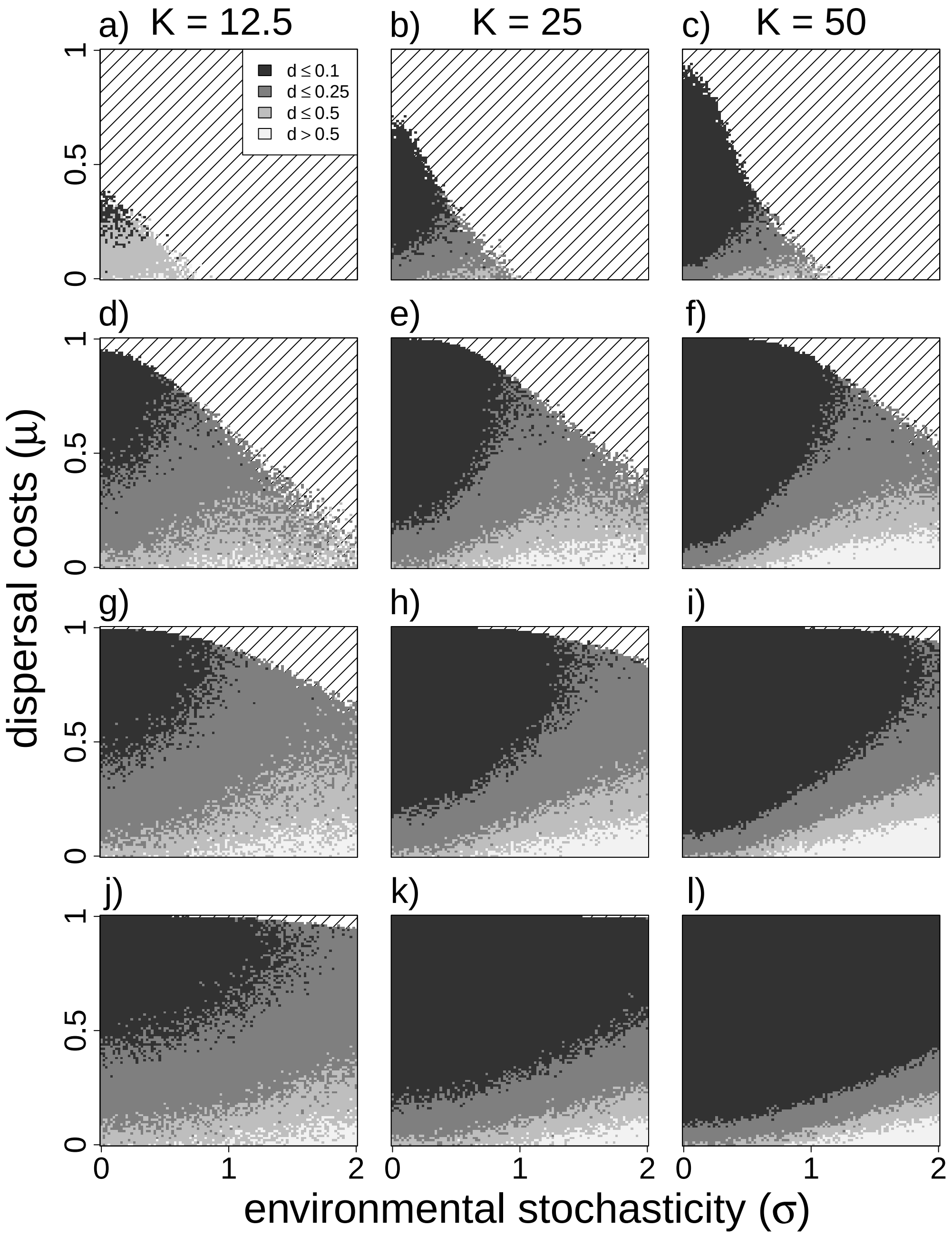

Figure 2.9: Influence of dispersal costs (μ), environmental stochasticity (σ), carrying capacity (K) and fertility (λ) on the evolution of emigration rates (density independent) for asexually reproducing populations. Hatched areas indicate extinct populations. Dispersal costs (μ) clearly select against dispersal while environmental stochasticity (σ) increase emigration rates. Both, increasing carrying capacity (K) and fertility (λ) reduces the occurrence of global extinctions. Constant parameters: $\epsilon = 0$.

3

Evolution of dispersal distance: maternal investment leads to bimodal and fat-tailed dispersal kernels[1]

Contents

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[1] This chapter is in preparation as: Fronhofer, E.A., Poethke, H.J. and Dieckmann, U. Evolution of dispersal distance: maternal investment leads to bimodal and fat-tailed dispersal kernels.

Abstract

Dispersal is of central importance for the ecology and evolution of animals and plants. While dispersal research has focused on the eco-evolutionary dynamics of emigration rates, dispersal distances have been less well studied. It remains unclear what shape evolutionarily stable dispersal kernels have. Detailed knowledge about dispersal kernels (the statistical distribution of dispersal distances) is of pivotal importance for understanding diversity patterns, the accurate prediction of species invasions or range shifts. We examine the evolution of dispersal kernels in continuous space using an individual-based simulation model of a population of sessile organisms (trees, corals). We analyse the influence of three potentially important processes on the shape of the dispersal kernel: distance-dependent inter-individual competition, distance-dependent dispersal costs and maternal investment which reduces dispersal costs of the offspring through a trade-off with maternal fecundity.

Without maternal competition and dispersal costs lead to unimodal and fat-tailed dispersal kernels. Increasing costs reduce the width and the tail weight of the kernel. However, maternal investment inverts this effect: for high dispersal costs kernels become bimodal. Kernels increase in tail weight (long-distance dispersers) and in the amount of non-dispersers. Furthermore, maternal investment increases population viability. The results are robust against a majority of tested parameter combinations.

3.1 Introduction

Understanding and eventually predicting the distribution of species in space and time has never been more important. The spatial distribution of organisms is mainly influenced by their dispersal abilities (Kokko and López-Sepulcre 2006). Although it is well known that a dispersal event is characterized by three stages — departure, transition and settlement (Clobert et al. 2009) — most theoretical and empirical work is firmly rooted in the tradition of metapopulation ecology, focuses mainly on emigration and assumes global or nearest-neighbour dispersal (Bowler and Benton 2005). Yet, there is growing evidence that such classical metapopulations may indeed be rare (e.g. Baguette 2004; Driscoll et al. 2010; Fronhofer et al. 2012). Consequently, a system with a strict distinction between unsuitable matrix and clearly defined habitat patches is just a special case of spatially structured populations in a continuous world. In this context dispersal research should focus more on movement strategies and dispersal distance.

The last decade has seen a rapid development of models for actively moving animals (among many others Nathan et al. 2008a; Getz and Saltz 2008; Fronhofer et al. in press). In contrast, models of passive dispersal in sessile organisms, such as trees, have already for a long time relied on so-called dispersal kernels, i.e. the statistical distribution of propagules in space (Cousens et al. 2008; Hovestadt et al. 2012). The specific form of such kernels defines not only the mean dispersal distance, but also the occurrence of potentially important but rare long-distance dispersal events (LDD; Kot et al. 1996; Muller-Landau et al. 2003). 'Fat-tailed' distributions, which imply a relatively large proportion of LDD, increase the velocity of species invasions (Kot et al. 1996; Caswell et al. 2003), their ability to cope with fragmentation (Dewhirst and Lutscher 2009) and may influence species diversity patterns (Chave et al. 2002; Nathan 2006). A number of possible dispersal kernel shapes have been proposed (e.g. reviewed in Cousens et al. 2008) but very often, negative-exponential, power-law or Gaussian distributions are assumed for simplicity (for a critical discussion see Kot et al. 1996).

In addition, the term 'dispersal kernel' is not always clearly defined. A kernel may describe two distinctly different probability density functions (pdf): (i) the density pdf which describes the density of propagules to be expected at a certain distance and (ii) the distance pdf which describes the distribution of distances the propagules are dispersed to (see also Cousens et al. 2008; Hovestadt et al. 2012). Of course, both definitions are correct and kernels can be expressed in both terms, yet the form will differ characteristically. If one takes a uniform distribution of seeds per area as an example, the density pdf will logically be a rectangular distribution in a finite world, while the distance pdf will be a linearly increasing function of distance. This is simply due to the fact that in two dimensions the area of a circle increases with the radius and if the density is to be constant more propagules have to be dispersed to larger distances. If not indicated otherwise we will here use the distance pdf as dispersal kernel.

In spite of the immense relevance of the specific form of the dispersal kernel, it is still unclear what an optimal and evolutionarily stable kernel should resemble. This question has been addressed for the first time by Hovestadt et al. (2001) who find that in autocorrelated landscapes fat-tailed dispersal kernels evolve. A quantity of propagules will fall within the suitable habitat surrounding the parental plant but a significant amount of propagules will exhibit long-distance dispersal, i.e. disperse more or less uniformly over the landscape, in order to minimize kin competition (Hamilton and May 1977). The shape of the dispersal kernel is a result of two opposing forces: kin competition would be minimized by a completely uniform distribution of propagule densities, while distance-dependent dispersal costs (for a review see Bonte et al. 2012) select against long dispersal distances. Hovestadt et al. (2001) include dispersal costs only implicitly via increasingly unsuitable habitat. The effect of distance-dependent dispersal costs has been analysed explicitly by Rousset and Gandon (2002). For monotonically increasing dispersal cost functions these authors predict unimodal dispersal kernels (distance pdf). While the mean dispersal distance depends on the intensity of kin competition, fat tails are not predicted to occur in two-dimensional landscapes. Recently Starrfelt and Kokko (2010) have analysed the evolution of dispersal distance and kernel shapes in the context of parent-offspring conflict. They could show that maternal control of dispersal leads to longer dispersal distances as predicted by Hamilton and May (1977) and that during invasions fat-tailed and u-shaped kernels may evolve with a mass of propagules staying at the parental location and an additional peak at the maximal dispersal distance. This pattern emerges during range expansion especially under maternal control. During invasions the costs of dispersal, which select against LDD, are offset by kin- and spatial-selection (see e.g. Phillips et al. 2008; Kubisch et al. in press b). In the extreme case of no dispersal costs, and especially under maternal control Hamilton and May (1977) predict a uniform density pdf, i.e. an increasing distance pdf. As Starrfelt and Kokko (2010) show this interaction of dispersal costs and kin- and spatial-selection will lead to u-shaped distance pdfs, i.e. to fat-tailed density pdfs. All these models represent important steps towards a better understanding of the evolution of dispersal kernel shapes.

Two fundamental issues that are known to heavily influence the evolution of dispersal have not been taken into account by the above mentioned models: (i) the strength and spatial extent of competitive interactions and (ii) trade-offs, more specifically parental investment. Firstly, as Berger et al. (2008) point out competition is a process that importantly shapes plant communities and that therefore should be modelled at the individual- and not only at the population-level. A large number of models in dispersal ecology are grid-based (e.g. Murrell et al. 2002; Gros et al. 2006; Bonte et al. 2010) which either implies that competition acts at the local population level, or — if only one individual is modelled per grid cell — that the competition kernel has a quadratic base, which is a somewhat artificial assumption. Secondly, it has been shown theoretically (Roff 1994; Fronhofer et al. 2011a) and empirically (Reznick 1985) that life-history trade-offs, e.g. between reproduction and dispersal ability, may deeply influence the evolution of dispersal and for example lead to polymorphisms with a coexistence of low- and high-dispersal morphs. In the context of sessile organisms with passive dispersal such trade-offs are inter-generational and more appropriately described as maternal investment that may offset the offspring's dispersal costs. Especially in plants, where seeds are surrounded by maternal tissue and may depend on these structures for dispersal it is sensible to include this aspect and to analyse the consequences of this investment.

Therefore, we present an individual-based model of a population of sessile organisms such as trees to investigate the evolution of the shape of the dispersal kernel. In contrast to a great majority of existing models (e.g. Murrell et al. 2002; Gros et al. 2006; Bonte et al. 2010; North et al. 2011) we do not *a priori* assume a specific kernel shape. We derive optimal kernel shapes while not taking into account constraints emerging from the realization of this kernel. We explicitly implement a total of three selective forces which should be of relevance for the evolution of the shape of the dispersal kernel, namely a competition kernel (see e.g. Roughgarden 1974), distance-dependent dispersal costs (for a review see Bonte et al. 2012) and maternal investment that reduces dispersal costs experienced by dispersing offspring.

Under the usual assumption of no maternal investment we find that the interplay between the competition kernel and distance-dependent dispersal costs generally leads to unimodal and fat-tailed kernels. While increasing dispersal costs reduce tail weight, maternal investment changes the evolutionarily optimal kernel form and selects for bimodal and heavily fat-tailed kernels. It is particularly interesting to note that maternal investment may severely increase population viability. Our results prove to be robust against the great majority of tested parameter combinations.

3.2 Model description

3.2.1 Reproduction and inheritance

In our model every individual is characterized by its specific dispersal kernel. We define the dispersal kernel as the probability distribution $P(d)$ of reaching a given distance (d) after a dispersal event, i.e. we use a distance pdf. As we do not determine a specific functional relationship *a priori* the kernel is implemented as a function-valued trait (see Dieckmann et al. 2006) with 21 values giving the probabilities of reaching a given distance class d_i ($d_1 = 0, 0 < d_2 \leq 1, 1 < d_3 \leq 2, ..., 19 < d_{21} \leq 20$). These values are positive and normalized to sum up to 1 (see also Hovestadt et al. 2001; Starrfelt and Kokko 2010). We thus approximate a continuous dispersal kernel with discrete values. We ran additional simulations with up to 31 distance classes and also analysed the effect of increasing the extent of the first distance class ($0 \leq d_1 < 0.1, 0 \leq d_1 < 0.2$). This will be discussed in detail below; our results were not affected qualitatively.

Generations are discrete and overlapping. Once per time step individuals reproduce sexually and produce a number of offspring drawn from a Poisson distribution with mean $\bar{\lambda}$. As our model is applicable for example to trees we assume that individuals are simultaneously monoecious, i.e. have male and female reproductive organs. Selfing is excluded and for simplicity we assume that an individual mates with its nearest neighbour.

As our model is phenotypic the offspring inherit for each distance class of the dispersal kernel the mid-parent value altered by a segregation kernel (Roughgarden 1979), a Gaussian distribution with the mid-parent value as mean and $\sigma_s = const. = 0.1$ as standard deviation. This allows us to include the biologically relevant effects emerging from the processes of segregation and recombination during meiosis.

In order to optimize simulation time we additionally assume rare mutation events. While the mutation rate is kept constant ($m = 0.001$) the strength of mutations, i.e. the amount by which an allele value may be changed (Gaussian distribution, mean zero, standard deviation σ_m, log-transformed) decreases with time (see also Poethke et al. 2010): $\sigma_m = e^{-5 \cdot \frac{t}{t_{max}}}$ with t as the actual time step and t_{max} as the total simulation time. To guarantee that segregation, recombination and mutations result in positive numbers for the kernel the values are log-transformed before the mid-parent values are altered by the segregation kernel and mutations.

3.2.2 Dispersal

As we investigate the evolution of the dispersal kernel of sessile organisms with passive dispersal, we assume maternal control of dispersal (see also North et al. 2011). This means that the mother's genotype defines the dispersal distance of the offspring. As Hamilton and May (1977) note optimal dispersal distances may be different depending on whether one maximises the inclusive fitness of the mother or of the offspring. Due to costs of dispersal applying directly to the offspring, dispersal distances under offspring control are often reduced. This has been analysed in detail by Starrfelt and Kokko (2010). We have run additional simulations with offspring control and found that the results corresponded well to their results.

The dispersal distance of an offspring is determined by randomly drawing a distance class d according to the maternal dispersal kernel ($P(d)$). The realized dispersal distance is drawn randomly with a uniform distribution from this interval, i.e. if $d = 0$ the dispersal distance is always zero, if $d = 1$ the dispersal distance is between 0 and 1 and so forth.

3.2.3 Dispersal costs and maternal investment

As we assume a constant per step mortality (μ_d^0) the probability of dying while dispersing over a distance δ follows an exponential function (figure 3.1)

$$\mu_d = 1 - e^{-\mu_d^0 \cdot \delta}. \tag{3.1}$$

Of course, the experienced dispersal costs will not depend on the net distance travelled, but on the realization of the dispersal event. Logically, equation 3.1 holds for a straight line walk. For any other realization the cost function will follow the general form $\mu_d = 1 - e^{-\mu_d^0 \cdot \delta^n / c}$. If the realization is a (correlated) random walk, i.e. follows a Lévy process, we find that $n < 1$ (results not shown). This does not change the shape of the dispersal mortality function qualitatively: $n < 1$ increases the slope of the function for small distances while it saturates later. Additional simulations show that our results are not influenced qualitatively by this assumption.

Dispersal costs may be offset — at least to some extent — by maternal investment which increases the dispersal ability of propagules. Such a trade-off implies that although investment of resources increases one component of fitness another component of fitness is reduced (Roff and Fairbairn 2007). Very often an increase in dispersal ability is correlated with a decrease in fertility (Zera and Denno 1997; Tanaka and Suzuki 1998; Roff 2002; Roff et al. 2002).

For simplicity we will assume two extreme scenarios: (i) either the offspring carry all costs as described above (see equation 3.1; scenario ‘offspring pay’) or (ii) the costs are completely covered by maternal investment (scenario ‘mother pays’). To keep both scenarios comparable we determine the maternally covered, kernel-dependent, costs by summing up the distance-dependent costs over the entire kernel $P(d)$ for all possible distance classes d:

$$\tau = \frac{\sum P(d) \cdot \mu_d}{\sum P(d)}. \tag{3.2}$$

Costs trade-off with fecundity (see also Burton et al. 2010; Fronhofer et al. 2011a) and the mean number of offspring is then calculated as:

$$\bar{\lambda} = \lambda_0 \cdot (1 - \tau). \tag{3.3}$$

with $\lambda_0 = 4$ as a standard value.

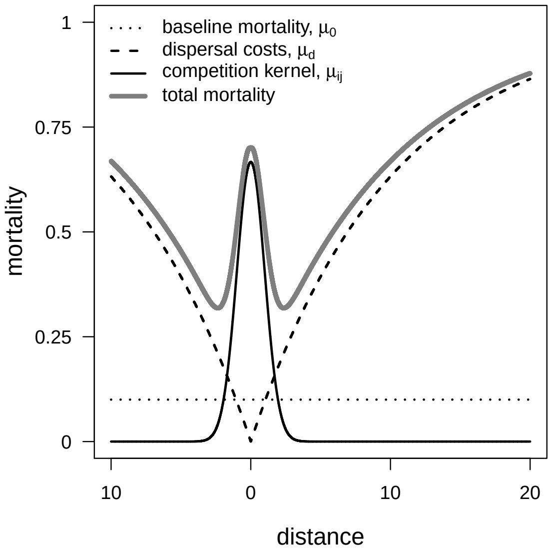

Figure 3.1: Overview of the components of distance-dependent mortality (equation 3.5). The shape of the competition kernel is very flexible and can vary from leptokurtic to platykurtic. Its height is a function of the focal organism's age (a; see equation 3.4 and text for details). Its width is determined by the standard deviation (σ). Distance-dependent dispersal costs are an asymptotic function (see equation 3.1) and depends only on the per distance unit mortality (μ_d^0). The depicted function is only correct in 'offspring pay' scenarios. In addition we assume a distance- and density-independent, constant baseline mortality (μ_0). Note that the figure ignores effects of neighbouring individuals. Parameter values: $\gamma = 2$, $\sigma = 1$, $a = 6$, $H_a = 3$, $\mu_d^0 = 0.1$, $\mu_0 = 0.1$.

3.2.4 Competition and mortality

No matter whether competition is for space, light or nutrients it will always depend on inter-individual distances. In addition we include age-dependence since competition will be asymmetric between established trees and seedlings, for example (see figure 3.1). In our model competition acts by increasing mortality and not by decreasing fertility. This allows us to derive a density-dependent individual mortality term, i.e. the probability of dying in the present time step (μ_i). For the form of this competition kernel — often termed zone or sphere of influence (for a review of modelling approaches see Berger et al. 2008) — we assume a general and very flexible functional relationship (analysed in detail by Roughgarden 1974). This approach is similar to the sphere of influence model presented by Schiffers et al. (2011). The effect of an individual j on the focal individual i is calculated as:

$$\mu_{i,j} = e^{-\left(\frac{\Delta_{i,j}}{c}\right)^{\gamma}} \cdot \frac{a_j}{a_j + H_a} \tag{3.4}$$

with $c = \sigma\sqrt{\Gamma(\frac{1}{\gamma})}/\sqrt{\Gamma(\frac{3}{\gamma})}$; Γ is the gamma function. The first term of the function reflects distance- and the second term age-dependence. $\Delta_{i,j}$ is the euclidean distance between trees i and j. σ is the standard deviation of the competition kernel and γ the kurtosis. $\gamma = 2$ yields a Gaussian normal distribution, values smaller than 2 lead to a leptokurtic run (thin peak, fat tails) values over 2 to a platykurtic function (broad peak, thin tails). The kurtosis ($\gamma = 2$ as standard value) thus reflects how far inter-individual competition reaches into space, while the standard deviation ($\sigma = 1$ as standard value) determines the width of the competition kernel.

Age-dependence is a simple asymptotic function with a as the age of tree j and H_a as the half-saturation constant, i.e. the age at which a tree reaches half of its maximal competitive ability ($H_a = 3$ as standard value). Note that the age-dependent term is important since without it competition between adults and seedlings is symmetric.

The total competition related mortality (μ_i) of individual i may additionally include a baseline mortality ($\mu_0 = 0.1$ as a standard value) which is density independent (see figure 3.1):

$$\mu_i = 1 - (1 - \mu_0) \cdot \prod_{i \neq j} (1 - \mu_{i,j}). \tag{3.5}$$

3.2.5 Simulations

All simulations were run in a world of 100 x 100 distance units with periodic boundary conditions. Depending on parameter combinations populations sizes varied roughly between 400 and over 7000 individuals. Simulation time was set to $t_{max} = 10,000$ time steps, a time span that allowed all simulations to reach equilibrium. The results shown below are means over 25 replicates. Please see table 3.1 for a summary of relevant parameters and tested values.

Table 3.1: Important model parameters, their meaning and tested values.

parameter	**values**	**meaning**
λ_0	2, 4, 8	fecundity
μ_0	0.05, 0.1, 0.2	baseline mortality (density independent)
σ	0.5, 1, 2	width of the competition kernel (standard deviation)
γ	1, 2, 4	kurtosis of competition kernel
H_a	1.5, 3, 6	age-dependence of competition (half-saturation constant)
μ_d^0	0.05, 0.1, 0.15, ... , 0.4	dispersal costs (per distance unit)

3.3 Results

3.3.1 Evolution of fat-tailed kernels

In all scenarios without maternal investment, i.e. when the offspring pay distance-dependent dispersal costs according to equation 3.1, we find that the evolutionarily stable dispersal kernel is unimodal and fat-tailed (figure 3.2 A). This results from the interaction between the competition kernel and dispersal costs as shown in figure 3.1. Increasing dispersal costs lead to narrower, more peaked and less fat-tailed kernels (figure 3.2 B). This is due to an increase in the slope of the dispersal mortality function (figure 3.1).

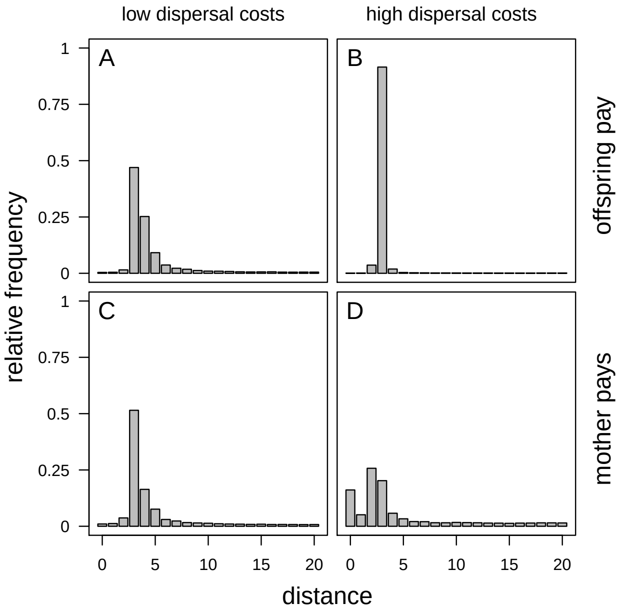

Figure 3.2: Maternal investment and the evolution of dispersal kernels. All four panels show evolutionarily stable dispersal kernels (distance pdfs). The upper row (A, B) depicts the influence of dispersal costs without maternal investment, i.e. when offspring pay distance-dependent dispersal costs according to equation 3.1. The competition kernel (equation 3.4) leads to unimodal and fat-tailed distributions (A). Increasing dispersal costs lead to narrower and more peaked kernels (B). The lower row (C, D) shows kernels for scenarios with maternal investment, i.e. the mother pays kernel-dependent dispersal costs (equation 3.2) and reduces her fecundity in order to maximize offspring survival during dispersal (equation 3.3). Maternal investment leads to heavily fat-tailed kernels (C, D) and to bimodality at high dispersal costs (D). Parameter values: $\lambda_0 = 4$, $\mu_0 = 0.1$, $\gamma = 2$, $\sigma = 1$, $H_a = 3$; left panels (A, C) $\mu_d^0 = 0.1$, right panels (B, D) $\mu_d^0 = 0.35$.

3.3.2 Maternal investment leads to bimodal kernels

In general, maternal investment increases the occurrence of LDD, i.e. the weight of the kernel's tail (figure 3.2 C). Interestingly, maternal investment inverts the effect of dispersal costs on long-distance dispersal: here increasing dispersal costs lead to an increase in tail weight (figure 3.2).

In addition, the evolutionarily stable dispersal kernel for high dispersal costs is bimodal (figure 3.2 D) with an important proportion of propagules remaining very close to the maternal individual and a mass of offspring showing LDD.

3.3.3 Dispersal costs

A more detailed analysis of the influence of dispersal costs shows that, as one would assume, the mean dispersal distance decreases with costs in the 'offspring pay' scenario (figure 3.3 A). Yet, with maternal investment ('mother pays') the relationship becomes u-shaped, i.e. higher dispersal costs favour higher mean dispersal distances (figure 3.3 A). Clearly, this is due to the asymmetry and tail weight of the kernels (figure 3.2) since the median dispersal distance decreases monotonically with dispersal costs (figure 3.3 B). The median reaches a steady value which is defined by the width of the competition kernel (see also figure 3.4). The scenario assumed, i.e. distance costs paid by the offspring ('offspring pay') vs. kernel costs paid by the mother ('mother pays'), does not influence the median dispersal distance.

As mentioned above, increasing dispersal costs lead to narrower kernels if the offspring pay distance dependent dispersal costs (figure 3.3 C). However, in the case of maternal investment this tendency is reversed for sufficiently high dispersal costs (figure 3.3 C; here $\mu_d^0 > 0.2$) which is due to the above described bimodality (figure 3.2 D).

A similar pattern can be observed for tail weight (figure 3.3 D). In the 'offspring pay' scenario increasing dispersal costs reduce tail weight, here measured as the 95th percentile of the kernel. Maternal investment inverts this pattern: as soon as the kernel becomes bimodal its tail weight increases with dispersal costs (figure 3.3 D).

3.3.4 Shape of the competition kernel

The qualitative results presented above, i.e. the emergence of fat-tailed dispersal kernels in general and bimodality in scenarios with maternal investment, are robust against variation in all model parameters (figures 3.4 and 3.5). Not surprisingly, the width of the competition kernel influences the mean and the median of the dispersal kernel, i.e. the location of the peak (figure 3.4 A, B). Wider competition kernels, i.e. higher values of the standard deviation σ, lead to bimodal dispersal kernels at lower dispersal costs in the 'mother pays' scenario (figure 3.4 C, D). The pattern is not lost for narrower

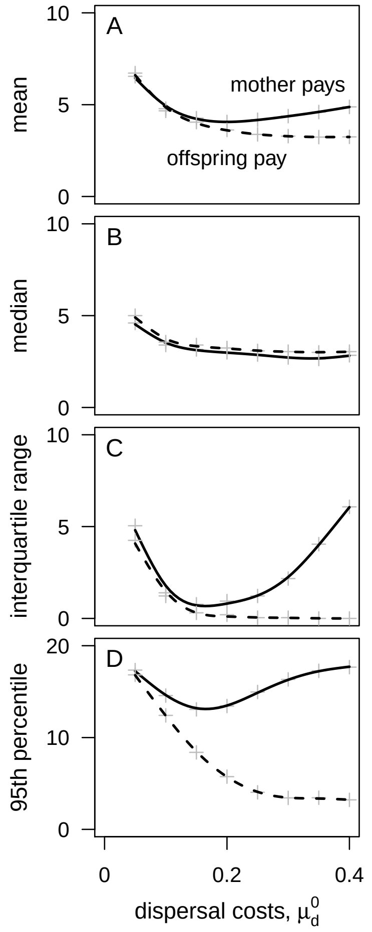

Figure 3.3: Maternal investment and dispersal costs. The graphs represent a systematic analysis of the influence of dispersal costs (μ_d^0) on mean (A), median (B), interquartile range (C) and the position of the 95% percentile (D) of the evolutionarily stable dispersal kernels. Here and in the following figures the solid line represents results for scenarios with maternal investment ('mother pays') and the dashed line without ('offspring pay'). For 'mother pays' scenarios the mean dispersal distance shows a u-shaped relation with increasing dispersal costs while median does not (A, B). The interquartile range (C) captures the emerging bimodality in 'mother pays' scenarios. The 95th percentile is a good indicator for fat tails (D). Parameter values: $\lambda_0 = 4$, $\mu_0 = 0.1$, $\gamma = 2$, $\sigma = 1$, $H_a = 3$. The grey crosses represent data points and the lines are smooth spline regressions ($\lambda = 0.3$).

competition kernels, yet requires higher dispersal costs to emerge ($\mu_d^0 > 0.5$; not shown). The kurtosis (γ) of the competition kernel has only very slight effects. More leptokurtic shapes lead to slightly smaller dispersal distances (figure 3.4 E, F) because the costs inflicted by competition decrease at a faster rate at small distances. As a consequence more platykurtic competition kernels lead to bimodality in 'mother pays' scenarios at lower dispersal costs (figure 3.4 G) and to more pronounced fat tails (figure 3.4 H).

The shape, especially the hight of the competition kernel, also depends on the focal individual's age (equation 3.4). We find that the slower an individual's competitive ability increases ('slow growth' in figure 3.4; larger values of the half-saturation constant H_a) the smaller dispersal distances become (figure 3.4 I, J). Under such conditions the usual pattern of higher dispersal distances in scenarios with maternal investment is inverted (figure 3.4 J) which is due to a more pronounced bimodality (figure 3.4 K) with a higher peak at distance zero. This is primarily due to the lower competitive ability of a focal maternal individual. In turn, this pattern interacts with increasing dispersal costs and allows the emergence of a heavier tail (figure 3.4 L; black and grey solid lines intersect). Maternal investment allows to increase the amount of LDD, i.e. tail weight, by increasing the height of the peak at distance zero, i.e. the number of non-dispersers (see also equation 3.2).

3.3.5 Fecundity and mortality

In the 'mother pays' scenario higher fecundities (λ_0; figure 3.5 A–D) reduce bimodality and tail weight while the median dispersal distance is not affected. Note that the bimodal pattern is not lost, but requires higher dispersal costs to emerge. Higher fecundity increases competition, especially with kin, which leads to a reduction of the peak at zero. This in turn reduces tail weight, as described above. Baseline mortality (μ_0; figure 3.5 E–H) has no qualitative effect and no interpretable quantitative effect on our results.

3.4 Discussion

Our results represent an important step towards a better understanding of dispersal in sessile organisms such as plants. By relaxing the somewhat arbitrary assumption of a world with discrete habitat patches and modelling competition explicitly at the individual level in continuous space through a competition kernel we could show that in plants with overlapping generations kernels should be unimodal and fat-tailed (figure 3.2). This is true for both distance and density pdfs. While it is not surprising that our model predicts increasing dispersal costs to lead to smaller dispersal distances the introduction of maternal investment inverts this pattern (figure 3.3). It has been shown in other contexts that trade-offs may shape the evolution of dispersal considerably (e.g. Roff 1994; Burton et al. 2010; Fronhofer et al. 2011a). We here demonstrate for sessile organisms that trading fecundity for an increased survival of dispersing offspring, i.e. maternal investment, is highly advantageous. Maternal investment characteristically influences the form of the dispersal kernel. Bimodal kernels emerge for sufficiently high

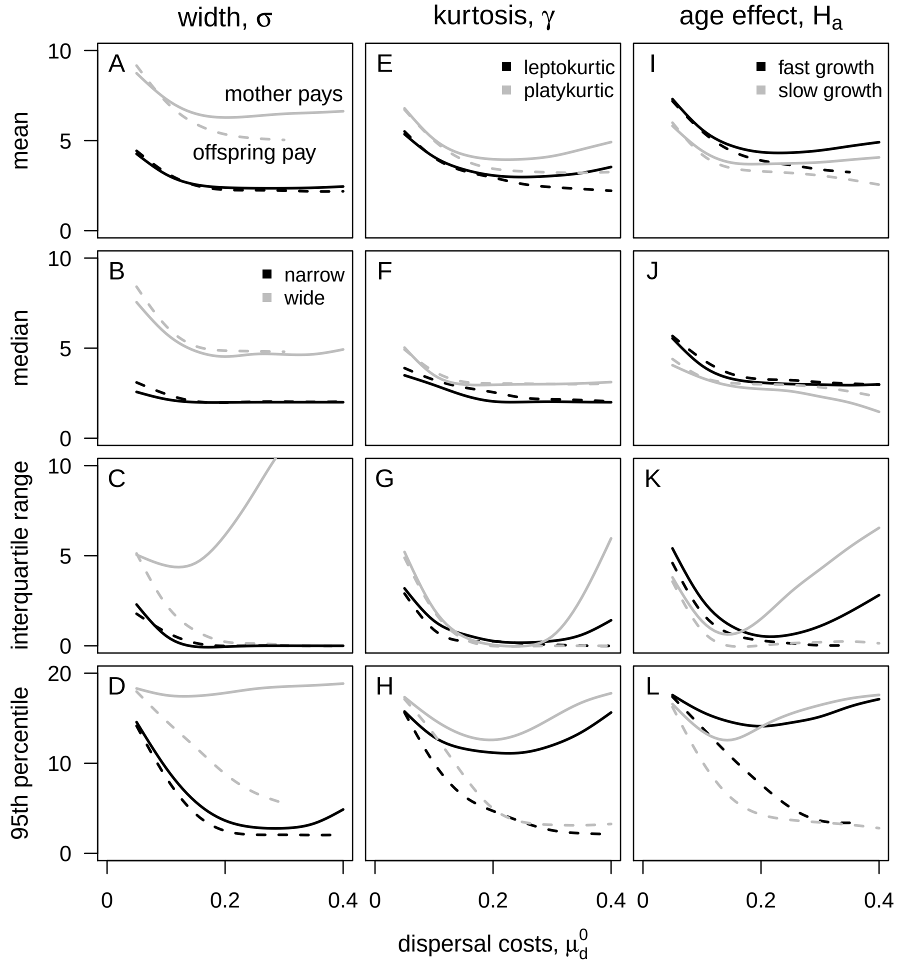

Figure 3.4: Influence of the shape of the competition kernel. The competition kernel (figure 3.1 and equation 3.4) is determined by its width (standard deviation σ; panels A–D), by its kurtosis (γ; panels E–H) and by its height, which is a function of the focal individual's age (half-saturation constant H_a; panels I–L). As in the previous figure solid lines show results for scenarios with maternal investment ('mother pays') and dashed lines without ('offspring pay'). Black curves always indicate scenarios in which the focal parameter value was halved and grey curves scenarios in which the value was doubled. The characteristic patterns shown before, i.e. bimodal and fat-tailed kernels for maternal investment, are stable. Wide kernel lead to larger dispersal distances (A, B), a more pronounced bimodality (C) and extremely fat tails (D). Bimodality emerges also with very narrow competition kernels, yet requires higher dispersal costs. More platykurtic competition kernels tend to underline the described effects, while leptokurtic competition kernels do not lead to a loss of fat tails or bimodality (E–H). Slow growth reduces dispersal distances and underlines the differences between scenarios with and without maternal investment (bimodality; K). Parameter values: $\lambda_0 = 4$, $\mu_0 = 0.1$. Narrow: $\sigma = 0.5$, wide: $\sigma = 2$; leptokurtic: $\gamma = 1$, platykurtic: $\gamma = 4$; fast growth: $H_a = 1.5$, slow growth: $H_a = 6$. The lines are smooth spline regressions ($\lambda = 0.3$).

dispersal costs and at the same time the kernels become heavily fat-tailed (figures 3.2 and 3.3). These results prove to be robust against variation in all tested simulation

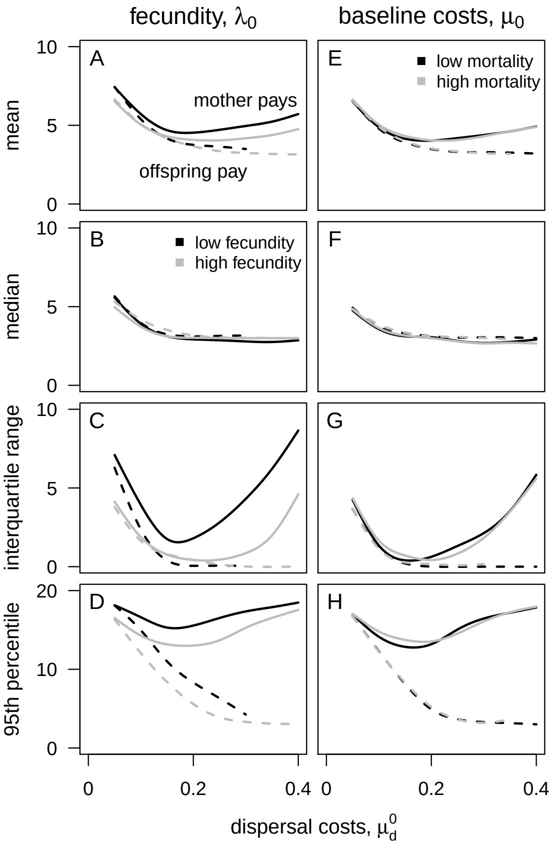

Figure 3.5: Influence of fecundity and mortality. As in the previous figure solid lines show results for scenarios with maternal investment ('mother pays') and dashed lines without ('offspring pay'). Black curves always indicate scenarios in which the focal parameter value was halved and grey curves scenarios in which the value was doubled. Low fecundities (λ_0) underline the effects described above (A–D), but higher fecundities to not destroy the patterns, i.e. fat-tails and bimodality for maternal investment at sufficiently high dispersal costs still arise. Density independent baseline mortality (μ_0; E–H) does not influence our results in a quantitatively relevant way. Parameter values: $\gamma = 2$, $\sigma = 1$, $H_a = 3$. Low fecundity: $\lambda_0 = 2$, high fecundity: $\lambda_0 = 8$; low mortality: $\mu_0 = 0.05$, high mortality: $\mu_0 = 0.2$. The lines are smooth spline regressions ($\lambda = 0.3$).

parameters (figures 3.4 and 3.5).

In scenarios with maternal investment bimodality of the dispersal kernel emerges mainly because of two mechanisms: (i) as the mother pays dispersal costs defined by the dispersal kernel (equation 3.2) increasing the variance of the kernel through a bimodal distribution with a peak at zero (or at very small distances) allows to decrease the costs while keeping the mean dispersal distance constant or even increasing it through a heavily fat tail. Thus, by reducing the dispersal distances of some offspring the mother may achieve LDD for other propagules. Higher dispersal distances are evolutionarily advantageous because they minimize kin competition (Hamilton and May

1977). This effect is especially pronounced for maternal control of dispersal (Hamilton and May 1977; Starrfelt and Kokko 2010) and would ultimately lead to a uniform density pdf or a steadily increasing distance pdf. (ii) Furthermore, the maternal location characteristically implies a minimal influence of the nearest neighbours' competition kernels. Locally this specific point in space maximizes an individual's survival and non-dispersers will thus be able to inherit this locally optimal location ('territorial inheritance').

Although a distance class of zero is usually used in models as we present here (see e.g. Hovestadt et al. 2001; Rousset and Gandon 2002; Starrfelt and Kokko 2010) it is certainly a quite artificial assumption since it implies the potential emergence of infinite densities. We therefore tested the impact of increasing the extent of this first distance class, which is at the same time a test of the validity of the above proposed explanation for bimodality. Additional simulations show that the bimodality reported here is not an artefact resulting from the assumption of a infinitely narrow first distance class. Our results are stable for a width of the first distance class of up to $0 - 0.2$. This sensitivity is the consequence of the above discussed advantages of territorial inheritance and underlines the possible artefacts resulting from grid-based models in general.

The two mechanisms discussed above also explain the influence of the age-specific component of the competition kernel (figure 3.4) and of fecundity (figure 3.5). Increased local competition through fast growth leads to a reduction of kernel bimodality in scenarios with maternal investment. Although there is an advantage for mothers keeping a fraction of offspring close by for territorial inheritance fast growth leads to an important increase in local competition between the mother and her non-dispersing offspring and between these. This leads to a reduction to the peak at distance zero, i.e. the number of non-dispersers. The same effect will emerge from increased numbers of offspring. As the kernel costs resulting from the formation of a fat-tail are offset by the production of 'cheaper' non-dispersers, reducing the latter will lead to a reduction of tail weight.

In general, maternal investment also allows the persistence of stable populations despite low fecundities, high mortalities and high competition, conditions that otherwise lead to global extinctions. This can be seen e.g. in figure 3.5 A–D: for low fecundities and if the offspring pay distance dependent dispersal costs populations are not viable for dispersal costs > 0.3. This is not the case in scenarios with maternal investment. Additional simulations show that maternal investment allows populations to survive dispersal costs over 0.8 (not shown).

Due to asymmetric competition between the mother and the offspring a majority of non-dispersers may actually die. This of course begs the question why mothers produce these offspring in the first place. If this was just a strategy to spare resources for the production of more expensive long-distance dispersers and these 'cheap' propagules were thus only produced to reduce the costs of offspring production, mothers could as well simply reduce the number of offspring produced and put all resources into long-distance dispersers. In order to explore this question we ran additional simulations including evolvable fecundities and a trade-off between fecundity and baseline mortality. Individuals reducing their fecundity could thus increase their survival. In all these simulations the bimodality was evolutionarily stable. Regardless of the form of the assumed trade-off function (concave, linear, convex) we observed evolution towards short lived, sometimes annual, but very fecund individuals showing an increasingly bimodal kernel. Dytham and Travis (2006) analyse the concurrent evolution of longevity and dispersal distance. Their results show that shorter life spans lead to shorter dispersal distances. Although our model is significantly different, the increasing bimodality, i.e. the higher frequency of non-dispersers we find is a similar phenomenon. It results from reduced kin competition and the possibility of territorial inheritance. Yet, as the form of our kernel may evolve freely, a reduced life span does not lead to smaller dispersal distances in general. On the contrary, as noted above, in scenarios with maternal investment the kernels are bimodal and heavily fat-tailed with an important fraction of long-distance dispersers.

Our model is applicable to sessile organisms such as plants. Most plants will show maternal investment, at least to some degree, since fruit and seed production is obviously maternally regulated. The bimodal dispersal kernel which we predict can be realized for example by seed polymorphisms, a phenomenon that has been frequently observed (for a review see Imbert 2002). The Asteraceae *Heterotheca latifolia* for example shows a dimorphism in achene structure: while disc achenes, which have a pappus, are wind dispersed and responsible for LDD ray achenes are not (Venable and Levin 1985). This polymorphic seed structure will lead to bimodality in the dispersal kernel and increased tail weight (see also van Mölken et al. 2005; Brändel 2007). The same effect can be achieved by polychory, i.e. the use of more than one seed dispersal agent (see e.g. Berg 1966; Jordano et al. 2007). For example in *Prunus mahaleb* small birds are responsible for short distance dispersal while fruits eaten by mammals and larger birds are dispersed over long distances (Jordano et al. 2007). In a very broad sense our results may be of significance for territorial animals, although the model has not been designed for actively moving animals. Of course, in this case competition will be more prone to act on fertility than on mortality, but the resulting patterns may be similar. A dimorphism can often be observed between non-dispersers that wait, eventually help their parents, and bet on territorial inheritance and dispersers that try to colonize new, eventually empty territories (e.g. Kokko and Ekman 2002).

As in any tractable model we include some simplifying assumptions, a number of which we have already dealt with throughout this paper. A central simplification we have made is that dispersal strategies, i.e. the dispersal kernel, are not age-dependent, although we assume overlapping generations. Maternal age-dependent dispersal has been analysed by Ronce et al. (1998) who provide theoretical and empirical evidence that such a strategy is evolutionarily advantageous, for both maternal and offspring control of dispersal. As we have discussed above the emerging bimodal dispersal kernel is a result of cost optimization in order to allow LDD and at the same time insures territorial inheritance. Yet, these two aspects are advantageous respectively early and late in the life of an individual. We hypothesize that age-dependent kernels would be fat-tailed in early life stages and more biased towards short-distance dispersal and the production of non-dispersing offspring later on in order to reduce (kin) competition but still allow territorial inheritance.

A further simplification is the uniformity and stability of the landscape we assume. Although space is continuous in our model, it is homogeneous and shows no habitat structure or turnover. As Hovestadt et al. (2001) predict fat-tailed dispersal kernels to emerge in autocorrelated landscapes, we are confident that the introduction of spatial structure would not alter our results fundamentally (see North et al. 2011, for a detailed treatment of the influence of habitat structure on dispersal distance). Of course, patch size would interact with the competition kernel and influence the evolving mean dispersal distance and the location of the dispersal kernel's maximum or second peak for bimodal kernels. Yet, as the introduction of suitable and non-suitable habitat basically leads to an increase in dispersal costs we hypothesize that spatial structure would only underline our results for both scenarios. Especially in scenarios with maternal investment the bimodality of the dispersal kernel should be more pronounced, provided that patches are large enough to support more than one individual. A bimodal kernel is highly advantageous in fragmented landscapes with patch turnover as well, since the fat tail and resulting LDD allows individuals to colonise distant and empty patches. At the same time the non- and short distance-dispersers emerging from the same kernel in the next generation guarantee a successful and sustained establishment (see also North et al. 2011).

Although the concept of a dispersal kernel is not new only little work has been done on the evolution of the shape of dispersal kernels. In contrast to previous work (Hovestadt et al. 2001; Rousset and Gandon 2002; Starrfelt and Kokko 2010) we have concentrated on two important aspects that have been ignored in this context up to now: (i) the effects of individual competition kernels in continuous space and (ii) maternal investment. We could show that including these two processes leads to novel results. We predict the emergence of heavily fat-tailed and bimodal dispersal kernels for sessile organism with overlapping generations.

4

Assortative mating counteracts the evolution of dispersal polymorphisms[1]

Contents

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[1] This chapter is published as: Fronhofer, E.A., Kubisch, A., Hovestadt, T. and Poethke, H.J. (2011) Assortative mating counteracts the evolution of dispersal polymorphisms Evolution 65: 2461–2469.

Abstract

Polymorphic dispersal strategies are found in many plant and animal species. An important question is how the genetic variation underlying such polymorphisms is maintained. Numerous mechanisms have been discussed, including kin competition or frequency-dependent selection.

In the context of sympatric speciation events genetic and phenotypic variation is often assumed to be preserved by assortative mating. Thus, recently, this has been advocated as a possible mechanism leading to the evolution of dispersal polymorphisms. Here, we examine the role of assortative mating for the evolution of trade-off driven dispersal polymorphisms by modelling univoltine insect species in a metapopulation. We show that assortative mating does not favour the evolution of polymorphisms. On the contrary, assortative mating favours the evolution of an intermediate dispersal type and a uni-modal distribution of traits within populations. As an alternative mechanism, dominance may explain the occurrence of two discrete morphs.

4.1 Introduction

Besides birth and death events emigration and immigration are the major processes that govern the dynamics of spatially structured populations. Therefore, dispersal behaviour is a key life-history attribute and its evolution is of central importance for ecology. Major advances in this field have been summarized recently by e.g. Bowler and Benton (2005) or Ronce (2007). In short, there are a number of selective forces that favour dispersal as for example kin competition (Hamilton and May 1977; Poethke et al. 2007), the avoidance of inbreeding (e.g. Bengtsson 1978; Ravigné et al. 2006) or habitat variability — either spatio-temporal (McPeek and Holt 1992) or demographic (Travis and Dytham 1998; Cadet et al. 2003). In the extreme case of local population extinctions dispersers may recolonize empty habitat patches (Comins et al. 1980; Roff 1994). Yet, dispersal may bear important physiological costs (e.g. Zera and Mole 1994). Furthermore, increased predation pressure during the migratory phase or the risk of not finding suitable habitat (e.g. Cody and Overton 1996) are some of the costs associated with dispersal. These forces lead to a reduction of dispersal.

A large number of theoretical studies are concerned with the prediction of one evolutionary stable dispersal rate (Gandon and Michalakis 1999; Poethke et al. 2003). Some models highlight the conditions necessary for a coexistence of more than one dispersal strategy (Leimar and Norberg 1997; Roff 1994; Holt and McPeek 1996; Doebeli and Ruxton 1997; Mathias et al. 2001; Parvinen 2002; Bonte et al. 2010). Such polymorphisms may be behavioural, phenotypic or genotypic. Behavioural polymorphisms can be found in any model and in many animal and plant species: only a fraction of individuals disperse while the others stay in their patch of origin. Polymorphisms may be phenotypic as in social insects or aphids (Itô 1989), for example. Finally, polymorphisms may be found at the genetic level (e.g. Bonte et al. 2010). Of course, any combination is possible. Here, we will focus on polymorphisms that arise at the genetic level and are expressed in the phenotype (by adaptations to the specific behaviour). Evidently, a behavioural response is the final result. In general, such dispersal polymorphisms can evolve when dispersal is costly, i.e. selection favours residents at the local population scale, while empty habitat patches guarantee a high fitness gain to individuals establishing new populations. Spatially and temporally varying environments may similarly lead to the evolution of polymorphisms (e.g. McPeek and Holt 1992; Parvinen 2002; Poethke et al. 2011).

Dispersal polymorphisms are known from a large variety of plant (Levin and Muller-Landau 2000) and insect taxa — e.g. the sand field cricket *Gryllus firmus* (Roff 1994; King and Roff 2010), the soapberry bug *Jadera haematoloma* (Winchell et al. 2000) or the silver-spotted skipper *Hesperia comma* (Hill et al. 1999). Individuals of such species differ in their dispersal abilities due to differences in e.g. wing size or load, flight muscles or fat reserves (Harrison 1980) — in most cases individuals of the macropterous morph also show a higher tendency to disperse (e.g. Roff and Fairbairn 1991)

A question of central importance is how variation can be maintained within a species or population and finally lead to the evolution of clearly distinct strategies. Some possible mechanisms have been summarized e.g. by Roff (1994) and comprise for example frequency-dependent selection (Cockerham et al. 1972; Clarke 1979). Furthermore, it has been shown theoretically (Roff 1994) and empirically for many species (Reznick 1985) that the evolution of such polymorphisms is often shaped by trade-offs between life-history parameters.

Trade-offs imply that although a specific investment of resources increases one component of fitness another component of fitness is reduced at the same time (Roff and Fairbairn 2007). In the above cited examples an increase in dispersal ability is correlated with a decrease in fertility (Zera and Denno 1997; Tanaka and Suzuki 1998; Roff 2002; Roff et al. 2002). It is widely accepted that trade-offs play an important role in shaping evolutionary trajectories. Yet, at least theoretically, it is less clear how life-history trade-offs and the evolution of polymorphisms are exactly connected (Roff and DeRose 2001; Roff and Fairbairn 2007).

In a laboratory study on the dimorphic planthopper *Prokelisia dolus* Langellotto et al. (2000) found evidence for assortative mating based on wing form. This mating pattern is seen as a requirement for evolutionary branching in sexually reproducing species (e.g. Doebeli 1996; Dieckmann et al. 1999) and is commonly found in many insects (Crespi 1989). In general, assortative mating is a mechanism that underlines and stabilizes differences especially in the context of sympatric speciation (Dieckmann et al. 1999; Doebeli and Dieckmann 2003; Gavrilets 2003) because it preserves genetic and phenotypic variation (Wright 1921).

Here, we are interested in the effects of assortative mating on the evolution of dispersal polymorphisms. In contrast to a majority of theoretical studies on dispersal evolution (for a discussion see Ronce 2007) we use a diploid system. We additionally construct an analogous haploid model in order to analyse the influence of the genetic system assumed (see also Parvinen and Metz 2008). As outlined above investment in dispersal ability reduces the amount of resources available for reproduction. As a logical consequence, we incorporate a trade-off between dispersal ability and fertility into our model (for recent examples of the few studies that do account for such trade-offs see Burton et al. 2010; Travis et al. 2010). Using an individual based simulation model, we will firstly screen the parameter space for regions with polymorphic dispersal strategies. Secondly, we hypothesize that assortative mating underlines and stabilizes trade-off driven dispersal polymorphisms and eventually expands regions with polymorphic strategies in parameter space. To our knowledge the connection between dispersal polymorphisms evolving due to fitness trade-offs and assortative mating has never been investigated theoretically in a diploid model before.

4.2 The Model

We use an individual based simulation approach (see e.g. Travis and Dytham 1999; Poethke and Hovestadt 2002; Kubisch et al. 2010), which can be thought to reasonably describe any annual univoltine insect living in a metapopulation. The focal organisms are diploid. An individual has two evolving loci, one coding for emigration probability ($0 \leq \bar{d} \leq 1$) and a second one for the relative investment in dispersal ability ($0 \leq \bar{\rho} \leq 1$). This investment involves a reduction in fertility which will be described in more detail below. Since both loci influence dispersal we assume genetic linkage between them, i.e. no recombination. Intuitively this is clear, since it makes no sense to trade (large) amounts of fertility for dispersal ability while being a non-dispersive individual and vice versa (for a formal analysis of the joint evolutionary dynamics of dispersal tendency and ability see Yukilevich 2005). We nevertheless tested this in preliminary simulations and could confirm our assumption: without linkage intermediate values for $\bar{d}$ and $\bar{\rho}$ evolved; polymorphisms were never found.

4.2.1 Genetics

As the modelled organisms are diploid we implemented maternally and paternally inherited alleles at both loci (d_1, d_2 and ρ_1, ρ_2). These can mutate with a fixed probability of $m_1 = 0.001$. If a mutation occurs, the allele values inherited from the parents are changed by adding a random value drawn from a uniform distribution ($0 \pm \Delta_m$, with $\Delta_m = 0.1$). Reflecting conditions are assumed at the lower and upper limits. This implementation was chosen in order to avoid an artificial fixation to extreme values (0 or 1). We tested our model with other mutation procedures (i.e. resetting values smaller than 0 and larger than 1 respectively to 0 and 1) and found no qualitative effect.

In order to check whether the mode of inheritance has any influence on our results we implemented (i) a linear relationship between geno- and phenotype, i.e. the individual emigration probability ($\bar{d}$) as well as the relative investment in dispersal ability ($\bar{\rho}$) are calculated as mean values from the two respective alleles and (ii) dominant/ recessive inheritance. In the latter case dominance (implemented as an extra locus x_1^d, x_2^d and x_1^ρ, $x_2^\rho \in \{0; 1\}$) is allowed to evolve for both alleles at all loci. If an allele is dominant ($x = 1$) and the other not ($x = 0$), the phenotype is determined uniquely by the value of the dominant allele. If both alleles were either dominant or recessive, we calculated the phenotype as the arithmetic mean (see Eq. 4.1).

$$\begin{aligned}\bar{d} &= \begin{cases}\frac{1}{2}(d_1+d_2) & \text{if} \quad x_1^d = x_2^d \\ x_1^d d_1 + x_2^d d_2 & \text{if} \quad x_1^d \neq x_2^d\end{cases} \\ \bar{\rho} &= \begin{cases}\frac{1}{2}(\rho_1+\rho_2) & \text{if} \quad x_1^\rho = x_2^\rho \\ x_1^\rho \rho_1 + x_2^\rho \rho_2 & \text{if} \quad x_1^\rho \neq x_2^\rho\end{cases}\end{aligned} \tag{4.1}$$

Mutation between the dominant and the recessive state was possible with a rate of $m_2 = 0.0001$. We assume this lower mutation rate, since the switch between dominance and recessivity has an important qualitative impact on the observed phenotypes, while the evolving life-history parameters (d and ρ) only change quantitatively in a restricted interval (Δ_m). In addition to these two diploid models we ran simulations with an analogous haploid (clonal) model.

4.2.2 Population structure and dynamics

We assumed a metapopulation with a total of 1000 habitat patches. We implemented global natal dispersal and random external patch extinctions that occurred with a probability ϵ. Locally, a Beverton-Holt model for logistic population growth was assumed (Beverton and Holt 1957). The patch specific mean number of offspring $R_{t,p}$ can then be calculated for every time step (t) as

$$R_{t,p} = \lambda_{t,p} \cdot \frac{1}{1 + aN_t} \tag{4.2}$$

with the susceptibility to crowding $a = \frac{\lambda_0 - 1}{K}$. The carrying capacity was set to $K = 100$ individuals for all patches.

Mean individual fecundity at the global scale is given by λ_0. Every patch is characterised by temporally variable environmental conditions. This has been incorporated into our model by drawing a patch-specific mean fecundity $\lambda_{t,p}$ from a log-normal distribution with mean λ_0 and standard deviation σ. σ thus determines the magnitude of (annual) environmental fluctuations in growth conditions. Such habitat variability is known to have important effects on dispersal strategies as increasing σ favours more dispersive individuals (reviewed e.g. in Bowler and Benton 2005). Heterogeneous landscapes are also assumed to favour evolutionary branching (e.g. McPeek and Holt 1992; Parvinen 2002).

4.2.3 The trade-off: fertility vs. dispersal ability

After mating with a randomly chosen male in its patch, every female produces a certain number of offspring drawn from a Poisson distribution with mean $R^I_{t,p}$, the mean individual number of offspring. $R^I_{t,p}$ is determined by the patch specific mean number of offspring ($R_{t,p}$) and the individual relative investment into dispersal ability ($\bar{\rho}$) of the female:

$$R^I_{t,p} = R_{t,p} \cdot (1 - \bar{\rho}). \tag{4.3}$$

Similar approaches have been taken by Burton et al. (2010) in their study of a three-trait trade-off between dispersal, reproduction and competitive ability during range expansion or by Travis et al. (2010) who model a trade-off between seed production and investment in inflorescence height which of course influences dispersal distance.
During dispersal emigrants die with the probability μ^I. The individual mortality risk depends on the landscape specific dispersal mortality (μ_0) and on the genetically determined amount of resources allocated to dispersal ability ($\bar{\rho}$): the more an individual invests into dispersal ability the lower its mortality risk becomes; yet, at the same time its fertility is reduced (see Eq. 4.3). An increase in dispersal ability, e.g. by accumulating more fat reserves, growing larger wings, or developing better flight muscles, is equivalent to reducing dispersal mortality (μ_I). We assume that the resulting individual mortality risk (μ^I) follows a negative exponential function

$$\mu^I = \mu_0 \cdot e^{-\gamma\bar{\rho}} \tag{4.4}$$

governed by γ, which determines the steepness of this function. Consequently, γ represents the payoff, i.e. the efficiency of investment into dispersal ability: if the payoff (γ) is small, large amounts of fertility would have to be traded for a comparatively small reduction in dispersal mortality and vice versa. To test the generality of our model we ran additional simulations with linear and sigmoid trade-off functions. However, the results presented below hold for all three types of trade-off functions tested.

4.2.4 Assortative mating

Assortative mating is implemented as follows: instead of choosing a random male from the local population for mating the females choose — with a certain probability (α) — a mate according to their euclidean distance in phenotype space. This was implemented as a weighted lottery. The parameter α is the proportion of females mating non-randomly and can be seen as the strength of assortative mating (O'Donald 1960). For female f in patch p the distance in phenotype space to male m is calculated as:

$$distance_{f,m} = \sqrt{(\bar{d}_f - \bar{d}_m)^2 + (\bar{\rho}_f - \bar{\rho}_m)^2} \tag{4.5}$$

with $\bar{d}$ and $\bar{\rho}$ being the phenotype of the individuals, i.e. incorporating dominance if evolved (see Eq. 4.1).

4.2.5 Simulations

The allele values of the two evolving loci (d_1, d_2 and ρ_1, ρ_1) were initialized with random values drawn from a uniform distribution between zero and one. In order to allow the system to reach an equilibrium state, simulations were run for 10000 generations. Typically, equilibrium was reached after a much shorter time span, i.e. within 2000 to 5000 time steps. For each parameter combination simulations were replicated 25 times. For an overview of the parameter space tested refer to Tab. 4.1.

Table 4.1: Model parameters and meanings with tested values.

parameter	values	significance
K	100	habitat capacity
σ	0, 0.5, 1, 1.5	environmental stochasticity
ϵ	0, 0.02, 0.04, ..., 0.2	random patch extinction probability
λ_0	2, 3, 4	fecundity
μ_0	0, 0.1, 0.2, ..., 1.0	landscape specific dispersal mortality
γ	0, 1, 2, ..., 20	payoff, i.e. efficiency of investment into dispersal ability
α	0, 0.05, 0.1, 0.25, 0.3, 1.0	strength of assortative mating
d	*evolving* $\in [0, 1]$	emigration probability
ρ	*evolving* $\in [0, 1]$	relative investment in dispersal ability
x	*evolving* $\in \{0; 1\}$	dominance ($x = 1$), recessivity ($x = 0$)
m_1	0.001	mutation rate for life-history traits
Δ_m	0.1	mutation width for m_1
m_2	0.0001	mutation rate for dominance

For the systematic analysis of large ranges of parameter space we used an index indicating the presence of dispersal polymorphisms: we computed Hartigan's Dip Test Statistic for Unimodality for the distribution of the emigration probability alleles (d). This statistic increases with increasing departure from unimodality (package "Diptest"; R Development Core Team 2010). Since the focal behaviour here is the reduction of dispersal mortality, i.e. investment in increased dispersal ability, the figures do not show the trait $\bar{\rho}$ but the relative reduction of dispersal mortality calculated as $1 - e^{-\gamma\bar{\rho}}$ (see Eq. 4.4).

4.3 Results

4.3.1 The evolution of dispersal polymorphisms

A clear dispersal polymorphism evolved for a wide variety of parameter combinations. Figure 4.1 A shows a typical example: while the alleles for dispersal propensity (d)

and ability (ρ) showed a bimodal distribution, a trimorphism evolved in phenotype space due to heterozygous individuals. Of central influence for the evolution of polymorphisms is the payoff (γ, Eq. 4.4), i.e. the efficiency of investing into dispersal ability. Depending on the other parameters, deviations from the monomorphic state could evolve for intermediate values of the payoff parameter (Fig. 4.2 A). Below $\gamma \leq 5$ (unprofitable and low payoff) a single dispersal phenotype evolved with low emigration probability ($\bar{d} < 0.4$ depending on the other parameters) and an accordingly small investment in dispersal ability ($\bar{\rho} \ll 0.05$). For the other extreme (ca. $\gamma > 18$; advantageous payoff) one single highly dispersive phenotype ($\bar{d} > 0.8$) evolved which invested heavily in dispersal ability ($\bar{\rho} > 0.15$). Another factor of considerable influence is the external extinction probability (ϵ). Stable polymorphisms emerged for intermediate values (Fig. 4.2 B).

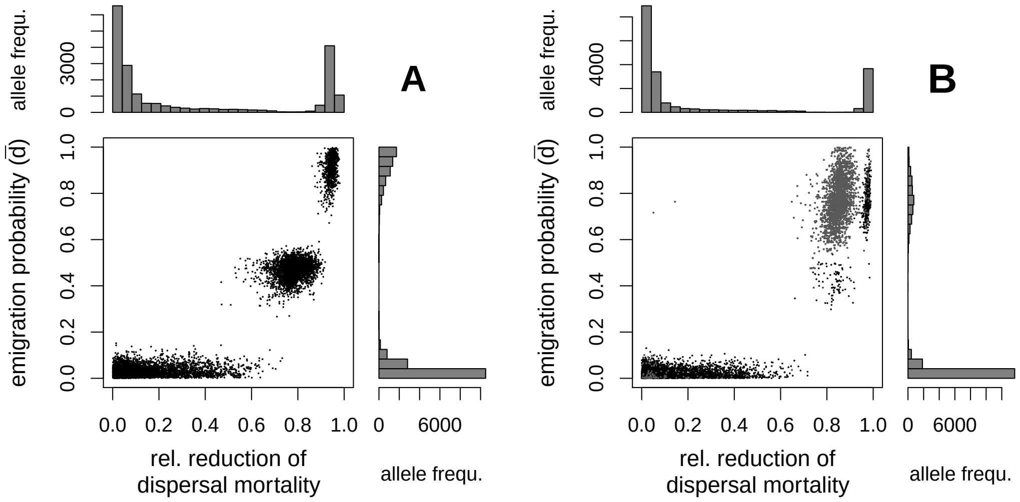

Figure 4.1: Evolution of dispersal polymorphisms under random mating ($\alpha = 0$). The scatter plots show phenotype space. Every point represents a diploid organism. The histograms show the allele distribution for both traits. Panel A shows results when we assumed intermediate inheritance (i.e. a linear relationship between geno- and phenotype): a clear polymorphism with homozygous dispersers and non-dispersers as well as an intermediate type (heterozygous individuals) evolved. For panel B dominance was allowed to evolve, which lead to a dimorphism in phenotype space. The grey points indicate heterozygous individuals for emigration probability with a dominant allele. Due to mutations at the dominance locus some heterozygous individuals still have an intermediate phenotype. Dominance only evolved for the emigration probability (d) and not for the locus determining the relative investment in dispersal ability (ρ).
Scatter plots and histograms are based on 10000 individuals randomly chosen from the last generation of 25 simulation repeats. Simulation parameters were : $\gamma = 12$, $\lambda_0 = 3$, $\sigma = 1.0$, $\mu_0 = 0.5$, $\epsilon = 0.05$.

Increasing dispersal mortality (μ_0) selected for polymorphic strategies (Fig. 4.2 A and B). A similar effect was found for environmental stochasticity (σ): more inter-patch variability led to polymorphisms even when the payoff was low (small values of γ). In general, fecundity (λ_0) had little influence on the evolution of dispersal dimorphisms. These findings are robust regardless of the mode of inheritance implemented: if we assumed a linear relationship between geno- and phenotype a phenotypic trimorphism evolved, while a clear bimodal distribution was found for both traits at the allele level (Fig. 4.1 A). A dominant/ recessive mode of inheritance did not alter the results fundamentally: dominance always evolved for emigration probability (d) and led to a clear dimorphism at the phenotype level (Fig. 4.1 B) while the underlying allele distribution did not change qualitatively. Nevertheless, note that the dispersal morph alleles became rarer. More exactly, dominance only evolved for alleles coding for high emigration probability while non-dispersive alleles evolved to be recessive. No dominance evolved for the relative investment in dispersal ability (ρ).

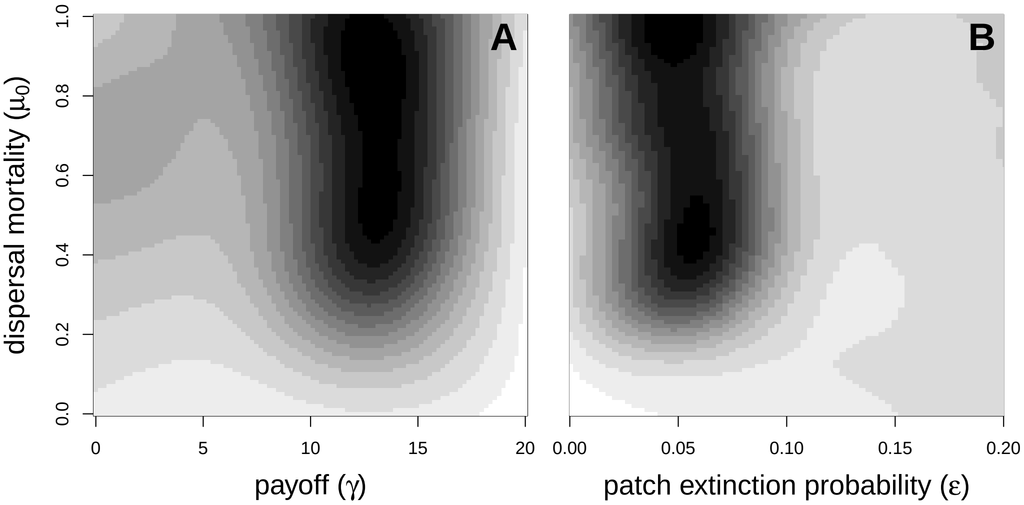

Figure 4.2: Evolution of dispersal polymorphisms under random mating ($\alpha = 0$) as a function of landscape specific dispersal mortality (μ_0) and (A) the payoff, i.e. the efficiency of investing in dispersal ability (γ) and (B) patch extinction probability (ϵ). As an index for the evolution of dispersal polymorphisms we used Hartigan's Dip Test Statistic for Unimodality. Darker colours indicate a stronger departure from unimodality (indication of polymorphism) in the distribution of the emigration probability (d). Note that the results are identical for the distribution of the relative investment in dispersal ability ρ. Each panel shows a thin plate spline regression of 650 simulation results each with three repeats. Fixed model parameters were: $\sigma = 1.0$ (A, B); $\lambda_0 = 3.0$ (A, B); $\epsilon = 0.05$ (A); and $\gamma = 12$ (B).

4.3.2 The role of assortative mating and ploidy

In contrast to our hypothesis and to existing suggestions (see introduction) assortative mating did not enhance the evolution of dispersal polymorphisms. On the contrary, with assortative mating only intermediate dispersal strategies evolved (Fig. 4.3 A). This result was obtained regardless of the mode of inheritance. In addition to this, we could show that if assortative mating was introduced to the system after a stable polymorphism had been allowed to evolve ($t > 5000$), the polymorphism vanished (not shown). Note that already a small tendency for assortative mating (α) leads to a complete homogenization of the metapopulation: if more than one fourth of all females mated assortatively ($\alpha > 0.25$) no dispersal polymorphism evolved in our simulations. Qualitatively we found the same result for the haploid (clonal) model (Fig. 4.3 B). Although we scanned the parameter space as for the diploid model (results not shown) we did not find polymorphic dispersal strategies (the parameter values tested are listed in Tab. 4.1).

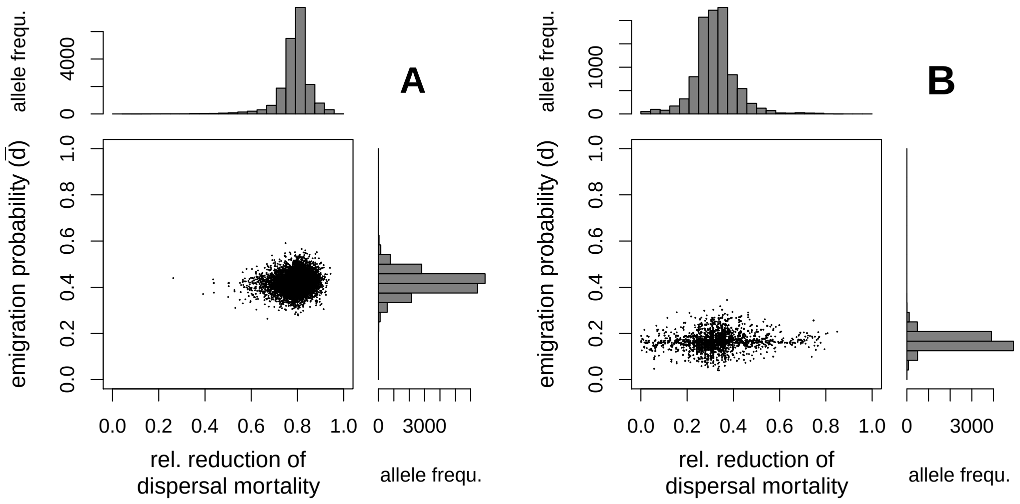

Figure 4.3: Evolution of dispersal strategies with assortative mating (panel A; $\alpha = 0.3$) and clonal reproduction (haploid individuals; panel B). No polymorphisms evolved under these assumptions. The scatter plot shows phenotype space. Every point represents a diploid organism after 10000 generations of evolution. Here, 10000 randomly chosen individuals from 25 simulation repeats are shown. The histograms visualize the allele distribution of both traits.
For panel A we assumed a linear relationship between geno- and phenotype. Note that the results are identical if dominance was assumed. Simulation parameters were : $\gamma = 12$, $\lambda_0 = 3$, $\sigma = 1.0$, $\mu_0 = 0.5$, $\epsilon = 0.05$.

4.4 Discussion

It is intuitively clear that investment into dispersal ability should only evolve when environmental conditions favour the evolution of a sufficiently high level of dispersal. Basically, three evolutionary relevant forces influence dispersal propensity: dispersal mortality (μ_0) selects against high emigration probabilities ($\bar{d}$) while random patch extinctions (ϵ) and environmental stochasticity (σ) have the opposite effect (Comins et al. 1980; Ronce et al. 2000; Poethke and Hovestadt 2002; Poethke et al. 2003). It is trivial that individuals will not invest into dispersal ability (low values for traits $\bar{d}$ and $\bar{\rho}$) when dispersal is not favoured (low values for ϵ and high values for μ_0), especially since the two loci governing these features are genetically linked. An equally monomorphic evolutionary stable strategy evolves when dispersal is highly advantageous (high values for ϵ and low values for μ_0). Individuals under such conditions will heavily invest into dispersal ability (high values for traits $\bar{d}$ and $\bar{\rho}$).

Of course, a prerequisite for substantial investments into dispersal ability is a sufficiently high efficiency of the investment, i.e. an advantageous payoff (γ). The steeper the trade-off function (Eq. 4.4) the smaller the costs — in terms of fertility — become to achieve a certain reduction in dispersal risk. This explains why low efficiency, i.e. a small payoff γ, favours monomorphic populations following a resident (or low-dispersal) strategy with no investment into dispersal ability. High efficiency (high values of γ) leads to monomorphic populations in which all individuals show relatively high emigration probabilities and large investment into dispersal ability.

For intermediate efficiencies (Fig. 4.2 A) the dispersive phenotype still profits from the advantages of dispersal e.g. reduced kin competition (Hamilton and May 1977; Poethke et al. 2007) or colonizing empty habitat patches (for reviews see Bowler and Benton 2005; Ronce 2007), while mitigating the associated costs of dispersal. By contrast, a non-dispersive phenotype benefits from higher fertility, i.e. such individuals have a growth advantage in direct competition with the dispersive morphs. This allows non-dispersers to invade locally any population of dispersers. Yet, since the persistence of local populations is limited by patch extinctions, a purely resident strategy cannot persist. Thus, in a haploid system neither strategy is evolutionarily stable (Fig. 4.3 B). However, in a diploid system with random mating heterozygotes with intermediate phenotypes are produced. This allows the resident haplotype (low values for d and ρ) to "hitch-hike" in heterozygous individuals together with the dispersive haplotype. Thus, it can persist even in unstable environments as long as there is a sufficiently high frequency of haplotypes for dispersive behaviour. It is immediately clear that here selection is frequency-dependent (Roff 1994) since a rising frequency of haplotypes for dispersiveness in the population increases the mobility as well as the advantage of the undispersive type in local competition.

At the same time this example of genetic "hitch-hiking" explains why our results indicate that assortative mating does not favour the evolution of polymorphic strategies but destabilizes polymorphisms once evolved (Fig. 4.3 A). Assortative mating in a population leads to a lack of heterozygotes and thus prevents non-dispersive haplotypes from hitch-hiking on heterozygous individuals together with dispersive ones. Consequently, an intermediate phenotype which in itself represents the optimal compromise between fertility and investment into dispersal ability will evolve under such circumstances.

Note that some models of speciation come to similar conclusions (for a review see e.g. Ritchie 2007). However, the underlying mechanisms are distinctly different: Kirkpatrick and Nuismer (2004) argue that a widely accepted key assumption of speciation models is that all individuals have equal reproductive success. Yet, obviously in nature rare phenotypes are penalized by assortative mating, since they are less likely to find a mate than very common phenotypes. Thus, assortative mating may counteract the evolution of polymorphic strategies. By contrast, in our model assortative mating penalizes the more frequent, non-dispersive haplotype.

As Parvinen and Metz (2008) note, the evolutionary stable dispersal rate in haploid and diploid models may be considerably different in quantitative and qualitative terms. For our model this is in part explained above. Note that the evolutionary stable emigration probability for the haploid model (Fig. 4.3 B) is considerably smaller than in the other simulations. This is due to the fact that the effective population size in the diploid model is considerably smaller than in the haploid case because we used the same values for carrying capacity ($K = 100$) while omitting the males. In the diploid model, especially with non-random mating, an important number of males will not be able to reproduce. Such an effect and its influence on the evolutionary stable dispersal rate has been quantified by Gros et al. (2009) for a different system of non-random mating (harem formation). Furthermore, the effective population size in the sexual system may be further diminished due to skewed sex-ratios after recolonization events. In general, such smaller population sizes select for higher dispersal rates (Travis and Dytham 1998).

The evolution of dominance in our simulations (Fig. 4.1 B) indicates that the intermediate (heterozygote) strategy is less fit than both extreme morphs (Pimm 1979; Udovic 1980). Dominance prevents the expression of the intermediate phenotype (van Dooren 1999) without destroying the polymorphism. Now the population consists of two distinct phenotypes. Obviously, dominance is an effective mechanism allowing the maintenance of alternative strategies. Note that it is always the allele for dispersiveness that becomes dominant. This is due to the fact that the undispersive genes need the dispersive type to reach new patches. As dominant alleles for the dispersive type are more “effective” in realizing dispersal, the dispersal morph alleles become rarer with dominance (Fig. 4.1 B). The same is true for the investment into dispersal ability. Since the relation between investment and dispersal mortality reduction is non-linear (Eq. 4.4), the heterozygotes achieve nearly the same relative reduction in dispersal mortality compared to homozygous dispersers (Fig. 4.1 B).

In their study on the wing dimorphic planthopper *Proklesia dolus* Langellotto et al. (2000) demonstrate that a trade-off between flight capability and reproduction exists in this species. Furthermore, the authors show that this trade-off can not only be found in females but also in males. In addition to these findings, the authors present some evidence for non-random mating: assortment seems to be based on wing form. Yet, the results obtained from single-choice preference experiments overall only suggest a trend. The authors nevertheless do conclude that individuals of *Proklesia dolus* mate assortatively.

Our model does not support the hypothesis that assortative mating plays a role in the establishment or stabilization of trade-off driven dispersal polymorphisms. Therefore, either Langellotto et al. (2000) overrated the significance of their results or the proportion of assortatively mating individuals in the examined population was very small. Our model would support the latter interpretation since it predicts the evolution of dispersal polymorphisms as long as less than ca. 25% of the individuals mate assortatively ($\alpha < 0.25$).

In summary, our results suggest that, in contrast to dominance, assortative mating is not a mechanism relevant for the maintenance of dispersal polymorphisms. Furthermore, we were able to underline the importance of frequency-dependent selection for the evolution of dispersal polymorphisms due to fitness trade-offs. In our model the local patch extinction rate is a key component favouring dispersal polymorphisms. We thus confirm the significance of turnover due to local extinctions (Roff 1994; King and Roff 2010).

Our findings underline the importance of carefully choosing an appropriate relationship between genotype and phenotype when modelling dispersal evolution. A majority of theoretical studies assume a simple clonal form of reproduction (e.g. Doebeli and Ruxton 1997; Mathias et al. 2001; Bonte et al. 2010). Exceptions can be found when sex-specific strategies are investigated (e.g. Perrin and Mazalov 2000; Bonte et al. 2009). Here, we demonstrate that such assumptions may strongly alter model predictions, quantitatively as well as qualitatively (see also Parvinen and Metz 2008).

Finally, our work leads to testable hypotheses. i) The evolution of trade-off driven dispersal polymorphisms is limited to spatio-temporally variable metapopulations (Hanski 1999) or to expanding ranges (Phillips et al. 2010). In the latter case spatial selection has the same consequences as spatio-temporal variation, i.e. patch turnover, in equilibrium metapopulations (Duckworth 2008). ii) Trade-off driven dispersal polymorphisms should only be found in species without (strong) assortative mating. In general, dimorphisms at the phenotype level can be favoured by the evolution of dominance.

5

Picky hitch-hikers: vector choice leads to directed dispersal and fat-tailed kernels in a passively dispersing mite[1]

Contents

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[1] This chapter is submitted as: Fronhofer, E.A., Sperr, E.B., Kreis, A., Ayasse, M., Poethke, H.J. and Tschapka, M. Picky hitch-hikers: vector choice leads to directed dispersal and fat-tailed kernels in a passively dispersing mite. Oikos.

Abstract

Dispersal is a central life-history trait for most animals and plants: it allows to colonize new habitats, escape from competition or avoid inbreeding. Yet, not all species are mobile enough to perform sufficient dispersal. Such passive dispersers may use more mobile animals as dispersal vectors. If multiple potential vectors are available an active choice can allow to optimize the dispersal process and to determine the distribution of dispersal distances, i.e. an optimal dispersal kernel.

We explore dispersal and vector choice in the neotropical flower mite *Spadiseius calyptrogynae* using a dual approach which combines experiments and an individual-based simulation model. *S. calyptrogynae* is found in lowland rainforests in Costa Rica. It inhabits inflorescences of the understorey palm *Calyptrogyne ghiesbreghtiana* and is phoretic on a number of flower visitors including bats, beetles and stingless bees. We hypothesised that the mites should optimise their dispersal kernel by actively choosing a specific mix of potential phoretic vectors.

In a simple olfactometer setup we showed that the flower mites do indeed discriminate between potential vectors. Subsequently we used an individual-based model to analyse the evolutionary forces responsible for the observed patterns of vector choice. The mites combine vectors exhibiting long-distance dispersal with those allowing for more localized dispersal. This results in a fat-tailed dispersal kernel that guarantees the occasional colonization of new host plant patches (long distance) while optimizing the exploitation of clumped resources (local dispersal). Additionally, kin competition results in a preference for small vectors that transport only few individuals at a time. At the same time, these vectors lead to directed dispersal towards suitable habitat, which increases the stability of this very specialized interaction. Our findings can be applied to other phoretic systems but also to vector-based seed dispersal, for example.

5.1 Introduction

Dispersal is a central life-history trait for all animal and plant species: emigration and immigration are the only processes besides birth and death events that influence population dynamics. Many of the evolutionary forces driving emigration are quite well understood, at least from a theoretical point of view (for reviews see Bowler and Benton 2005; Ronce 2007). On the one hand, the avoidance of kin competition, for example, is an important factor selecting for dispersal (Hamilton and May 1977). Besides this, habitat variability in space and time (McPeek and Holt 1992), demographic fluctuations (Travis and Dytham 1998; Cadet et al. 2003) and local extinctions (Comins et al. 1980; Roff 1994) also favour increased dispersal rates. On the other hand, dispersal may be a very costly behaviour: in addition to increased predation risk during transition and physiological costs (i.e. energy spent during dispersal, investment in movement and flight apparatus; see e.g. Zera and Mole 1994) dispersers may not find suitable habitats and perish (Cody and Overton 1996). Dispersing individuals may also pay opportunity costs which are, for example, due to maladaptation to new habitat conditions or loss of social rank (for a recent review see Bonte et al. 2012). As a consequence, these factors select against dispersal.

Particularly for species that inhabit ephemeral habitats, such as small ponds, river banks prone to flooding, dung pats, carcasses or — as in this study — flowers, dispersal is necessary to guarantee the (long-term) persistence of the lineage. Individuals have to leave their habitat and disperse to new resources before the habitat completely degenerates and the local populations goes extinct. The resulting evolutionary dynamics of dispersal may be highly complex (see e.g. Travis and Dytham 1999). If such systems show high degrees of specialization — as in this study — successful dispersal may become an important challenge. Depending on the system of interest, dispersal may happen through space or through time by dormant stages. Since our study species, *Spadiseius calyptrogynae*, does not exhibit any dormant stages, we will focus on dispersal through space.

As dispersal is vital for species living in ephemeral habitats it is surprising to find highly non-mobile species specialized to such environments, such as — among many other examples — mites living in patchily distributed flowers (Colwell 1973; Tschapka and Cunningham 2004; Guerra et al. 2012), nematodes living in tropical figs (Krishnan et al. 2010) or annelids and ostracods found in bromeliads (Lopez et al. 2005). Individuals of such non-mobile species have evolved to use other more mobile taxa as means of transportation. This behaviour, known as phoresy, allows non-mobile species to persist in unstable spatially structured populations (Colwell 1985; Houck and OConnor 1991; Soroker et al. 2003; Niogret et al. 2006).

In such harsh but predictable environments — and especially if the individuals have to rely on other species for dispersal — one can assume that the use of information is highly adaptive since it may confer a substantial evolutionary advantage over a random strategy (Ronce 2007). This is especially relevant if the focal species is specialized to a specific habitat, i.e. plant species. It has for example been shown that mites inhabiting dung pats (Niogret et al. 2004, 2006), broad mites (Soroker et al. 2003) and fig nematodes (Krishnan et al. 2010) use chemical signals to locate potential phoretic hosts and to discriminate between alternatives.

Here, we will analyse dispersal and vector choice by the neotropical bat flower mite *Spadiseius calyptrogynae* (Acari: Mesostigmata; Lindquist and Moraza 2008). This species is particularly interesting because it shows highly specialized habitat requirements and is only found on a single understorey palm species (*Calyptrogyne ghiesbreghtiana*) in the tropical lowland rainforest of Costa Rica (Tschapka and Cunningham 2004). The palm flowers year round and often occurs in swamps. Since these occur in patches the palm shows a clumped distribution. Inflorescences are protandrous, i.e. they first develop male flowers that are followed by females flowers, over an inforescence lifespan of ca. 9–11 days. Only one inflorescence flowers at any given time per palm (Cunningham 1995), which forces the flower mites to change their habitat at least once and possibly up to 2–3 times during their lifetime. For detailed studies on the biology of *Calyptrogyne ghiesbreghtiana* see Cunningham (1995, 1996, 1997a,b, 2000).

The flower visitors are on the contrary not specialized to the palm species. The inflorescences are visited by bats (*Artibeus watsoni/phaeotis*), one stingless bee species (*Trigona fulviventris*) and two beetles (*Chasmodia collaris* — Scarabeidae, *Cholus curialis* — Curculionidae). The bats are frugivorous (Lopez and Vaughan 2007) and the stingless bee is a generalist and visits a large number of flowering plants (Janzen 1983). Very little is known about the coleopterans and we thus cannot completely exclude that these are specialized on *Calptrogynae ghiesbreghtiana* although personal observations indicate a more generalist behaviour (Sperr pers. obs.).

In addition to variation in the quality of their interaction with the host palm (mutualistic pollination to floral herbivory), theses four flower visitors differ markedly in terms of (1) visitation pattern, (2) size, i.e. transportation capacity and (3) mobility, i.e. the dispersal kernel. We will now detail these differences (for a summary see table 1) and forward some hypotheses how these may influence the quality of the dispersal vectors from the point of view of phoretic mites. The following paragraphs allow the reader to become more familiar with the system under study. Note that the data referred to in the following paragraphs are taken from Sperr and Tschapka (in prep.) if not indicated otherwise.

(1) The most frequent visitors to the palm are the stringless bees (*Trigona fulviventris*)

with approximately 30–35 visits per day (the numbers were corrected for duration since too short visits do not allow a mite to climb onto a potential phoretic vector). The second most common visitors are bats (*Artibeus* spp.; the data come from video recordings and thus the two visiting species *A. watsoni* and *A. phaeotis* cannot be distinguished; even in the field this is problematic; see Timm and LaVal 1998) with ca. 2–3 visits per night. Finally, the coleopterans are rare visitors with respectively 1 and less than 1 visit per day for *Cholus curialis* (Curculionidae) and *Chasmodia collaris* (Scarabeidae). In addition *Trigona fulviventris* and *Cholus curialis* show a marked preference for male flowers, as they feed on pollen.

(2) In terms of transportation capacity, the bat species, *Artibeus* spp., may carry a large number of mites on their wings (up to 360 individuals) while the scarabid beetle, *Chasmodia collaris*, has a slightly lower transportation capacity, the weevil *Cholus curialis* was found to carry no more than 50 mites and the maximal mite load for *Trigona fulviventris* was 7 mites.

(3) The dispersal distances covered by *Artibeus* spp. can be estimated from their home range area that covers between 3 and 4 hectares (Chaverri et al. 2007). This is comparable in size to the territory of a *Trigona fulviventris* colony (ca. 180 m in diameter; see Janzen 1983). *Cholus curialis* were found be very philopatric and leave a *Calyptrogyne* stand only very rarely while *Chasmodia collaris* exhibits long-distance movement of up to 800 m in a few days.

From this short overview of the system's natural history we forward the following hypotheses: (1) As dispersal is obligate and very frequent, the mites should either rely on very frequent visitors — such as *Trigona fulviventris* and *Artibeus* spp. — or not discriminate between phoretic hosts at all. (2) Mites should rely on small vectors — such as *Trigona fulviventris* or *Cholus curialis* — in order to avoid inbreeding (Bengtsson 1978; Ravigné et al. 2006) and minimize kin competition (Hamilton and May 1977; Poethke et al. 2007). Of course, group dispersal may be advantageous to overcome Allee effects (for a summary see Courchamp et al. 2008) and mites could avoid kin competition and inbreeding by disembarking on different subsequently visited palms. Yet, depending on the revisitation probability, such a behaviour could be extremely costly. (3) Directed dispersal towards early stage inflorescences should be evolutionarily advantageous. Since dispersal is costly (Bonte et al. 2012) the phoretic mites should be selected to minimize the number of dispersal events which would favour *Trigona fulviventris* and *Cholus curialis*. These vectors visit inflorescences early after the onset of flowering, i.e. during the male flowering phase (*Calyptrogyne ghiesbreghtiana* is protandrous). Even if females lay eggs multiple times on different inflorescences, an early stage inflorescence facilitates the successful development of its offspring. (4) In terms of dispersal distances we hypothesise that the phoretic mites should show a preference for vectors with intermediate dispersal distances — such as *Artibeus* spp. — which would allow the mites do disperse within host plant patches but also to occasionally colonize new patches.

We investigate the preferences exhibited by *Spadiseius calyptrogynae* in dual-choice and cafeteria olfactometer setups. In addition, we develop an individual-based model that includes the necessary system-specific features (for other approaches combining theoretical and empirical work see e.g. Ronce et al. 1998; Baiser et al. in press). This allows us to revisit our hypotheses, to test whether we have included all critical assumptions that lead to the system-specific behaviour and to analyse the effects of these assumptions. This study is the first to analyse insect cuticular components and volatiles isolated from bat fur as potential cues which enable informed phoretic dispersal decisions in flower mites and to combine this with a formal individual-based model to explore evolutionarily stable phoretic dispersal strategies.

In more general terms this study allows us to test whether theory developed for more classical active and passive dispersal modes can also be applied to phoretic dispersal. Phoretic systems are by far more complex and selective pressures less clear since emigration decisions define the subsequent dispersal phases, i.e. transition and immigration.

5.2 Material and Methods

5.2.1 Study site

The study was conducted from March to April 2012 at La Selva Biological Station, a nature reserve located at the confluence of the rivers Puerto Viejo and Sarapiquí in the north-eastern Caribbean lowland rainforest of Costa Rica (10°26' N, 83°59' W). The station receives roughly 4000 mm of precipitation per year with on average more than 100 mm per month. Seasonality is not very pronounced, a period of less rainfall occurs from February to April (Sanford et al. 1994).

To guarantee the most natural environmental conditions while keeping a controlled experimental setting, the experiments were performed in the ambient laboratory of the field station between 19:00 h and 06:00 h. This time frame was chosen based on the study species' and its phoretic vectors' natural activity peaks.

5.2.2 Organisms

Spadiseius calyptrogynae were kept on collected *Calyptrogyne ghiesbreghtiana* inflorescences in the ambient laboratory. Experimental individuals were randomly collected from the inflorescence.

For extraction of cuticular components and other scent cues *Chasmodia collaris* (two individuals), *Cholus curialis* (four individuals) and *Trigona fulviventris* (10 individuals) were caught directly on *C. ghiesbreghtiana* inflorescences using an insect net. Bats (*Artibeus watsoni* or *A. phaeotis*, two individuals; *Glossophaga* sp., probably *G. commissarisi*, one individual) were captured with mist nets (mesh size 16 mm, 6 m x 2.5 m, Vohwinkel, Germany) set in front of flowering *C. ghiesbreghtiana.* Species were identified using the key by Timm and LaVal (1998).

5.2.3 Experiments

All choice tests followed the same design. Glass Petri dishes (diameter: 50 mm) were divided into four sectors of equal size. Identical scent extracts (treatments) were applied to diagonally opposite sectors. Experiments always started 15 min. after extract application in order to guarantee a solvent-free surface. Single mites were placed in the center of the Petri dish using a fine artist brush. The time a mite spent in a specific sector was recorded for 180 sec. or until it left the experimental arena. Petri dishes and tweezers were cleaned with acetone, hexane and 90% ethanol before use. Every 10 consecutive tests the Petri dish was cleaned and new extracts were used. Previous experiments indicate that the results are not biased by this protocol. We did not record any evidence that scents decay during this time or that mites produce scent tracks.

5.2.4 Scent collection and dual-choice tests

In order to determine whether *S. calyptrogynae* use olfactory cues during phoretic vector choice, extracts of two flower visitors were tested in the above described experimental setup against each other. Individual of *C. collaris*, *T. fulviventris* and *C. curialis* were extracted in 2 ml of hexane for 20 sec. after having been frozen (−20°C for 3 days Niogret et al. 2006). Before extraction we made sure to remove all traces of pollen, mites or other particles from the insects. In addition, ca. 10 mg of fur (2 cm^2 from the back of the animals with clean scissors) was collected from *Artibeus* sp. and *Glossophaga* sp. as a control and extracted for 48 h (room temperature, darkness) in 2 ml hexane (Ghanem 2008). Extracts were stored at -20°C until used.

Glossophaga sp. fur extract is used as a control. Individuals of this species do visit *C. ghisbreghtiana* (Tschapka 2003), yet their hovering flight style (these bats are actually nectarivorous) prevents prolonged body contact with the inflorescences which does not allow mites to use this species as a phoretic vector (Tschapka and Cunningham 2004). In order to make the volatile concentration in extracts comparable to each other, the concentrations were normalized to the surface of the vectors (mean values from all sampled individuals; surface estimated as an ellipsoid; *Chasmodia collaris*: 5.9 cm^2, *Cholus curialis*: 1.0 cm^2, *Trigona fulviventris*: 0.4 cm^2, bats: 2 cm^2 from the back of

the animals). We tested the effect of this normalization by running additional cafeteria experiments (see below) with a two-fold increased concentration of *Artibeus* sp. extract and found no qualitative influence on our results (results not shown).
30 μl of each normalized extract was directly applied to opposing Petri dish sectors and tested against the same amount of extract from an other vector (or control). As described above, the time each mite (for all dual-choice experiments: $N = 50$ mites; except when explicitly indicated otherwise) spent in a specific sector was recorded for 3 min. or until it left the experimental arena.

5.2.5 Cafeteria experiment

These dual-choice experiments were supplemented by cafeteria experiments in which normalized extracts of all four vectors (*Chasmodia collaris*, *Cholus curialis*, *Trigona fulviventris* and *Artibeus* sp.) were tested simultaneously against each other, which mimics a more complex environment. The experiments were performed as described above with $N = 100$ mites.

5.2.6 Statistical methods

The statistical analysis for all choice experiments (dual-choice and cafeteria) was performed using generalized linear mixed models (GLMM; "glmmPQL" function of package "MASS" version 7.3-19; R 2.15.1). For the dual-choice tests the time a mite spent in sectors containing the same extract (of the 4 sectors 2 contained the same extract) was added. We implemented the extract and mite instar (categories: larvae, protonymphs, deutonymphs, males or females; see Lindquist and Moraza 2008) as fixed effects and the individuals as random effects in order to account for the two (four) values obtained per mite in the dual-choice (cafeteria) experiments. If necessary the data were transformed to allow a Gaussian error distribution. If this was not possible we chose a "Tweedie" GLMM (package "tweedie" version 2.1.1; R 2.15.1; see also Smyth and Verbyla 1999). This error distribution is a compound Poisson distribution and allows a mass of values at zero and continuous non-negative real numbers, as is the case for our time measurements. For the cafeteria experiment we ran an additional Tukey post-hoc test (function "glht" of the package "multcomp" version 1.2-12).

5.2.7 Individual-based simulation model

In order to derive evolutionarily stable phoretic dispersal strategies for the system under investigation we use a well established individual-based simulation approach (see e.g. Travis and Dytham 1999; Poethke and Hovestadt 2002; Fronhofer et al. 2011a, 2012). Such models can be reasonably well applied to a large number of arthropod species.

Note that individual-based simulations include the effects of kin competition by default (Poethke et al. 2007). Of course, some system-specific features were introduced and will be described in detail below (for a summary of parameters see table 5.1).

Our spatially explicit model is grid-based and uses a fractal landscape (generated in R with package "ecomodtools" version 0.1-1; see Chipperfield et al. 2011) which allows us to control the autocorrelation (Hurst index; standard $H = 0.25$; here and in the following we will indicate standard parameter values in brackets. To test the influence of these specific parameter values we ran a sensitivity analysis; see Appendix table 5.3) and the proportion of suitable habitat (standard: $p_H = 0.5$). Decreasing Hurst indices indicate more fragmented landscapes. The grid (1024 cells) is wrapped around a torus in order to simulate an infinite world.

One cell represents ca. 10 x 10 m of tropical lowland rainforest. For simplicity we assume that such a cell, if suitable, contains one flowering individual of the palm *Calyptrogyne ghiesbreghtiana* at any time. Note that this will not always be the same individual, but subsequently different palms. One grid cell thus hosts one local population of the flower mites *Spadiseius calyptrogynae*. We assume a local carrying capacity of $K = 100$ mites and a maximal patch age of $t_{max} = 3$ generations after which the local population goes extinct deterministically. This is a realistic parametrisation if we assume a generation time of 3–4 days (pers. obs.). The patch may be recolonized in the next time step.

Our model is semi-continuous which means that we assume discrete, non-overlapping generations, while iterating the dispersal step which approximates continuous time. This allows us to balance technical constraints (e.g. simulation time) while analysing the process of interest, i.e. phoretic dispersal, in detail (see below). For simplicity we implement a clonal model and assume logistic population growth in local populations (Beverton and Holt 1957). The mean number of offspring a female mite produces per generation is calculated as:

$$\lambda = \lambda_0 \cdot \frac{1}{1 + aN_t} \tag{5.1}$$

with $\lambda_0 = 4$ as fecundity, N_t as the actual population size and the susceptibility to crowding $a = (\lambda_0 - 1)/K$. The realized number of offspring is then drawn from a Poisson distribution with mean λ.

Every offspring inherits from its parent a vector-valued trait which codes for the genetically fixed preferences for the four phoretic vectors, i.e. bats (*Artibeus* spp.), bees (*Trigona fulviventris*), and the two coleopterans (*Chasmodia collaris* and *Cholus curialis*). These four preferences (real numbers between 0 and 1) are subject to evolution and we therefore assume that these preferences may mutate. Mutations occur rarely (mutation rate $m = 0.001$). If such a mutation occurs the preference values inherited

Table 5.1: System summary (data from Sperr and Tschapka in prep.) and model parameters.

phoretic vector	**visitation rate** (per day)		**dispersal distance** (mean, cells)		**dispersal mortality**		**vector capacity**		**patch preference**
Artibeus sp.	high	3	intermediate	5	intermediate	0.5	very high	75	none
T. fulviventris	very high	35	intermediate	4	intermediate	0.5	very low	5	early
C. collaris	low	1	high	10	low	0.4	high	50	none
C. curialis	intermediate	2	low	1	high	0.6	low	10	early

are changed by adding a random number drawn from a uniform distribution ($0 \pm \Delta m$, with $\Delta m = 0.2$). Since the values are limited between zero and 1 we assume reflecting boundary conditions.

For the sake of simplicity, and because exact information about the life-history of the flower mite *Spadiseius calyptrogynae* is still lacking, we assume natal dispersal, i.e. only one dispersal event before reproduction. As stated above, the dispersal step is simulated in continuous time (see e.g. Allen and Dytham 2009). The dispersal procedure is event-based with 150 iterations per patch and generation. An event is a visitation by a certain flower visitor and happens for every suitable habitat patch (inflorescence) according to visitation probabilities estimated from flower visitation data ($p(Artibeus) = 0.07$; $p(Chasmodia) = 0.02$; $p(Cholus) = 0.04$; $p(Trigona) = 0.7$; these values are calculated from table 5.1 and take into account the number of iterations and generation time). After the visitation event has been determined all mites may decide to use this phoretic vector or not, according to their individual preferences (see above). If the number of potential dispersers is greater than the phoretic vector's capacity ($K(Artibeus) = 75$; $K(Chasmodia) = 50$; $K(Cholus) = 10$; $K(Trigona) = 5$) a subset of dispersers is chosen randomly.

For every phoretic vector a dispersal distance is drawn from a skewed dispersal kernel with probability density $P(d) = \alpha^2 d e^{-\alpha d}$ and mean $M = 2/\alpha$ following Gros et al. (2006). Note that we tested other kernel shapes (e.g. negative-exponential) and found that our results were not altered qualitatively. Every vector is characterized by a specific mean dispersal distance which reflects data from field observations (see Introduction and table 5.1) relative to the underlying landscape ($M(Artibeus) = 5$; $M(Chasmodia) = 10$; $M(Cholus) = 1$; $M(Trigona) = 4$). As we have to fit the resulting dispersal distances to the underlying grid, we assume area-to-area dispersal.

In order to incorporate the characteristic preference for early stage inflorescences (i.e. male, depletion of pollen) by *Cholus curialis* and *Trigona fulviventris* we implemented a second, informed dispersal step. After arriving in the target patch defined by the dispersal kernel, vectors may relocate to one of the 8 nearest neighbours of the target cell. In order to avoid strong artefacts all vectors prefer suitable over non-suitable patches, i.e. *Calyptrogyne* over non-*Calyptrogyne* patches. Yet, *Cholus curialis* and *Trigona fulviventris* will relocate deterministically to the youngest patch (equivalent to male flowering phase) if suitable cells are encountered. If more than one patch has the same age, the target is chosen randomly amongst those.

In addition, phoretic vectors may not revisit any conspecific plant, which corresponds e.g. to a return to the bat roost or bee colony or to some other activity which does not include visiting a new plant. This results in an additional mortality term for the phoretic mites ($\mu(Artibeus) = 0.5$; $\mu(Chasmodia) = 0.4$; $\mu(Cholus) = 0.6$;

$\mu(Trigona) = 0.5$). These parameters are the only ones that we cannot directly estimate from field data. Since *Artibeus* spp. and *Trigona fulviventris* are not specialized pollinators to *C. ghiesbreghtiana* (although the bats are the main pollinators; see e.g. Tschapka 2003) we assume that the revisitation probabilities are low and thus the mortality term is high. Visitation patterns of *Chasmodia collaris* and *Cholus curialis* remain unknown. From personal observations (Sperr and Fronhofer pers. obs.) we estimate *Chasmodia collaris* to revisit *Calyptrogyne ghiesbreghtiana* more often than *Cholus curialis*. The influence of changing these values is analysed in the Appendix (sensitivity analysis; table 5.3). Note that this mortality term greatly influences the variance of a phoretic dispersal event, since all phoretic mites on a vector are prone to die simultaneously.

Simulations were run for 3000 generations in order to allow the system to reach equilibrium. The results presented below are mean values over 25 replicate simulation runs. For the sensitivity analysis we used 10 replicates for every tested parameter combination.

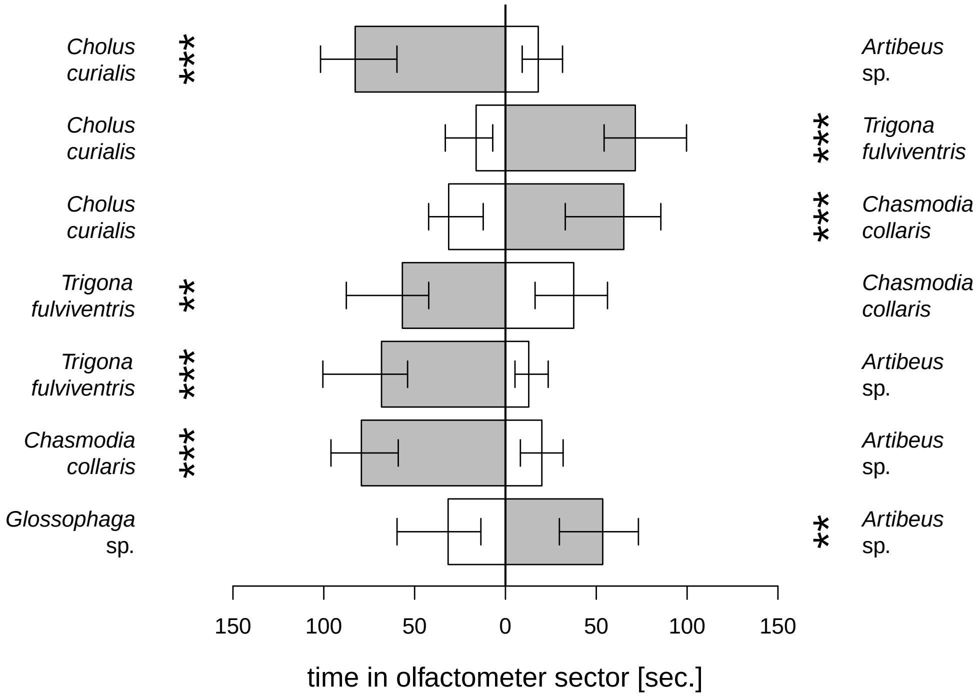

Figure 5.1: Dual-choice tests. Vector extracts (see plot margins) were tested in a basic olfactometer setup against each other. Bars show the time mites spent in the corresponding sectors (median, 25% and 75% percentiles for $N = 50$ mites in each experiment). See text for the statistical analysis (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

5.3 Results

5.3.1 Dual-choice tests

The results of our olfactometer dual-choice experiments show that *Spadiseius calyptrogynae* does indeed discriminate between phoretic vectors using olfactory cues (figure 5.1). *Artibeus* sp. scent was preferred over fur extract of the bat *Glossophaga* sp. (GLMM: $N = 50$; $t = -2.98$; $p = 0.0045$). In all experiments mite instar was found to have no significant effect (results not shown). *Cholus curialis* cuticular extract was significantly preferred over *Artibeus* sp. (GLMM: $N = 50$; $t = 11.94$; $p < 0.001$). *Chasmodia collaris* cuticular extract was significantly preferred over *Artibeus* sp. (GLMM: $N = 50$; $t = 12.7$; $p < 0.001$) and over *Cholus curialis* (GLMM: $N = 50$; $t = -4.53$; $p < 0.001$), but not over *Trigona fulviventris* (GLMM: $N = 50$; $t = 3.01$; $p = 0.004$). *Trigona fulviventris* cuticular extract was significantly preferred over all other tested extracts, i.e *Artibeus* sp. (GLMM: $N = 50$; $t = 8.3$; $p < 0.001$) and *Cholus curialis* (GLMM: $N = 50$; $t = 9.33$; $p < 0.001$).

5.3.2 Cafeteria experiment

We found the same pattern in our cafeteria experiment (figure 5.2 A) indicating that cuticular extracts of *Trigona fulviventris* are preferred over all other choices (Tukey's test; *T. fulviventris* vs. *Artibeus* sp.: $z = 7.74$; $p < 0.001$; *T. fulviventris* vs. *C. collaris*: $z = 3.27$; $p = 0.005$; *T. fulviventris* vs. *C. curialis*: $z = 6.97$; $p < 0.001$) while *Chasmodia collaris* fares better than the two remaining extracts (Tukey's test; *C. collaris* vs. *Artibeus* sp.: $z = 5.14$; $p < 0.001$; *C. collaris* vs. *C. curialis*: $z = -4.13$; $p < 0.001$). In the cafeteria experiment the mites did not differ significantly in their choice of extracts of *Artibeus* sp. and *Cholus curialis* (Tukey's test: $z = 1.19$; $p = 0.63$).

5.3.3 Individual-based simulation model

The individual-based model described above and parametrized as detailed (table 5.1) fits the empirical data remarkably well (compare figures 5.2 A and 5.2 B). Figure 5.2 B shows the evolutionarily stable phoretic vector preferences. In general, all individuals have a pronounced preference for *Trigona fulviventris* as a phoretic vector. Some mites also show a lower but still substantial preference for *Chasmodia collaris* and *Cholus curialis*. A remarkable pattern is the important variance exhibited in the preferences for *Chasmodia collaris* and *Cholus curialis*. Upon closer investigation (figure 5.3) we found that the preferences were distributed multimodally. Note that this occurs across simulations and not within. Figure 5.3 shows two axes of phenotype space. The two remaining axes can be ignored since all individuals exhibit uniformly low preferences

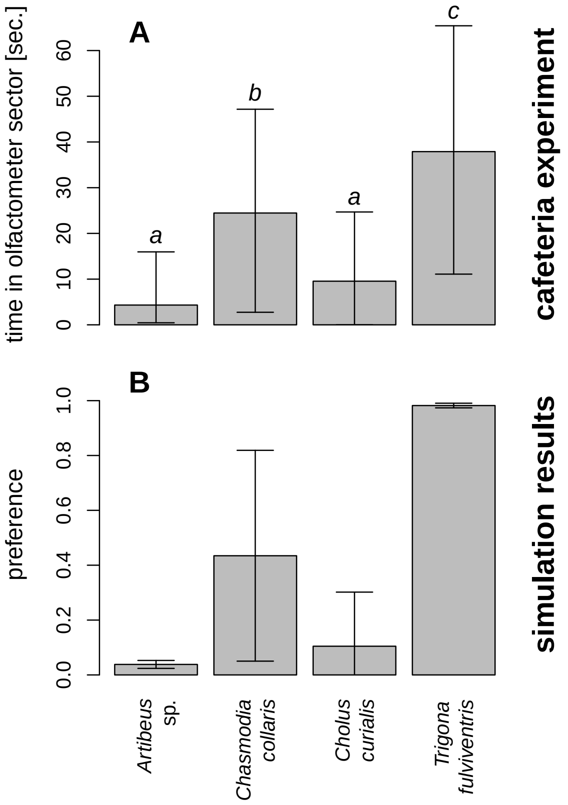

Figure 5.2: Cafeteria experiment and simulation model results. Figure A shows the results of the cafeteria experiment which is analogous to the dual-choice test with the difference that four vector extracts are tested against each other simultaneously ($N = 100$ mites). The letters indicate significantly different values (Tukey's test after GLMM; see text for results). Bars represent the median with the 25% and 75% percentiles as error bars. Figure B shows results from the individual-based simulation. The values depicted are mean preferences ($\pm s.d.$) for the different vectors. Note the corresponding variances between figures A and B.

for *Artibeus* sp. and high preferences for *Trigona fulviventris.* While some individuals rely completely on the *Trigona* bees for dispersal (individuals in the lower left part of figure 5.3) others rely on both *Trigona fulviventris* and *Chasmodia collaris* (individuals in the lower right part of figure 5.3), while a third group does not discriminate between these two vectors and *Cholus curialis.*

This multimodality can also be found in the empirically collected data (figure 5.4 and table 5.2). Note that since the data gained from the dual-choice test are paired (one time measure for each of the two extracts per tested individual) we show the differences in figure 5.4. Table 5.2 indicates that the bimodality can be found for preferences of *Chasmodia collaris* and *Cholus curialis*, as our individual-based simulation model suggests (figure 5.3).

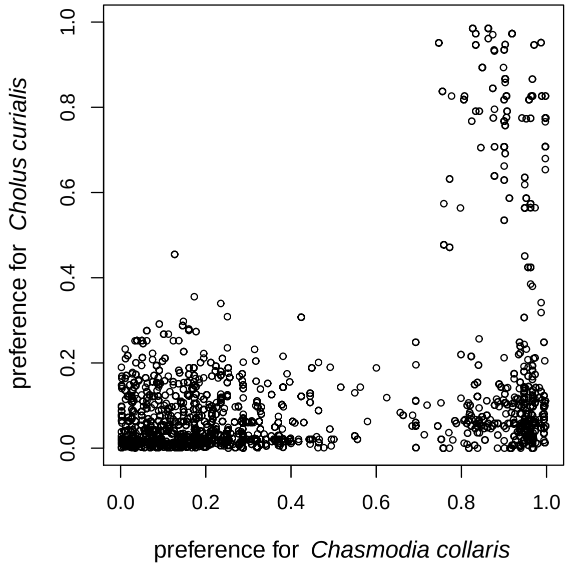

Figure 5.3: Simulation model results: phenotype space. This figure shows the same results as figure 5.2 B, yet here every individual is represented by a dot. Phenotype space has four dimensions (the four dispersal vectors), yet since preference for *Artibeus* sp. is constantly low and preference for *Trigona fulviventris* is constantly high (see figure 5.2 B) we have omitted these two dimensions for clarity. Note the three distinct dispersal strategies (lower left: preference for *Trigona fulviventris* only; lower right: preference for *Trigona fulviventris* and *Chasmodia collaris*; upper right: preference for *Trigona fulviventris*, *Chasmodia collaris* and *Cholus curialis*). The multimodality occurs across and not within simulation runs. The figure shows 10000 randomly drawn individuals from 25 simulation repeats.

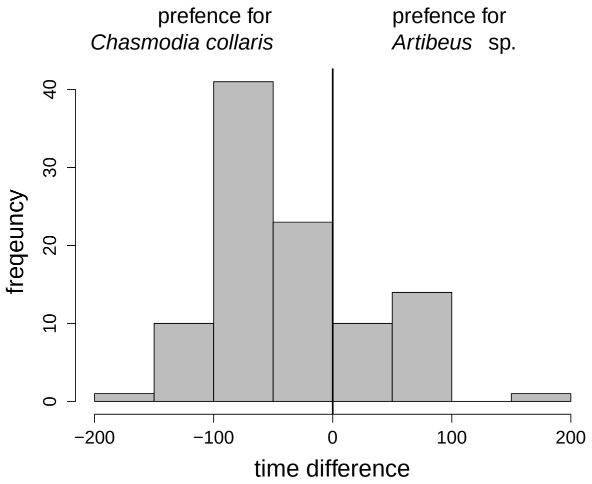

Figure 5.4: Preference distribution. Distribution of the time differences for a new repeat of the dual-choice test *Chasmodia collaris* vs. *Artibeus* sp. ($N = 100$ mites). We chose to show the distribution of the differences since the time a mite spend in one sector and in the other is not independent ("paired"). The histogram shows a clear bimodality.

5.4 Discussion

In summary, since *Spadiseius* mites live in an ephemeral habitat dispersal is obligatory. As the mites are not mobile enough they have to rely on phoresy. A number of flower visitors are potentially available as vectors. These differ in a large number of attributes. Our empirical work indicates that the mites are able to discriminate between these flower visitors using olfactory cues isolated from cuticles and fur. Our simulation results confirm that discrimination between these vectors is evolutionarily advantageous as the patterns obtained from the simulations are in good accordance with the empirical results. Especially in such possibly very stochastic and specialized systems information use is crucial for population viability. Kin competition is a major driving force for the evolution of dispersal and responsible for the choice of small vectors. The autocorrelated occurrence of the host plant selects for fat-tailed dispersal kernels which is achieved by mixing short- and long-distance dispersal vectors. In addition, vector choice does not only influence emigration and transition, but also immigration into new patches (directed dispersal). We will now discuss each of these point in more detail.

5.4.1 Dispersers use chemical cues for vector choice

Our results indicate that the phoretic bat-flower mites of the species *Spadiseius calyptrogynae* use chemical cues present on flower visitors to make informed decisions for phoretic dispersal. In accordance with our first hypothesis these flower mites are quite choosy in terms of phoretic vectors (figures 5.1 and 5.2). Our individual-based simulation model confirms that the exhibited informed dispersal strategy is evolutionarily stable and thus fares better than (random) other strategies.

Our results are consistent, regardless of the exact experimental set-up: the dual-choice and cafeteria experiments yield comparable results (figures 5.1 and 5.2). It is particularly interesting that the mites have apparently evolved to use insect cuticular hydrocarbons — which are known to be important in a large number of ecological contexts for recognition (for reviews see Howard and Blomquist 2005; Blomquist and Bagnères 2010) — but also scent cues from mammalian vectors. In addition, the latter cues used by the mites seem to be vector specific and not generally mammalian since the mites were able to discriminate between vector and non-vector bat species (*Artibeus* sp. vs. *Glossophaga* sp.; figure 5.1). This might also be relevant for discriminating between visits by perching bats and rare visits by mouse opossums (Sperr et al. 2009).

Our empirical data indicate that mite instar has no influence on vector choice, although it is assumed that adult females are the main dispersers (Lindquist and Moraza 2008). Yet, larvae, nymphs and males do have to disperse when their inflorescence whithers and these individuals may have the same sensory capacities and preferences as females do. We suggest that all stages may at least potentially use information from vector scent cues to determine an appropriate vector. Note that phoresy by all stages has been observed in other flower mite species (see Lindquist and Moraza 2008, and literature cited therein).

5.4.2 Kin competition influences vector choice

The empirically collected data (figure 5.1, 5.4 and 5.2 A, table 5.2) and the simulation results (figure 5.2 B and 5.3) suggest that, as predicted by our second hypothesis, most mites exclusively use individuals of the stingless bee species *Trigona fulviventris* as phoretic vectors. This vector has multiple advantages (see also table 5.1): it is quite reliable since visitation rate is high. In addition, using *Trigona fulviventris* as a dispersal vector is the best option for avoiding kin competition (Hamilton and May 1977). Kin competition has repeatedly been shown to be a very important factor influencing dispersal evolution (e.g. Poethke et al. 2007).

Additional simulations show that the low preference for *Artibeus* is mainly due to its large size. If both vectors are implemented as completely identical except for their carrying capacity the evolutionarily stable preference is always for the smaller vector.

5.4.3 Vector choice leads to directed dispersal

Regardless of other possible disadvantages (e.g. low revisitation frequency) *Trigona fulviventris* prefers early stage inflorescences as the bees collect pollen. As suggested by our third hypothesis, this allows an optimal exploitation of such a short lived habitat as a flower since it maximises the time between arrival and patch extinction. This reduces dispersal mortality over subsequent generations and allows eggs to hatch.

The most important pollinator of *C. ghiesbreghtiana* — *Artibeus* spp. (Tschapka 2003) — is not a preferred vector. Of course, it may be critical to compare insect cuticular components to extracts from bat fur. As we have tested the effect of increasing (doubling) the concentration of *Artibeus* sp. extract in the cafeteria experiment we are confident that our results are not artefacts of simple concentration or intensity effects. Furthermore, the mites are faced with exactly the same choice in the field. The only difference is that we tested fur from the bats' backs (in order to avoid important contamination with pollen and other plant substances) and that mites only attach to the bats' wing membranes. Nevertheless, our empirical and simulation results both indicate that *Artibeus* spp. are not prime dispersal vectors. We think that different evolutionary forces are relevant for plants and mites: while the palms should rely on visitors that transfer pollen from male to female inflorescences, the phoretic mites on the contrary should favour vectors that revisit early stage inflorescences since this alleviates the pressure of immediate relocation and allows egg development. Our empirical results may further be influenced by the fact that we have conducted our field study during the ‘dry’ season (note that even during these months precipitation is not low; see Sanford et al. 1994) which implies a lower number of flowering *Calyptrogyne* palms. During this period *Artibeus* spp. may be especially poor phoretic vectors because of lowered revisitation probabilities since the bats have to rely on other food sources. If vector preference is a plastic trait higher densities of flowering *Calyptrogyne* individuals may have led to a higher preference for *Artibeus* spp. as a vector. Here again, we can use the results from the individual-based model to formulate an informed hypothesis. Even if we decrease fragmentation and increase habitat availability (see sensitivity analysis; Appendix table 5.3) our model does not indicate that *Artibeus* sp. may become more attractive. Due to these spatial effects we would hypothesise that long-distance dispersal with *Chasmodia collaris* becomes less important, as is is too costly. The stingless bees remain the most appropriate dispersal vectors.

Directed dispersal has recently been demonstrated in animal dispersed palms in Barro Colorado Island (Hirsch et al. 2012). These authors show that scatter-hoarding seed dispersers lead to seed dispersal away from areas with high conspecific densities and thus high competition and mortality. Our study demonstrates the importance of the same principle for phoretic animals in ephemeral habitats. Directed dispersal in our case leads to colonization of habitats that have just recently become suitable. This reduces intra-specific competition and allows the establishment of new local populations with maximal longevities.

In this study we have only analysed information use for emigration decisions, but of course immigration is just as important. We here suggest that emigration decisions are influenced by and determine immigration: the use of certain vectors, such as the stingless bees, leads to directed dispersal towards early stage inflorescences. Informed immigration may still be evolutionarily advantageous, especially in this bat-flower mite system since most of the phoretic vectors are not specialized on *Calyptrogyne ghiesbreghtiana*. This question will be dealt with in detail elsewhere.

5.4.4 Vector mixing leads to fat-tailed dispersal kernels

An important fraction of dispersers exhibit an equally pronounced preference for *Trigona fulviventris* and a comparatively rare dispersal vector: the scarab beetle *Chasmodia collaris* (figure 5.4, 5.2 and 5.3). This vector has one central advantage, which is its long-distance flights (table 5.1). As the host palm *Calyptrogyne ghiesbreghtiana* frequently occurs in swamps, which leads to a clustered distribution, long-distance dispersal events allow the (re-)colonization of new host plant clusters. Although this dispersal behaviour is very risky, i.e. bears an important mortality risk, the pay-off for colonizing distant, eventually empty patches seems to balance these costs.

Hovestadt et al. (2001) show that in autocorrelated landscapes 'fat-tailed' dispersal kernels evolve. This is due to the antagonistic effects of kin competition — which would select for a uniform distribution of individuals of a lineage throughout the landscape (Hamilton and May 1977) — and dispersal costs — which increase with distance due to the autocorrelation of the habitat. Long-distance dispersal and fat-tailed dispersal kernels are extensively being studied in plants (Nathan 2006; Nathan et al. 2008b) but observations of long-distance dispersal are limited (Gillespie et al. 2012). The host palm shows exactly such an autocorrelated distribution and our results suggest that mites achieve a heavily fat-tailed dispersal kernel by mixing a short-distance (*Trigona fulviventris*) and a long-distance dispersal kernel (*Chasmodia collaris*).

This interpretation leads immediately to the question why our results suggest that mites showing only short-distance dispersal with *Trigona fulviventris* seem to coexist with the individuals using a mixed strategy. Additional simulations show that coexistence is actually not evolutionary stable. Since the long-distance vectors (*Chasmodia collaris*) are very rare and imply high levels of dispersal mortality selection acts very slowly. The high intrinsic stochasticity of the system under study may lead to the fixation of short-distance dispersers using exclusively the stingless bees. Further simulations indicate that populations monomorphic for the mixed strategy cannot be invaded by individuals showing a preference for short-distance dispersal only. Conversely, a population monomorphic for *Trigona fulviventris* can be (slowly) invaded by a strategy characterized by a mixed kernel.

Note that a third strategy, which is actually a minority (figure 5.3), seems to be rather unspecific and disperses additionally on *Cholus curialis* (see also figure 5.1 and 5.2). This vector has the advantage of most probably staying in the present *Calyptrogyne* stand but preferring, just as *Trigona fulviventris*, early stage inflorescences. The overall costs associated with this choice seem to be low enough for selection to act slowly.

Such patterns of short-distance movement and long-distance dispersal are not found in the closely related hummingbird-flower mites (e.g. Colwell 1973). As most hummingbird-flowers (e.g. *Heliconia* spp.) flower over longer periods of time and may have subsequently flowering inflorescences on one plant, these mites can often simply walk to the next flower as soon as the currently inhabited one withers. In flower mites inhabiting *C. ghiesbreghtiana* this is not possible — as only one inflorescence flowers at any given time — and the corresponding short-distance movements have to be effected by phoretic dispersal on appropriate vectors, e.g. *Trigona fulviventris* or *Cholus curialis.*

Although in the field other cues may also be used to determine the identity of a vector, such as body temperature or movement patterns, chemical cues seem to play a pivotal role. Chemical communication is wide spread (for a review see Steiger et al. 2011) although in this case 'communication' may be the wrong term since the vectors probably provide the cues that help to identify them unintentionally ('chemical eavesdropping'). A number of other studies have analysed the importance of chemical cues for phoretic dispersal (Soroker et al. 2003; Niogret et al. 2004; Krishnan et al. 2010). Yet, none of these found evidence for non-random use of multiple vectors in order to combine short-distance movement with long-distance dispersal events.

5.4.5 Robustness of simulation results

To our knowledge our study is the first to combine chemo ecological experiments in the field with a simple individual-based model. This allows us to analyse in more detail the underlying eco-evolutionary dynamics that lead to the observed and measured patterns. Of course, our individual-based model is far from capturing all the complexities of the system we are analysing. For instance, we assume non-overlapping generations, clonal reproduction (i.e. we model only female mites) and the same specific dispersal kernel form (although the means are different) for all vectors. Of course, the landscape is highly artificial and the annual dynamics of *Calyptrogyne ghiesbreghtiana* are ignored. Yet, this is exactly the advantage of such a model (see e.g. Kokko 2005). In this modelling study we were interested in optimal phoretic dispersal strategies. Thus, although simplifying the life-history of animals and plants greatly we modelled the crucial dispersal step quasi continuously. And although or especially because all elements included in the model are greatly simplified the model stays tractable and the results are understandable. The model helped us interpret such abstract features as the variance exhibited by the behaviour of the mites in the dual-choice and cafeteria experiments as representing different dispersal strategies. The simulations show that the stingless bee *Trigona fulviventris* should be the preferred phoretic vector. Note that this pattern is consistent throughout the sensitivity analysis (see Appendix table 5.3) even when this vector is penalized by high mortality rates. Similarly clear is the result that *Artibeus* sp. is not an adaptive choice. *Chasmodia collaris* — the long-distance disperser — very rarely drops in attractivity below preferences of 0.2, except when high additional mortalities are assumed. This is not surprising since the mortality for a disperser on *Chasmodia collaris* is already very high in the standard scenario. The adaptive value of *Cholus curialis* depends somewhat more on the parameter combinations.

5.4.6 Concluding remarks

We have shown that the use of (chemical) information is highly adaptive for taking emigration decisions, because non-random emigration allows to influence the shape of the dispersal kernel and may lead to directed dispersal. We have analysed our hypotheses using a dual approach and presented empirical results from chemo-ecological studies with tropical flower-dwelling mites and individual-based simulation results.

The evolutionary forces discussed above are relevant to any phoretic species. They are especially important for specialized interactions, as such systems can only be stable if the (more) mobile partner is able to reach its host. Our conclusions can also be applied to other systems, for example to animal dispersed seed plants as appropriate vectors are crucial for the realization of optimal dispersal kernels. 'Vector choice' in plants can be achieved by fruit morphology, for example (e.g. Flörchinger et al. 2010). In animal dispersed plants kin competition should also favour small vectors. In autocorrelated habitats vector mixing can be used to achieve fat-tailed dispersal kernels (Nathan et al. 2008a).

We hope that our results also show how helpful such dual approaches, combining experimental work *in situ* and *in silico*, can be for a better understanding of ecological and evolutionary dynamics and their feedback loops. Such studies are particularly important to bridge the gap between empirical and theoretical ecology (Restif et al. 2012).

5.5 Appendix

Normality of data obtained by dual-choice test. Sensitivity analysis of the individual-based model.

Table 5.2: Distribution of the data from the dual-choice experiments. Since per tested mite two values (one for each extract) were collected the data are paired and we analyse the differences, as in a paired t-test for example. The distribution of these differences is tested for normality (Shapiro-Wilk test of normality). Significantly non-normally distributed differences indicate bimodality as in figure 5.4.

vectors	**normality of difference distribution**
Artibeus sp. vs. *Glossophaga* sp.	$W = 0.98$, $p = 0.68$
Trigona fulviventris vs. *Chasmodia collaris*	$W = 0.99$, $p = 0.99$
Cholus curialis vs. *Chasmodia collaris*	$W = 0.98$, $p = 0.67$
Artibeus sp. vs. *Trigona fulviventris*	$W = 0.97$, $p = 0.16$
Cholus curialis vs. *Trigona fulviventris*	$W = 0.98$, $p = 0.54$
Artibeus sp. vs. *Chasmodia collaris*	$W = 0.96$, $p = 0.004$
Artibeus sp. vs. *Cholus curialis*	$W = 0.93$, $p = 0.007$

Table 5.3: Individual-based simulation model: sensitivity analysis. The table basically shows the same results as figure 5.2 B (cafeteria experiment; simulation results). For every phoretic vector the mean and the standard deviation of the evolutionarily stable preference is shown ($mean \pm s.d.$). The first results row shows the standard run for comparison. The first column indicates which parameter was changed and the second column the corresponding tested value. The results are means from 10 simulation runs.

		***Artibeus* sp.**	***C. collaris***	***C. curialis***	***T. fulviventris***
standard		0.033 ± 0.013	0.452 ± 0.409	0.192 ± 0.298	0.985 ± 0.008
λ	3	0.035 ± 0.019	0.208 ± 0.271	0.362 ± 0.347	0.986 ± 0.003
	4	0.058 ± 0.008	0.460 ± 0.359	0.046 ± 0.015	0.982 ± 0.007
t_{max}	2	0.015 ± 0.004	0.043 ± 0.015	0.148 ± 0.202	0.982 ± 0.010
	4	0.130 ± 0.048	0.867 ± 0.302	0.072 ± 0.062	0.879 ± 0.306
H	0	0.041 ± 0.014	0.585 ± 0.372	0.088 ± 0.126	0.982 ± 0.009
	0.5	0.044 ± 0.015	0.284 ± 0.312	0.098 ± 0.098	0.979 ± 0.008
p_H	0.3	0.031 ± 0.011	0.319 ± 0.346	0.691 ± 0.337	0.981 ± 0.009
	0.4	0.023 ± 0.009	0.294 ± 0.307	0.440 ± 0.402	0.977 ± 0.010
	0.6	0.041 ± 0.009	0.229 ± 0.254	0.167 ± 0.270	0.983 ± 0.005
$M(Artibeus)$	6	0.034 ± 0.011	0.266 ± 0.258	0.044 ± 0.018	0.984 ± 0.006
	4	0.046 ± 0.012	0.316 ± 0.342	0.288 ± 0.390	0.980 ± 0.006
$M(Chasmodia)$	11	0.039 ± 0.016	0.446 ± 0.430	0.142 ± 0.294	0.986 ± 0.004
	9	0.036 ± 0.014	0.550 ± 0.420	0.147 ± 0.281	0.980 ± 0.010
$M(Cholus)$	2	0.033 ± 0.006	0.250 ± 0.250	0.122 ± 0.227	0.977 ± 0.005
$M(Trigona)$	5	0.045 ± 0.020	0.739 ± 0.357	0.249 ± 0.333	0.980 ± 0.011
	3	0.045 ± 0.164	0.531 ± 0.366	0.155 ± 0.255	0.985 ± 0.005
$\mu(Artibeus)$	0.4	0.218 ± 0.044	0.402 ± 0.384	0.059 ± 0.023	0.986 ± 0.008
	0.6	0.016 ± 0.005	0.525 ± 0.423	0.121 ± 0.159	0.982 ± 0.007
$\mu(Chasmodia)$	0.3	0.045 ± 0.014	0.963 ± 0.023	0.191 ± 0.307	0.980 ± 0.008
	0.5	0.031 ± 0.009	0.063 ± 0.030	0.247 ± 0.357	0.982 ± 0.008
$\mu(Cholus)$	0.5	0.032 ± 0.008	0.235 ± 0.249	0.936 ± 0.043	0.981 ± 0.010
	0.7	0.045 ± 0.011	0.221 ± 0.243	0.025 ± 0.009	0.981 ± 0.008
$\mu(Trigona)$	0.4	0.018 ± 0.006	0.172 ± 0.287	0.021 ± 0.006	0.981 ± 0.010
	0.6	0.118 ± 0.061	0.526 ± 0.322	0.803 ± 0.270	0.880 ± 0.306

6

From random walks to informed movement[1]

Contents

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Abstract

The analysis of animal movement is a large and continuously growing field of research. Detailed knowledge about movement strategies is of crucial importance for understanding eco-evolutionary dynamics at all scales — from individuals to (meta-)populations. This and the availability of detailed movement and dispersal data motivated Nathan and colleagues to published their much appreciated call to base movement ecology on a more thorough mechanistic basis. So far, most movement models are based on random walks. However, even if a random walk might describe real movement patterns acceptably well, there is no reason to assume that animals move randomly. Therefore, mechanistic models of foraging strategies should be based on information use and memory in order to increase our understanding of the processes that lead to animal movement decisions.

We present a mechanistic movement model of an animal with a limited perceptual range and basic information storage capacities. This 'spatially informed forager' constructs an internal map of its environment by using perception, memory and learned or evolutionarily acquired assumptions about landscape attributes. We analyse resulting movement patterns and search efficiencies and compare them to area restricted search strategies (ARS) and biased correlated random walks (BCRW) of omniscient individuals.

We show that, in spite of their limited perceptual range, spatially informed individuals boost their foraging success and may perform much better than the best ARS. The construction of an internal map and the use of spatial information results in the emergence of a highly correlated walk between patches and a rather systematic search within resource clusters. Furthermore, the resulting movement patterns may include foray search behaviour. Our work highlights the strength of mechanistic modelling approaches and sets the stage for the development of more sophisticated models of memory use for movement decisions and dispersal.

6.1 Introduction

The ability to move is fundamental to life and very relevant to the fitness of most animal species. It influences foraging success, the ability to escape predators, or to target mating partners — to name just a few aspects. Similarly, the impact of dispersal — a large-scale phenomenon resulting from the movement of individuals — on the eco-evolutionary dynamics of animal populations cannot be overestimated. The exchange of individuals between populations, respectively habitat patches, is central for the persistence of spatially structured populations (metapopulations: Levins 1969, 1970; Hanski 1998, 1999). Furthermore, dispersal is a key life-history attribute which may shape evolutionary trajectories of populations significantly (for recent comprehensive reviews see Bowler and Benton 2005; Ronce 2007). Yet, despite the central role movement plays in ecology and evolution the process is often not considered explicitly in models of spatially structured populations (e.g. Travis and Dytham 1998; Hanski 1999; Poethke et al. 2011; Fronhofer et al. 2011a). Instead, dispersal is approximated by diffusion processes or random walks (for a recent review see Codling et al. 2008) or the statistical properties of some dispersal kernel. These approaches typically do not consider the movement process at all but (only) the emergent consequences, i.e. the translocation of individuals from one place to another.

A number of models of animal movement and resulting inter-patch dispersal assume that the movement process can be described as a modified version of a random walk (Codling et al. 2008). Such models account for e.g. limited perceptual capabilities (detection range), directional persistence, i.e. correlation in the direction of consecutive movement steps (e.g. Bartumeus and Levin 2008), or a bias in movement directions (e.g. Conradt et al. 2003; Bartoń et al. 2009). They are based on the assumption that movement can be described by the statistical attributes of step length and turning angle distributions, for example. Movement decisions are seen as inherently random. However, the fact that the statistical properties of movement trajectories can adequately be described in this way should not be taken as evidence that the underlying generating processes are equally well described by such distributions (Benhamou 2007; Plank and James 2008; Boyer et al. 2009).

A first approach towards modelling movement as a more context-dependent process based on the ability to memorize a sequence of temporal events is found in the concept of the area restricted search (ARS Kareiva and Odell 1987; Benhamou 1992). In nature resources are often spatially autocorrelated (Conradt et al. 2003; Jelinski and Wu 1996), i.e. food plants are frequently surrounded by other food plants. Given that resources are rare and distributed in more or less discrete clusters (patches) encounters with resources reveal information on the probability of finding additional resources nearby.

ARS models assume that individuals remember the time since past encounters (possibly integrated by their hunger level, see Bartoń and Hovestadt 2013) and decrease the straightness (correlation) of their random walk upon detecting a resource item. Such patterns have been observed in various taxa, from microbes (Keller and Segel 1971) and invertebrates (Hassell and Southwood 1978) to birds (Tinbergen et al. 1967). Tailored to the search for spatially clustered resources this movement rule leads to a more intense search in areas of high resource density. If we equate 'resource aggregations' with the term 'habitat patches' — as frequently done in the metapopulation literature (for reviews see Hanski 1999; Hanski and Gaggiotti 2004a) — ARS models generate more or less straight inter-patch movement that can be differentiated from intra-patch foraging behaviour and the earlier may be qualified as dispersal (Ronce 2007). Note that ARS models do not assume any spatial memory or orientation: memory is only related to the temporal order of events, i.e. recent encounters with resource items. Furthermore, the ARS still is a modified random walk ('composite random walk'; Benhamou 2007) with a context-dependent directional correlation. Due to the lack of spatial memory the choice of the movement direction remains nonetheless a random process.

Like more simple random walk models the ARS models thus still assume that movement can be adequately described according to the statistical mechanics underlying the movement of physical particles, i.e. that movement can indeed be modelled as random walk. Only the statistical properties of the walk may change according to conditions. However, most animals possess (highly developed) perceptional and cognitive capabilities (including the ability to memorize, process information, and take decisions, as noted by Gautestad 2011). Individuals with such capacities can be expected to actively take informed, non-random decisions. Individuals from many taxa have indeed been shown to store information about their environment and use this memory to influence their behaviour (e.g. cognitive maps for navigation; for reviews see Moser et al. 2008; Moser and Moser 2008).

In summary, if we want to understand the (microscopic) mechanisms of movement the random walk framework appears to be ill suited. At a small scale mechanistic movement models should instead account for the physiological and behavioural processes that generate a sequence of (informed) movement decisions. This does not exclude, however, that random walk models may serve well as integrative tools for the description of large scale movement phenomena. While individual movement decisions may have a completely mechanistic and deterministic basis, the unpredictability of external conditions and signals (typically not recorded by a human observer) impacting upon individuals result in an apparent randomness of movement, especially over larger spatial and temporal scales.

Over the last years a number of approaches have been developed that model movement decisions based on individually or even evolutionarily 'learned' information about the spatial distribution of e.g. food resources. Some of these follow the 'patch-matrix' approach and thus do in fact not model movement but only emigration (Klaassen et al. 2006; van Gils 2010). Others still adhere, to a certain degree, to the random walk approach (Gautestad and Mysterud 2010a,b; Gautestad 2011; van Moorter et al. 2009) or assume that individuals learn optimal movement rules for a specific landscape during their life (Mueller et al. 2011).

In a conceptual paper, expanding the movement ecology paradigm of Nathan et al. (2008a), Getz and Saltz (2008) have compiled the general elements that are necessary to build mechanistic movement models. Their paper provides a framework for the construction of such models that account for an individual's motivation as well as its ability to perceive, memorize, or make inference based on past experience (see also Mueller and Fagan 2008). Here, we generally follow this framework, yet focus on the specific case of foraging behaviour (or more generally the search for any resource, i.e. host plants, oviposition sites) and expand it to account in more detail for the process of perception, memory building and use.

With great diligence Getz and Saltz (2008) explain the concept of 'fundamental movement elements' and 'canonical activity modes' — we will ignore these complexities here and simply assume that individuals move at constant speed. Further, Getz and Saltz (2008) point out that movement can be driven by different motivations and that movement decisions will be a consequence of some weighting of the different needs of the moving animal. Here, we will focus on movement motivated only by a single reason, i.e. the motivation to find food or host plants suitable for e.g. egg deposition. We do not account for competing motivations. In our model we are, however, more specific than Getz and Saltz (2008) with respect to three issues: (1) We clearly distinguish whether information about the landscape is based on perception or on memory of locations visited in the past; we allow for both (see also Mueller and Fagan 2008). (2) Furthermore, in our model an individual has the ability to make an informed guess (inference) about the state of unknown locations (neither perceived nor visited in the past) based on the information it has gathered. As outlined above, such an inference is sensible when the landscape is informative, i.e. when resources are distributed non-randomly. Note that this reasoning is always applicable, regardless of whether an observed cell was occupied or empty. This allows the focal animal to construct a 'spatial inference map' of the expected resource distribution based on the perceived and memorized locations of resources, and the learned or inherited knowledge about the statistical properties of the spatial distribution of these resources. Such an ability is also the core attribute of a 'Bayesian forager' (e.g. Klaassen et al. 2006; van Gils 2010). (3) Finally, any movement decision is the basis for future movement decisions, and therefore influences the availability of new options. Optimal movement decisions should therefore not only account for the immediate benefits of an action, but take into account the consequences for future movement. This aspect of 'anticipation' lays at the heart of the 'travelling salesman problem' (e.g. Wong et al. 2010; Lihoreau et al. 2012) and has not been discussed by Getz and Saltz (2008).

The model we propose in the following is a first step towards a mechanistic model of animal movement that simultaneously accounts for perception, memory, inference and anticipation. Although we make a number of severe simplifying assumptions. Already a very basic introduction of these processes leads to promising results, such as the emergence of highly efficient movement patterns that include (1) straight line search between patches (Zollner and Lima 1999), (2) systematic, grid-line search within patches and (3) foray search, i.e. loops returning to not yet fully depleted patches (e.g. Conradt et al. 2003).

6.2 Model description

6.2.1 Landscape

We modelled the movement of a single individual searching for resources distributed in a landscape of finite size, e.g. an insect foraging or searching for host plants. To simplify the storage (memory) and use of information our landscape is modelled as a hexagonal grid (500 x 500 cells). Cells are either empty or contain one resource item. To allow for different degrees of spatial correlation, resources were distributed using a Thomas process (R 2.14.1; package "spatstat" version 1.25-0). This allows us to control the number of clusters (κ), the degree of clustering (σ; standard deviation of the displacement from the cluster centre) and the number of items per cluster (μ). The resulting (continuous) coordinates were rounded to fit the underlying grid. No more than one non-renewable resource item was placed into a cell, i.e. duplications were omitted (resource content of cell i at time t: $C_{i,t} \in \{0, 1\}$). In addition to simulations with dense (1:$\kappa = 500$, $\sigma = 1$, $\mu = 150$) and three intermediate degrees of resource clustering (2: $\kappa = 500$, $\sigma = 2$, $\mu = 34$; 3: $\kappa = 500$, $\sigma = 4$, $\mu = 28$; 4: $\kappa = 500$, $\sigma = 6$, $\mu = 26$) we ran our model using a landscape with approximately randomly distributed resources (5:$\kappa = 500$, $\sigma = 20$, $\mu = 26$). Furthermore, we include results from one landscape that is heterogeneous in cluster size (6: including an equal number of clusters generated according to landscape 1 and additionally to $\kappa = 50$, $\sigma = 5$, $\mu = 1000$) and one that is heterogeneous in the degree of clustering (7: including and equal number of clusters generated according to landscapes 1 and 4). Parameters (especially μ) were tailored such that in all generated landscapes about 5% of cells contained a resource item (probability of containing a resource item $E_0 \approx 0.05$). Note that the initial landscape parameters do not correspond exactly to the resulting landscapes since the Thomas landscape is distorted by fitting the coordinates to the hexagonal grid. For every replicate simulation run a new landscape was generated. 100 replicates were used for the results presented below.

6.2.2 Movement model and rules

Movement decisions are deterministic. Exceptions may occur if two or more movement directions are equally attractive according to the criteria given below. The process leading to an individual's decision has four central elements: (1) perception, (2) memory, (3) inference and (4) anticipation. Firstly, information about the resource content ($C_{i,t}$) of visited and perceived locations (cells i at time t) is stored in the animal's memory. We assume here that perception and memory are free of errors. Secondly, the focal animal may infer from its memory (position of occupied and empty cells) and from learned or inherited knowledge about general landscape properties (mean resource density and correlation) the state of unknown cells. Initially, the probability of finding a resource at a given location i equals the mean resource content (E_0). With inference the probability of finding a resource may be higher or lower than this uninformed guess. Finally, while considering its movement options based on perception, memory and inference the individual may not only evaluate the direct benefits of the next movement step but also 'anticipate' — and take into account — how this decision affects its prospects for future movement. In the following, we will explain the rules implemented for each of the four components of the movement model in more detail.

6.2.3 Perception and memory

We assume that animals have a restricted perceptual capacity and can thus only perceive the content of cells within a defined perceptual range (radius of the perceptual range: P). The focal animal stores this perceived information in a map of the landscape. The internal map has two components: firstly, it contains information about the present resource content of a cell (cells containing a resource item: $C_{i,t} = 1$; empty cells $C_{i,t} = 0$). Secondly, it contains information about whether the cell has been previously harvested ($H_{i,t}$) or not (harvested cells are empty: $C_{i,t} = 0$ and $H_{i,t} = 1$; non-harvested cells: $H_{i,t} = 0$). This additional information is important because, on the one hand an individual should avoid revisiting a harvested cell (resources do not regrow), but on the other the information that the cell contained a resource item in the past remains valuable for the inference of the state of neighbouring cells.

6.2.4 Inference

In addition to the certain knowledge provided by direct perception and memory, an individual may also estimate the resource content of unobserved cells. Such an inference becomes possible if the general statistical attributes of the spatial distribution of resources (i.e. mean resource density and correlation) are known to the individual. If these general properties show temporal persistence it is very likely that such information is learned evolutionarily, i.e. saved in the genome. Without any prior information about the correlation of resources the expected probability that a cell contains a resource item equals the mean resource density in the landscape (E_0) — in our simulations $E_0 \approx 0.05$. However, when resources are correlated in space, information about the state of a cell confers information about the state of other cells in its vicinity: cells in the vicinity of an occupied cell have themselves an increased probability of containing a resource item (figure 6.1 A). Vice versa, the probability of finding a resource item in the surroundings of an empty cell is reduced (figure 6.1 B).

In our simulations we use a very simple approximation to calculate the expected

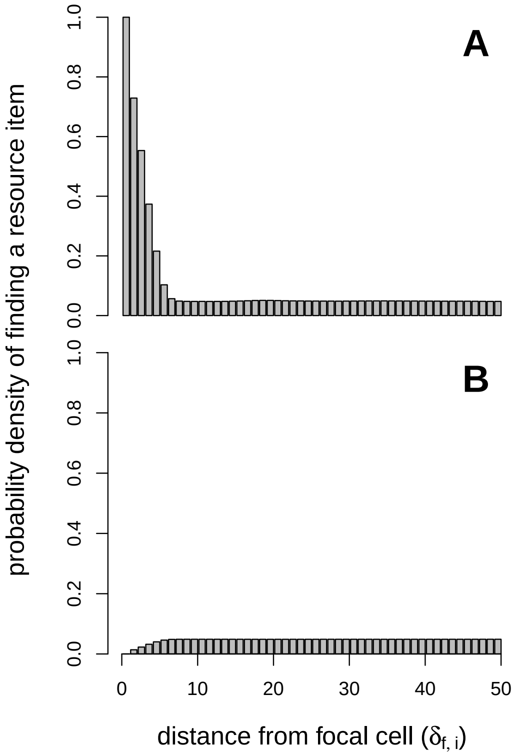

Figure 6.1: Probability of finding an occupied cell in the surroundings of a focal cell (occupied cells in panel A; empty in panel B) at a given distance ($\delta_{f,i}$) for a densely clustered landscape ($\sigma = 1$). For the meaning of the parameter values see text.

resource content of a focal cell ($E_{f,t}$) based on averaging the information of its surroundings (with inference radius R). This is only done for a cell that has not directly been observed. The expected probability that a cell f contains a resource item at time t is calculated as follows:

$$E_{f,t} = \begin{cases} 0 & \text{if} \quad C_{f,t} = 0 \\ \frac{1}{n}\sum_{r=1}^{n}(C_{r,t} + H_{r,t}) & \text{if} \quad C_{f,t} = unknown \\ 1 & \text{if} \quad C_{f,t} = 1 \end{cases} \tag{6.1}$$

with $C_{r,t} = E_0$ for so far unobserved cells. $n = 6 \cdot \sum_{i=1}^{R} i$ is the number of cells in the inference radius R around the focal cell f. As pointed out above, including $H_{r,t}$ in this calculation allows to derive correlative information from formerly occupied cells even when they have been harvested. Note that inference is only used when the state of the focal cell is unknown. Furthermore, inferred information is not saved for use in the next time step, i.e. inference is always based on secure knowledge. Note that the optimal inference radius (R), i.e. the inference radius that leads to the highest foraging success, should correlate with the average degree of clustering (σ).

As foraging is destructive in our model, i.e. resources do not regrow, inference is only spatial and not temporal. This is a valid approximation as long as the time scale under consideration is shorter than resource regrowth. At larger time scales temporal inference could, for example, be a driving force for the establishment of home ranges (e.g. van Moorter et al. 2009).

6.2.5 Anticipation

During each time step the animal decides to move to one of its six neighbouring cells (movement direction $\alpha = 30°, 90°, ..., 330°$; see figure 6.2), i.e. step length is fixed to 1. Based on its internal map which contains perceived and memorized as well as inferred information about these cells an individual will decide on its next movement step. Clearly, a rational forager should choose the direction resulting in the largest foraging success. It could thus choose the neighbouring cell with the largest $E_{i,t}$ value. Yet, as every step into a particular direction changes the position of the individual, it also influences the potential foraging success of following steps. Thus, individuals should base their movement decision not only on the resource content of the six directly neighbouring cells but also on that of subsequent cells. Indeed, the larger the area covered by the internal map the more the problem of an ideal anticipation resembles that of solving a ‘travelling salesman problem’. We sidestep the issue of resolving this rather complex problem here. Instead, we assumed that the movement decision is taken according to a simple hierarchical rule of thumb: (1) Generally, the animal moves into the directly neighbouring cell (direction α) with the highest expected resource content $E_{i,t}$. (2) If this is ambiguous, i.e. two or more cells have the same expected content, the animal will additionally take into account the content of neighbours to the potential target cells (see figure 6.2 for a detailed description of the process). We then calculate the specific attractivity of a direction α as the sum of the probability of resource encounter ($E_{i,t}$) in the target cell and the cells directly adjoining the target cell in that direction (see figure 6.2). If this does not yield an unambiguous result the refinement is repeated until a maximum of three cell rings have been used for the assessment. If at that moment two or more directions are still equally attractive the animal chooses randomly between these options. Exploratory simulations show that this happens rarely and that further increasing the number of cell rings used for anticipation does not change our results importantly.

Note that these movement rules, although being memory based, are rather local. Attraction by known resource patches far beyond the perceptual range (e.g. as known from primates: Normand and Boesch 2009; Presotto and Izar 2010) and the inference radius is not included. This simplification will not alter our results significantly, especially since foraging is destructive (see above).

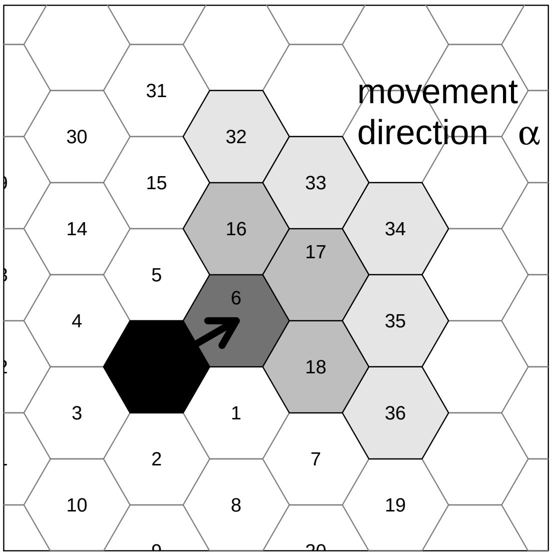

Figure 6.2: The attractivity of a movement direction (in this case $\alpha = 30°$ i.e. a movement to cell 6) is determined by the sum of the probability of resource encounter ($E_{i,t}$) in the focal cell in direction α (cell 6) and the three neighbours of this cell (cells 16, 17, 18) which are not themselves neighbouring the current position (cell 0) of the individual. If this does not yield an unambiguous result the refinement is repeated until a maximum of three cell rings have been used for the assessment. Here cells 32–36 could be used additionally.

6.2.6 Simulation experiments

In all simulation experiments the focal animal was released in the centre of the landscape. Simulations ended, whenever the foraging individual reached the border of the landscape (absorbing boundary conditions) or when the maximum number of movement steps ($N = 1000$) was reached. In order to compare the performance of different movement strategies we calculated the foraging success of a strategy as the number of resource items collected divided by the number of iteration steps (e.g. Bartumeus and Levin 2008) over all 100 replicate simulations runs. We analysed the influence of the parameters of our model by varying the perceptual range ($P \in \{0, 1, 2\}$) and the inference radius ($R \in \{0, 1, 2, .., 10\}$).

We compared the foraging success of our spatially informed forager with two implementations of a modified random walk: (1) an area restricted search (ARS) and (2) an omniscient, biased correlated random walk (BCRW). This is done in seven landscapes differing in the degree of clustering of resources (see above).

6.2.7 Area restricted search (ARS)

The concept of the area restricted search introduces the idea that individuals have the ability to memorize a sequence of temporal events. In such an ARS the correlation, i.e. the straightness of the walk, increases as a function of the time since the last encounter with a resource item (Kareiva and Odell 1987; Benhamou 1992). The correlation coefficient is calculated as $\rho_t = 1 + (\rho_{t-1} - 1) \cdot e^{-d \cdot \Delta t}$, with $\Delta t = 1$, and is thus bounded between 0 (no correlation, i.e. diffusion) and 1 (maximal correlation, i.e. straight walk). After each resource encounter ρ is reset to zero. In biological terms this means that a resource encounter fully satiates the focal animal; d can then be interpreted as the decay rate of the satiation. Step length was set to 1 cell as for the spatially informed forager and turning angles were drawn from a wrapped Cauchy distribution (e.g. Bartumeus and Levin 2008, for a discussion see Codling et al. 2008; R 2.13.1; package “CircStats” version 0.2-4) and transformed to the grid. We ran simulations for $d \in \{0.01, 0.1, 1, 10\}$. A maximum was always found within this interval.

6.2.8 Biased correlated random walk (BCRW) of omniscient individuals

In contrast to the ARS, this strategy is based on the assumption that an individual has an unlimited perceptual range and thus always perceives the complete landscape, i.e. is omniscient. In addition to a correlation of turning angles as in the ARS (see above) the BCRW thus assumes that the turning angles are biased towards a target. Here, the

target is always the nearest resource item.
We will use an implementation of a BCRW as proposed by Bartoń et al. (2009). The directional bias (β) is a function of the distance to the next resource item ($\delta_{f,i}$, measured as number of cells between the focal cell f and the next resource cell i) : $\beta = tanh\,(b\delta_{f,i})$ with b as the strength of the bias (for a detailed analysis of this movement strategy see Bartoń et al. 2009). The resulting mean turning angle of the BCRW (Φ_t; location parameter; modal angle of the wrapped Cauchy distribution) is influenced by both, the turning angle of the last time-step (Φ_{t-1}) and by the angle to the nearest resource item (Ψ_t): $\Phi_t = (1-\beta)\Phi_{t-1} + \beta\Psi_t$. For simplicity the correlation coefficient (concentration parameter ρ) is fixed. Although no grid is needed for these simulations we used the same landscapes as described above and set step length to 1 for a better comparability. We ran simulations for $b \in \{2,3,4\}$ and $\rho \in \{0.8, 0.9\}$ (sensible parameter values were extracted from Bartoń et al. 2009).

6.3 Results

6.3.1 Qualitative description and influence of perception, memory and inference

Our implementation of a spatially informed forager generates a broad spectrum of movement patterns. These show two characteristic attributes (see figure 6.3 B): (1) inter-patch movement is typically very straight and (2) larger turning angles emerge during a more or less systematic, grid-line ('meandering') search behaviour inside resource patches. To this respect the pattern resembles that generated by an ARS and is in good accordance with the behavioural dichotomy (correlated movement in the matrix and uncorrelated random walk in resource patches) observed e.g. in butterflies (Schtickzelle et al. 2007) or grasshoppers (Kindvall 1999; Hein et al. 2003). Depending on the landscape attributes (degree of clustering σ) the spatially informed forager is, however, much more efficient than the best ARS strategy (see below).

The driving mechanism behind these emergent path properties is the joint effect of perception, memory, inference and anticipation on movement decisions. Figure 6.3 illustrates the influence of the inference radius (R) on the movement pattern of an animal moving in a landscape with a high degree of resource clustering ($\sigma = 1$). Even in the absence of any inference ($R = 0$; figure 6.3 A) the movement pattern of an individual using an internal map is clearly different from that of individuals following a pure random walk (not shown): the movement in the matrix is obviously (relatively highly) correlated. This pattern emerges, because animals with memory typically do not reverse the direction of their walk — except if resources were detected — because they

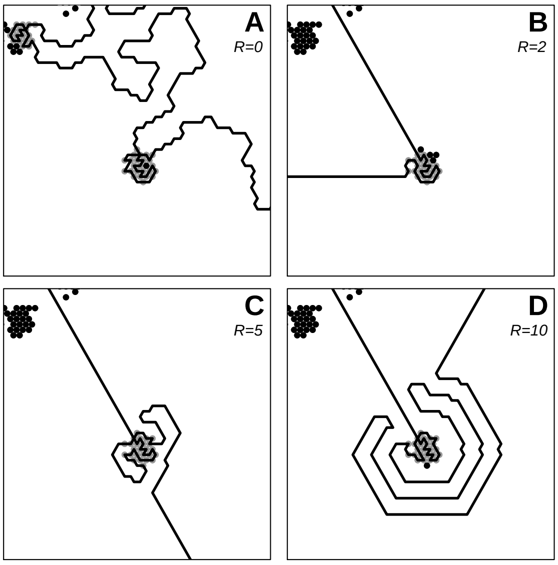

Figure 6.3: Influence of the inference radius (R) on the resulting movement path of a forager with a perceptual range of one cell ($P = 1$) in a densely clustered landscape ($\sigma = 1$). Panel A depicts the movement path of an animal with memory, but without spatial information (inference; $R = 0$). The movement path of a spatially informed forager using all cells in a radius of $R = 2$ to assess the status of so far unvisited cells is shown in panel B. The systematic, grid-line search pattern within patches is mainly a result of perception and memory use. In addition, the use of spatial information (inference) leads to straight walks between resource patches. A further increase of the inference radius (R) leads to foray loops (panel C) and an intense systematic search for new resources in the vicinity of patches discovered (panel D). Black dots are resource items, grey dots are harvested resource items.

have memorized that the observed cells behind them are empty. The most attractive, because unexplored, movement directions are thus the three cells lying ahead of the animal.

Introducing inference, i.e. the capacity to make an informed guess about the state of an unknown cell (e.g. inference radius $R = 2$; figure 6.3 B), leads to straight line walks as long as no resources have been detected. This is due to the fact, that the cell directly in front of the animal has the highest inferred $E_{i,t}$ value, since the distance to observed empty cells (behind the animal) is maximal. As soon as a resource patch has been detected this strategy shows a very systematic, grid-line search behaviour, because it has the capacity to memorize detected, but not yet harvested, resource items. Note that this pattern does not depend on inference in densely clustered resource aggregations, the size of the perceptual range and anticipation are decisive here.

In addition to this, foray searches — i. e. looping trajectories — may be observed if the inference radius (R) is further increased (e.g. $R = 5$; figure 6.3 C). This happens because the animal reorientates its movement towards a resource patch it has recently left, on the one hand due to the attractivity of perceived, but not yet depleted cells, and, on the other, due to a decline in its expectation (inferred probability of positive encounter) for the cells ahead. This expectation gradually declines the longer it moves without detecting a resource item. As such foray searches limit the total area an individual covers within a certain time interval they may reduce search efficiency in our simulations, as resources do not regrow (see figure 6.4). For very large inference radii ($R = 10$, figure 6.3 D) animals keep searching systematically in the surroundings of detected resources. If there is a large discrepancy between the assumed correlation distance (reflected by R) and the real correlation of resources in the landscape as in this example (figure 6.3 D), the animal will search intensely outside resource patches. This reduces the efficiency of inter-patch movement and leads to very inefficient search strategies.

6.3.2 Detailed model analysis

A more systematic analysis of the influence of perceptual range (P) and inference radius (R) is shown in figure 6.4. We compare the foraging success of the spatially informed strategy with area restricted searchers (ARS) and individuals following a biased correlated random walk (BCRW). Note, that for the sake of simplicity we only show the most efficient types of ARS and BCRW. For the ARS this value was a function of the decay rate (d) of the correlation: depending on the correlation of the landscape intermediate values of d ($d = 0.1$ for $\sigma = 1$, i.e. highly clustered landscape) or high values of d ($d = 1$ for $\sigma = 20$, i.e. random landscape) were optimal (see also Bartoń and Hovestadt 2013). The most efficient BCRW had high values for both correlation ($\rho = 0.9$) and strength of bias ($b = 4$). This ultimately leads to a straight (deterministic) walk towards the next resource item. While for the BCRW the perceptual range (P) covers by definition the whole landscape we restricted our simulation experiment with ARS to a detection radius of $P = 0$, i.e. the individual can only see the cell it presently occupies.

Obviously, the perceptual range (P) has an enormous influence on the search efficiency of individuals. Consequently, in all landscapes search efficiency increases with perceptual range and the BCRW searcher consistently outperforms any search strategy with a finite perception.

However, the results also show the enormous influence of spatial information use (i.e. inference) on foraging success. When individuals use an internal map but no inference ($R = 0$) they are not only outperformed by individuals following a BCRW but also by those following an ARS (obviously only if also $P = 0$ as assumed for the ARS). This holds for all types of landscapes analysed. Yet, as soon as individuals use spatial information (inference, $R > 0$) they perform better than those following an ARS. This

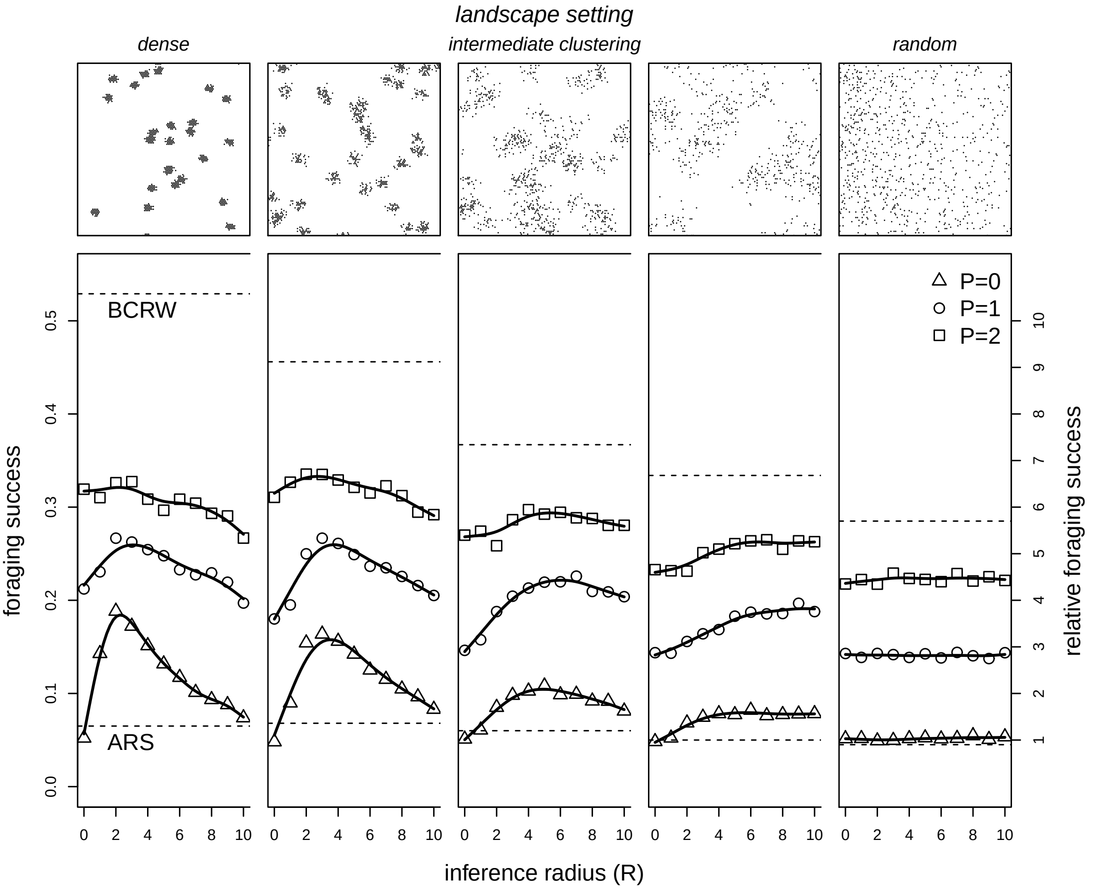

Figure 6.4: Systematic model analysis: influence of inference radius (R), perceptual range (P) and of landscape attributes (from left to right: dense clustering to a random landscape, depicted at the top; $\sigma = 1, 2, 4, 6, 20$) on foraging success, i.e. resource items found per iteration for 100 replicates. The relative foraging success can be read from the right y-axis (relative to the mean resource content of 5%, i.e. the foraging success of a straight line search). For comparison foraging success of the best ARS and BCRW are shown as dashed lines. The continuous smoothed lines are smooth spline regressions ($\lambda = 0.45$).

particularly holds if the resource distribution is clustered (high information content of the landscape) and the assumed inference radius (R) fits the correlation distance of resources in the landscape (maxima in figure 6.4; see below). In this case (e.g. figure 6.4; left panel; $P = 0$, $R = 2$) spatially informed individuals are over three times as successful as those following an ARS. In general, the optimal inference radii, i.e. maxima in figure 6.4, correlate quite well with the degree of clustering σ (see table 6.1).

The benefit of inference clearly depends on the statistical pattern of the resource distribution. The difference in search efficiency between area restricted searchers and spatially informed foragers decreases with decreasing resource clustering. Without any correlation of resources — i.e. in a random landscape — observations do not provide

Table 6.1: Optimal inference radii (R) depending on the degree of clustering (σ) of the landscape. The upper row shows the degrees of clustering (σ) assumed for each of the five tested landscape settings. The lower row sums up the results shown in figure 6.4 and shows the resulting optimal inference radii (R) for each landscape. Optimal values for R are those that lead to the highest foraging success. Note that since the landscape is grid-based R may only take integer values. The difference between the landscape clustering parameter (σ) and its estimate, i.e. the optimal inference radius (R), may be due to the distortion of σ while fitting the Thomas landscape to the hexagonal grid.

landscape clustering (σ)	1	2	4	6	20
optimal inference radius (R)	2	3	5	6	*no optimum*

information about the status of unobserved cells (see figure 6.4, right panel). In these landscapes there is no difference in performance between individuals following an ARS, and those using an internal map with or without spatial information.

Heterogeneity in cluster size (figure 6.5; left panel) does not alter the general findings reported above. The presence of larger clusters leads to a clear increase in foraging success for the optimal informed strategy in comparison to the ARS. The informed strategy shows a highly efficient intra-patch search behaviour (see figure 6.3) and avoids leaving a resource cluster before having harvested it thoroughly. Evidently, heterogeneity in the degree of clustering (figure 6.5; right panel) reduces the efficiency of all search strategies (including ARS and BCRW) since, without any behavioural plasticity, it is difficult do find an optimal strategy for such a landscape. Yet, as long as the landscape is not completely random (as in figure 6.4; right panel) the optimal informed strategy still performs better than an ARS.

6.4 Discussion

In the past several concepts and models for the movement of informed foragers have been presented (e.g. van Gils 2010; van Moorter et al. 2009; Mueller et al. 2011; Nathan et al. 2008a; Getz and Saltz 2008). To our knowledge the above presented model is among the first, however, to combine the effects of four fundamental cognitive abilities: perception, memory, inference and anticipation. In addition, it is not implemented as a derivate of a random walk (Gautestad and Mysterud 2010a,b; Gautestad 2011; van Moorter et al. 2009). Admittedly, the solutions employed here to save information in an internal map, to account for inference and implement anticipation are very simple and probably not optimal solutions for each of these sub-problems. For the problem of inference, for example, Bayesian approaches (e.g. Klaassen et al. 2006) may provide optimal solutions. Yet, note the good fit between the degree of resource clustering (σ) and

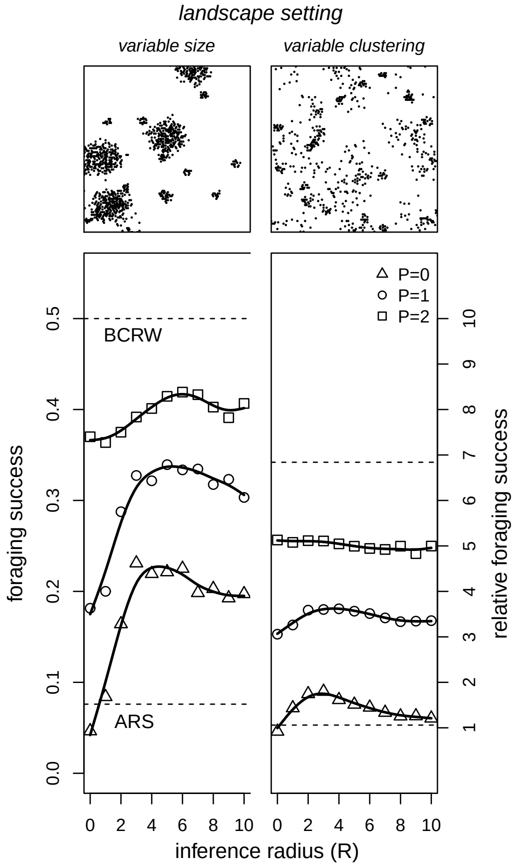

Figure 6.5: Heterogeneous landscapes: influence of inference radius (R), perceptual range (P) and of landscape attributes (from left to right: heterogeneity in cluster size, heterogeneity in degree of clustering) on foraging success, i.e. resource items found per iteration for 100 replicates. The relative foraging success can be read from the right y-axis (relative to the mean resource content of 5%, i.e. the foraging success of a straight line search). For comparison foraging success of the best ARS and BCRW are shown as dashed lines. The continuous smoothed lines are smooth spline regressions ($\lambda = 0.45$).

the estimate provided by the optimal inference radius (R; see figure 6.4 and table 6.1). Modified solutions of the travelling salesman problem (e.g. Wong et al. 2010) would constitute ideal anticipation algorithms. We chose not to combine these approaches — which are typically complex on their own — into a single unified movement model in order not to blur the main message we intend to convey. Moreover, nature itself may often provide only simple 'rules of thumb' that perform approximately as well as theoretically optimal solutions.

Due to the use of an internal map, the spatially informed search strategy improves efficiency of foraging at two scales: within patches and during the transition between patches. This can be seen in figure 6.3 B where the focal animal clearly changes from an (optimally) straight walk between resource clusters to a systematic search within such patches. Particularly in densely clustered landscapes foraging success may be more than tripled compared to an ARS (figure 6.4, left panel). Crucially, these patterns emerge from our implementation of basic cognitive attributes (perception, memory, inference and anticipation). Note that similar hybrid search strategies with high search efficiency have been described by Zollner and Lima (1999): their 'average-distance rule' incorporates straight-line search and a circling path. Yet, in their model these patterns are explicitly implemented and not emergent properties of an underlying mechanistic movement model (Mueller and Fagan 2008; Getz and Saltz 2008).

Here, we show that inference and anticipation based on perception and memory are crucial components of foraging behaviour leading to high search efficiencies. This is quite different from an ARS where search effort is also concentrated to resource patches but is nonetheless random and thus less efficient. Evidence for systematic searching has been found in numerous animal taxa (see Bartumeus and Catalan 2009, and literature cited therein). The adequacy of inference in our model crucially depends on the radius (R) used to infer the state of cells not yet visited. The optimal choice of R must reflect information about the statistical properties of the landscape (in particular the degree of clustering σ; figure 6.1, figure 6.4 and table 6.1). Individuals may learn such information in the course of their life. However, for many taxa that live in stable environments we may also assume that this information is 'learned' evolutionarily and stored in the genome.

We have also analysed the effect of increasing the radius of perception (P). We show that increasing the range of perception obviously increases foraging efficiency. At the same time it reduces the value of inference (figure 6.4 and 6.5). As a consequence a BCRW which assumes an infinite perceptual range does not need any inference. Note that for the ARS inference is implicitly included in the decay rate.

Interestingly, in addition to rather straight movement between patches and a grid-line search behaviour within patches our model may also generate looping behaviour (figure 6.3 C) similar to the 'foray searches' reported for many insect species, mammals and birds (e.g. Conradt et al. 2003; Conradt and Roper 2006). In our model the responsible mechanism underlying the emergence of this movement pattern is the use of spatial memory in combination with inference and anticipation. Individuals remember locations in which resources were present and assign a higher probability of finding resources to cells in the surroundings. Depending on the assumed correlation distance of resources this area may extend beyond a resource patch. This zone of influence of observed occurrences is further increased by anticipation. Foragers leaving a resource patch may then be re-attracted to a patch left a short while ago.

In our model we did not allow for any memory decay. Individuals remember everything they have perceived throughout their life. However, the ability to memorize presumably comes with a cost. It is thus interesting to ask how well our search strategy would perform if memory were restricted to a certain time span. Additional simulation runs with such limited memory show that restricting memory to even just the last 10 movement steps has a minor effect on foraging success. In fact, when individuals use much too large and suboptimal inference radii (e.g. $R = 10$ in a densely clustered landscape with $\sigma = 1$) limited memory may even increase foraging success. Such an overestimation of the degree of clustering of a landscape leads to intense search in the vicinity of resources (see figure 6.3 D). Limited memory compensates this error and, in this case, drives the individual away from already explored landscape areas. This phenomenon is similar to the observation of Boyer and Walsh (2010) who find in a BCRW model that — besides the inclusion of random steps — an intermediate use of memory is optimal. This happens because the use of memory alone results in a lack of exploratory behaviour which is important in changing landscapes. This idea also applies to our model, although the landscape changes only in space (resources are clustered) and not over time as in Boyer and Walsh (2010). Of course, the robustness of our model to memory loss is due to the destructive foraging scenario. If resource dynamics were included a movement strategy which infers resource content over space and time would be advantageous. Including an estimate for regrowth speed could be done in analogy to the inference radius.

The landscapes shown in figure 6.4 evidently assume a fairly constant degree of resource clustering (σ). Most natural landscapes though will be heterogeneous in this respect. This strict assumption is relaxed in figure 6.5. Although it might be impossible to find a truly optimal strategy in such cases (under the premise of no behavioural plasticity) we show that our movement rules are still advantageous in comparison to an ARS, regardless whether the landscape is heterogeneous in cluster size or the degree of clustering (see figure 6.5). From figures 6.4 and 6.5 it is clear that the inference radius becomes less important with increasing randomness of the landscape. The optimal spatially informed strategy still may have an advantage over an ARS since information use leads to a good exploitation of the dense clusters and is not relevant in those parts of the landscape showing only more or less randomly distributed resource items. In summary, for intermediate cases the efficiency of the informed strategy will be reduced in comparison to landscapes with homogeneous clustering and diminish with increasing proportions of less densely clustered resources, just as figure 6.4 suggests. Note that this only relates to heterogeneity in clustering, i.e. to the form of the boundary of resource clusters. Our results are not affected by varying cluster core sizes (see figure 6.5), since foraging success in a cluster core is not dramatically affected by suboptimal inference radii (see figure 6.3).

Our model focuses on the search for a single critical resource, which does not need to be food, but could also be e.g. plants suitable for oviposition. However, if the internal state of the focal animal was to shift from foraging to e.g. oviposition, mate finding, or search for shelter, several layers of internal maps representing the known or inferred distribution of different commodities could be included into the model (see Getz and Saltz 2008). Such multiple maps — appropriately weighted according to current needs and motivations — could then be overlaid and integrated to generate a more realistic movement decision.

The development of appropriate movement and dispersal models is central for a better understanding of population and evolutionary dynamics. This has important implications in applied ecology and conservation (e.g. metapopulation viability see Heinz et al. 2006). Nathan et al. (2008a) and also Mueller and Fagan (2008) have pointed out that modelling of animal movement should be more firmly based on mechanisms. Inspired by growing evidence that a large number of taxa use more or less complex internal maps for navigation (rodents: Hafting et al. 2005; Manns and Eichenbaum 2009; Wills et al. 2010; apes: Normand et al. 2009; Normand and Boesch 2009; birds: Thorup et al. 2007; for reviews see Moser et al. 2008; Moser and Moser 2008), we have proposed a very simple, yet novel model including perception, limited spatial memory and the use of spatial information. We could show that these simple assumptions lead to wide array of emergent phenomena reaching from optimal within and between-patch search to foray loops. To a certain degree our model is an approximation of a Bayesian forager with restricted perception who updates its prior information about the landscape to a posterior expectation depending on learned or inherited information about the resource distribution in the landscape. As it stands, the model represents a first step to a better understanding of the mechanisms behind movement behaviour. Further refinements should include a better statistical model for memory based inference of the state of so far not visited cells, a model of anticipation that allows to plan more than one movement step into the future and the inclusion of distance dependent (imprecise) perception as well as restricted and imprecise memory.

7

Discussion

Contents

7.1 Hierarchical levels of observation

As outlined in the introduction (p. 1), dispersal evolution is driven by forces arising at all levels of biological complexity, stretching from genes via individuals, populations and communities to landscapes (see figure 1.5, p. 10, and Kubisch et al. in prep.). It is important to realize that the eco-evolutionary consequences of all these forces can in turn be studied at different organizational levels (figure 7.1). One can analyse shifts in allele frequencies, phenotypic evolution and individual differences, effects on the dynamics of spatially structured populations such as changes in patterns of turnover and occupancy or shifts in the spatial distribution of species in landscapes.

If one thinks of dispersal as a three step process (see figure 1.4, p. 8) consisting of emigration, transition and immigration it is clear that, for a mechanistic understanding of SSP dynamics, the individual level plays an important role: individual behaviour during all three dispersal phases determines the dynamics observed at all other levels. In my work I have therefore concentrated on the individual level for both eco-evolutionary forces and the level of observation (see also figure 7.1). I have studied the consequences of mobility trade-offs and information use taking into account especially individual differences such as polymorphisms.

7.2 Individual level observations

7.2.1 Individual differences

In the last years research on individual differences has become a topic of widespread interest (Dall et al. 2012). Such differences among individuals in one population are particularly intriguing since they may be larger than between population differences, as in plants showing dimorphic seeds (heterocarpy; chapter 3, p. 39) or in wing-dimorphic insects (chapter 4, p. 57), for example. This topic has been studied and analysed using three more or less different frameworks: individual niche specialization, division of labour in social taxa, and more recently animal personalities (for a review and synthesis see Dall et al. 2012).

My work is best situated in the first framework, i.e. individual niche specialization. Chapter 3 (p. 39) for example shows how such individual differences may emerge. Maternal investment, i.e. a trade-off between maternal fecundity and the dispersal ability of propagules, leads to the evolution of a bimodal and fat-tailed dispersal kernel (figure 3.2, p. 48). This results in a polyphenism, as all individuals have the same genotype, i.e. dispersal kernel, yet show distinct phenotypes: some are long-distance dispersers and some only disperse short distances or not at all. These two types occupy two distinctly different “niches”: the non-dispersers inherit the mother’s location in space

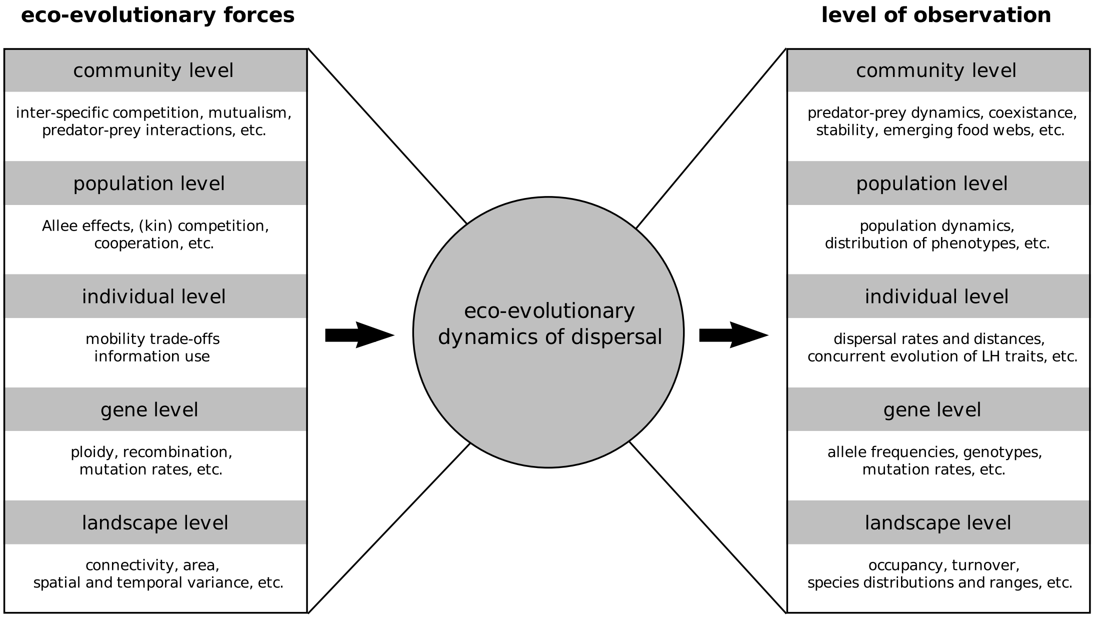

Figure 7.1: Overview of the eco-evolutionary forces arising from different levels of complexity (left) and the level on which their effects can be observed (right). My work mostly focuses on gene and individual level eco-evolutionary forces — such as ploidy or recombination and mobility trade-offs and information use — and their effects that can be observed at the individual level — such as evolutionarily stable dispersal rates and distances and especially individual differences in these life-history (LH) traits.
Note that some factors may appear on both sides of this graph. One example shown here are mutation rates. Mutation rates are an evolutionary force (left side), but mutation rates may in turn be subject to evolution ("second order evolution"; right side). As a consequence, it may be interesting to analyse the evolution of mutation rates during species invasions, for example. Another example are patch extinction rates (not shown). In an SSP showing deterministic succession (river banks prone to flooding, for example) extinction rates are evolutionary forces (left side) which are determined by the environment. Yet, extinction rates or turnover can also be observed and measured (right side). The values will probably differ because of rescue effects (see figure 1.4, p. 8).

and assure the local persistence of this genotype ("territorial inheritance") while the long-distance dispersers are responsible for spatial gene flow.

Such individual differences, e.g. wing-dimorphisms in the sand field cricket *Gryllus firmus* (e.g. Roff 1994; King and Roff 2010) or heterocarpy in the Asteraceae *Heterotheca latifolia* (Venable and Levin 1985), are always initially observed in the phenotype and do not have to be due to a true genetic polymorphism. In general, polymorphisms can occur at the genetic, phenotypic and behavioural level (see chapter 4, p. 57, for a discussion). Note that the conditions for the emergence of genetic polymorphisms can be quite restrictive. An example for a genetic polymorphism is presented in chapter 4 (p. 57), more specifically I show how gene (ploidy and linkage) and individual level mechanisms (mobility trade-offs and random vs. assortative mating) may lead to individual differences. I implemented a mobility trade-off and was able to show that the emergence of polymorphic dispersal strategies observed in chapter 3 (p. 39) in the specific context of maternal investment, is more generally valid. Given random mating and linkage of the diploid loci governing the trade-off and emigration rates polymorphic dispersal strategies evolve also at the gene level.

In such spatially structured populations turnover is decisive for the evolution of dispersal polymorphisms, as dispersers and non-dispersers are subject to quite different evolutionary pressures. In chapter 4 (p. 57) I show that this can lead to the concurrent evolution of high dispersal propensity and investment in dispersal ability. Of course, other life-history traits may show concurrent adaptations. SSPs with turnover include two distinct “niches”: patches with populations which have reached their carrying capacity, i.e. high competition environments, and empty, or low competition, patches as a consequence of turnover. This can lead to the emergence of r-and K-strategists (MacArthur and Wilson 1967) if one allows the concurrent evolution of dispersal and e.g. resource use efficiency (e.g. Fronhofer et al. in prep. b).

7.2.2 Individual movement

Knowledge about inter-individual differences and their ecological and evolutionary origins is certainly of great importance for a better mechanistic understanding of the dynamics of SSPs. Therefore, it is crucial to include individual level mechanisms and processes explicitly into models of animal and plant dispersal. All models presented in this thesis are mechanistic models of dispersal. Of course, as models are always simplifications of real systems (Kokko 2005), a number of details will not be included. One major aspect that is not taken into account in most models of dispersal evolution is the exact individual realization of the transition phase (figure 7.2). These models completely ignore the question how a given dispersal distance is realized by an individual movement strategy, i.e. the specific movement behaviour of individuals is not taken into account, and the models are not mechanistic at this microscopic scale.

The small number of models that do explicitly include the transition phase mostly adhere to the random walk framework (e.g. Bartoń et al. 2012). These models assume that individuals move randomly and ignore all attributes of their environment (but see Bartoń et al. 2009, for omniscient individuals). Even in models that take into account that individuals may have access to considerable amounts of information on the location of resources, for example, the resulting movement path is assumed to be inherently random (for a review of random walks models in biology see Codling et al. 2008).

This approach has been criticised previously by Nathan et al. (2008a) who propose a revolutionary movement ecology paradigm which assumes that an animal’s movement path is the result of its motion and navigation capacity as well as of its internal state and external factors. Based on this paradigm, I have developed a completely novel model of animal movement which relies on four key elements: perception, memory, inference and anticipation (chapter 6, p. 95). This is a first approximation of a complex transition process, yet the results are very promising. My implementation of this spatially informed forager leads to the emergence of a highly efficient search strategy by maximizing foraging efficiency at two levels: inter-patch movement is effectuated in a straight line walk, while discovered resource patches are depleted systematically in a grid-line search (see chapter 6, p. 95).

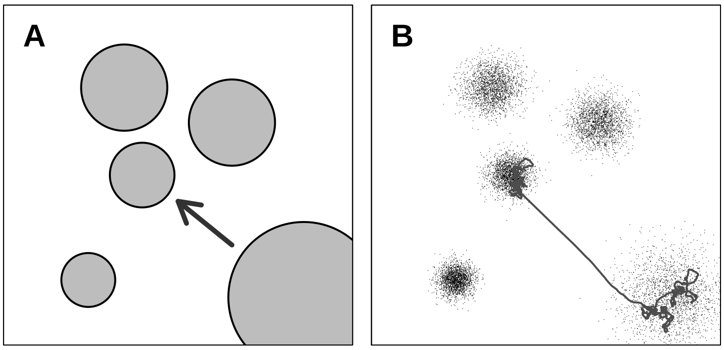

Figure 7.2: Dispersal in spatially structured populations. Most models of animal and plant dispersal are firmly rooted in the metapopulation concept (see chapter 2, p. 15) and assume discrete habitat patches separated by a hostile matrix (A). Yet, the idea of a spatially structured population is grounded in the fact that resources are often autocorrelated in space (B). Mechanistic models that include the transition phase should therefore model movement in a continuous world (B). Black points are resource items and the grey line represents the movement path of an individual performing an area restricted search (ARS; see chapter 6, p. 95).

7.2.3 From individual movement to dispersal and SSP dynamics

Ultimately, such models, which include mechanistic movement rules implemented at the individual level, will allow us to gain a better understanding of patterns that can be observed at higher levels of complexity (figure 7.1). Introducing regrowing resources, i.e. patch dynamics, into my mechanistic model of animal movement leads to the establishment of home ranges which means that individual animals tend to stay in their natal patch. Occasional dispersal events, i.e. home range shifts, are then an emergent phenomenon. This will allow me to bridge the gap between movement and dispersal ecology (figure 7.2) by modelling the eco-evolutionary dynamics of dispersal at a microscopic scale while being able to track the system's dynamics at all scales — stretching from individual movement paths to macroscopic landscape level dynamics such as range shifts.

7.3 Scaling up to landscape level observations

So far, I have considered the effects of gene and individual level eco-evolutionary forces and discussed the resulting patterns one can observe at the individual level (figure 7.1). Now, I would like to extrapolate from individual level observations and consider possible implications of my work for more macroscopic patterns that can be observed at the landscape level, such as species ranges, for example.

Trade-offs and the evolution of dispersal, fecundity and competitive ability during range expansions have been studied by Burton et al. (2010). Individuals at the range margin were found to be typically more fecund and dispersive, but less competitive than individuals in the range core, which may lead to an increase in the velocity of range expansions. This again is a typical example of r- and K-selection (see above). Note that such a three-way trade-off and the resulting pattern of highly dispersive and more fecund individuals at the range margin may explain why some field studies do not report a trade-off between fecundity and dispersal ability, but, on the contrary, a positive correlation (e.g. Saastamoinen 2007).

As described above and in chapter 4 (p. 57), the emergence of a stable dispersal polymorphism requires significant turnover, i.e. more or less classical metapopulation dynamics (see chapter 2, p. 15). Such metapopulation dynamics may be found at range margins since these are characterized by a dynamic equilibrium of colonizations and extinctions (see e.g. Holt and Keitt 2000; Oborny et al. 2009). In contrast, in the range core, an area showing no or very limited turnover, one should expect a homogeneous population with a lower dispersal rate.

Analogous effects can be observed if the focus lies on dispersal distance and not on dispersal rate. Starrfelt and Kokko (2010) have studied the evolution of dispersal distance in the context of parent-offspring conflict during species invasions and could show, among other phenomena, that mean dispersal distance increases during invasions. This is due to the evolution of heavily fat-tailed dispersal kernels, especially under maternal control of dispersal. I obtained a similar result already in an equilibrium scenario (chapter 3, p. 39) which suggests that the bimodality and high tail weight I report would only be reinforced in an invasion scenario.

In conclusion, mobility trade-offs do not only lead to the emergence of individual differences at the genetic and phenotypic level, but also to increased dispersal distances and invasion speeds (see also Elliott and Cornell 2012). These phenomena observed at the individual level may influence macroscopic patterns observed at the landscape level, such as the rate of species' range expansions. At this large scale, populations may become spatially inhomogeneous and show a marked difference between strategies found in the range core and at the range margin.

7.4 Bridging the gap between theoreticians and empiricists

Polymorphisms and individual differences have been studied for quite some time by empiricists (for an early review see Harrison 1980). In contrast, theoreticians are just beginning to unravel the underlying mechanisms and processes (see above). Empiricists are aware of condition dependent emigration, transfer or immigration and other complexities such as information use. Although these processes may critically influence population dynamics, a majority of theoretical work often does not include this necessary realism. Note that this asymmetry is not one-sided: theory has produced important predictions like the emergence of fat-tailed dispersal kernels (Hovestadt et al. 2001) that have only poorly been analysed in the field (but see chapter 5, p. 71). As a consequence, over the last decades a significant mismatch has developed between theory and empirical work in the context of dispersal ecology (Travis et al. 2012).

This disconnection could be overcome if more studies included both findings from theory or modelling and experimental work in the field. Unfortunately, such dual approaches are not common in (dispersal) ecology (but see for example Ronce et al. 1998). One example can be found in chapter 5 (p. 71), where I analyse the eco-evolutionary dynamics of non-random dispersal, i.e. information use, experimentally in the field and in an individual-based simulation model. These experiments were carried out in a lowland tropical rainforest in Costa Rica and explored the use of chemical cues for dispersal decisions in a phoretic flower mite. I could show that these mites non-randomly mix two different dispersal vectors in order to achieve fat-tailed dispersal kernels and directed dispersal towards suitable habitat. I simultaneously developed an individual-based simulation model, which is general enough to allow me to perform a detailed analysis and simple enough to understand the processes responsible for the observed dynamics. The model is still sufficiently complex to capture important system specific ecological processes. This dual approach was invaluable since it allowed me to correctly interpret the results (see figure 5.2, p. 84) and to understand important patterns such as the high variation present in both field and simulated data. In addition, modelling allowed me to pinpoint the eco-evolutionary processes acting in the system and to generalize my results appropriately.

Theory guided field work is essential for modern ecology (for a recent discussion see Restif et al. 2012). Besides being used as in chapter 5 (p. 71), modelling is important for the generation of sensible hypotheses that can then be tested in the field. Most eco-evolutionary dynamics are so highly non-linear that it may be difficult to forward (non-trivial) hypotheses about an ecological system of interest. In addition, simulation models may be used to test the planned experimental design, the appropriateness of the statistical methods and may allow to estimate effect sizes (see also Zurell et al. 2010, and the “virtual ecologist” approach).

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Author contributions

Chapter 2: E. A. Fronhofer, A. Kubisch, F. M. Hilker, T. Hovestadt, and H. J. Poethke. Why are metapopulations so rare? *Ecology*, 93(8):1967–1978, 2012.

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Chapter 3: E. A. Fronhofer, H. J. Poethke, and U. Dieckmann. Evolution of dispersal distance: maternal investment leads to bimodal and fat-tailed dispersal kernels. in preparation.

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Chapter 4: E. A. Fronhofer, A. Kubisch, T. Hovestadt, and H. J. Poethke. Assortative mating counteracts the evolution of dispersal polymorphisms. *Evolution*, 65(9):2461–2469, 2011.

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Chapter 5: E. A. Fronhofer, E. B. Sperr, A. Kreis, M. Ayasse, H. J. Poethke, and M. Tschapka. Picky hitch-hikers: vector choice leads to directed dispersal and fat-tailed kernels in a passively dispersing mite. *Oikos*, submitted.

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Chapter 6: E. A. Fronhofer, T. Hovestadt, and H. J. Poethke. From random walks to informed movement. *Oikos*, in press, DOI: 10.1111/j.1600-0706.2012.21021.x.

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I confirm that I have obtained permission from both the publishers and the co-authors for legal second publication.

I also confirm my primary supervisor's acceptance.

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1991 – 1995	Elementary school. German European School Singapore

Teaching experience

2010 – present	Supervision of Diploma and B.S. Theses
2011 – 2012	Teaching Assistant: “Systemanalyse und Simulation in der Ökologie”, ecological modelling (B.S.)
2010 – 2012	Teaching Assistant: “Grundlagen der Populationsökologie”, population ecology (B.S.)
2011	Teaching Assistant: “Globales Handeln in global und lokal vernetzten Entscheidungsprozessen”, game theory and strategic decisions in global networks, transferable skills course
2010 – 2011	Teaching Assistant: “Tierökologie 2: Grundlagen der Statistik”, statistics (B.S.)

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Professional activities

Refereeing	Ecology, Oikos, Behavioural Ecology and Sociobiology, Movement Ecology
Membership	European Society for Evolutionary Biology (ESEB), Gesellschaft für Ökologie (GfÖ), Society for Tropical Ecology (gtö)

Conference organisation

2012	Co-organiser of the 7th International Symposium of the Graduate School of Life Sciences, University of Würzburg.
2012	Co-organiser of the 7th Annual Workshop of the GfÖ AK "Young Modellers in Ecology" (YoMos) in Craheim
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Selected conference contributions

E. A. Fronhofer, E. B. Sperr, H. J. Poethke, and M. Tschapka. Host plant and vector recognition in a phoretic flower mite. Oral presentation, 42nd Annual Meeting of the Ecological Society of Germany (GfOE), Lüneburg, Germany, 2012.

E. A. Fronhofer, A. Kubisch, F. Hilker, T. Hovestadt, and H. J. Poethke. Why are metapopulations so rare? Oral presentation, Ecological Society of America (ESA) 97th Annual Meeting, Portland, OR, USA, 2012.

E. A. Fronhofer, J. Liebig, O. Mitesser, and H. J. Poethke. Variance manipulation and the dominance of despotism. Oral presentation, First Joint Congress on Evolutionary Biology, Ottawa, Canada, 2012.

E. A. Fronhofer, and H. J. Poethke. Moving from random walks to mental maps. Oral presentation, 12th Congress of the European Ecological Society (EEF), Ávila, Spain, 2011.

E. A. Fronhofer, A. Kubisch, T. Hovestadt, and H. J. Poethke. Genetic Linkage and the Evolution of Dispersal Polymorphisms. Oral presentation, 40th Anniversary Meeting of the Ecological Society of Germany (GfOE), Giessen, Germany, 2010.

K. Dolos, A. Kubisch, **E. A. Fronhofer**, T. Hovestadt, and B. Reineking. Bark beetle outbreak patterns: A theoretical study of the evolution of dispersal distance and aggregation strength. Poster presentation, 40th Anniversary Meeting of the Ecological Society of Germany (GfOE), Giessen, Germany, 2010.

E. A. Fronhofer, A. Kubisch, T. Hovestadt, and H. J. Poethke. Stray or Stay? Evolution of dispersal polymorphisms can be triggered by a mobility-fertility trade-off. Poster presentation, Ecological Society of America (ESA) 95^{th} Annual Meeting, Pittsburgh, PA, USA, 2010.

E. A. Fronhofer, O. Mitesser, and H. J. Poethke. Evolution of optimal group sizes in cooperative breeders. Poster, Evolution of Cooperation Conference (TECT IIASA), Vienna, Austria, 2009.

Invited talks

E. A. Fronhofer. Trade-offs and information use in spatially structured populations. Biodiversity Research Centre, Université Catholique de Louvain (UCL), Louvain-la-Neuve, Belgium, 2012.

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Publications

E. A. Fronhofer, H. J. Poethke, and U. Dieckmann. Evolution of dispersal distance: maternal investment leads to bimodal and fat-tailed dispersal kernels. in preparation.

E. A. Fronhofer, J. Liebig, O. Mitesser, and H. J. Poethke. Resource limitation favours the evolution of cooperative breeding and eusociality. in preparation.

E. A. Fronhofer, H. Märkle, and H. J. Poethke. Cooperative foraging and the evolution of group size polymorphisms in spatially structured populations. in preparation.

A. Kubisch, **E. A. Fronhofer**, and H. J. Poethke. Where am I and Why? Synthesising range biology and the eco-evolutionary dynamics of dispersal. in preparation.

E. B. Sperr, **E. A. Fronhofer**, M. Ayasse, and M. Tschapka. Host recognition in the phoretic flower mite *Spadiseius calyptrogynae*. in preparation.

E. A. Fronhofer, E. B. Sperr, A. Kreis, M. Ayasse, H. J. Poethke, and M. Tschapka. Picky hitch-hikers: vector choice leads to directed dispersal and fat-tailed kernels in a passively dispersing mite. *Oikos*, submitted.

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A. Kubisch, **E. A. Fronhofer**, H. J. Poethke, and T. Hovestadt. Kin competition as a major driving force for invasions. *Am. Nat.*, in press.

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