Evolution of dispersal and specialization in systems of interacting species

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Würzburg, den 22. November 2012

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Thotsapol Chaianunporn

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Chapter 1

Introduction: Evolution of dispersal and specialization in systems of interacting species

Nowadays, many species are threatened by human activities, such as habitat destruction (Brook et al. 2003) and global climate change (Walther et al. 2002; Parmesan and Yohe 2003; Thuiller et al. 2005; Thomas et al. 2004, 2006). Biologists indeed predict that a sixth mass extinction might be under the way (Barnosky et al. 2011). Specifically, species that closely interact with other species are considered especially vulnerable as their responses and adaptation might lead to temporal and spatial mismatch with partner species (Visser and Both 2005; Parmesan 2006; Schweiger et al. 2008; Berg et al. 2010; Kiers et al. 2010; Pelini et al. 2010) and possibly results in co-extinction of both species (Dunn et al. 2009). For this reason, the ecology and evolution of such interacting systems should be understood in order to assess their risk of extinction and to find right conservation strategies for them.

1.1. Examples of complex species interaction system

One example for a close interaction is the large blue butterfly *Maculinea arion*, an extremely specialised social parasite on *Myrmica* ant hosts. In summer (June–July), adult butterflies lay eggs between flower buds of a specific food plant (*Thymus* spp. or *Origanum vulgare*). Larva instars feed on flower heads for three weeks and develop from larva stage I to III, but gain little weight. After moulting to final larva stage (IV), a larva drops to the ground and waits to be discovered and picked up by *Myrmica* ant workers – while several different Myrmica species (*M. sabuleti*, *M. lobicornis* and *M. scabrinodis*) will do this, typically only a single host species (at one location) will ultimately care for the larva at one local area (Als et al. 2004; Thomas et al. 2005*b*). After discovery, ants carry the larva back to their nest and place it among their brood. A *M. arion* larva feeds on ant broods, mainly large ant larvae and gains about 98% of its final biomass by feeding on this diet. A larva pupates after ten months in the *Myrmica* nest and emerges as a butterfly 2 – 3 weeks later. Adult butterflies lives above ground and have no direct interaction with ants (Thomas et al. 2005*b*, 2009; Schönrogge et al. 2006).

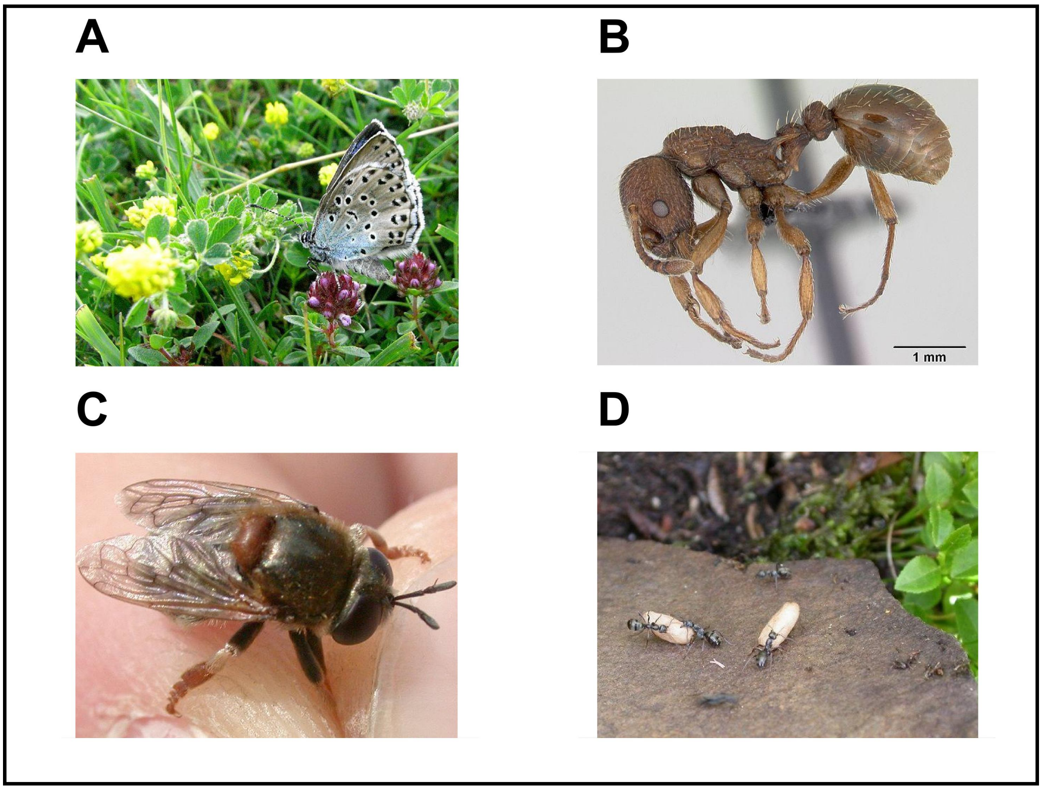

Figure 1.1: Examples of interacting species pairs: (A) large blue butterfly *Maculinea arion*; (B) *Myrmica sabuleti* host ant of *M. arion*; (C) hoverfly *Microdon mutabilis*; (D) *Formica lemani* host ant of *M. mutabilis.* (images by (A) Pengannel, 16 June 2008 via Flickr, Creative Commons Attribution; (B) April Nobile, 9 August 2007 via AntWeb.org, Creative Commons Attribution; (C) PaulT, 5 July 2002 via wikipedia.org, Creative Commons Attribution; (D) © Copyright Derek Parkinson, 4 July 2008 via geograph.org.uk, Creative Commons Attribution.).

Another example for close interactions comes from a hoverfly species *Microdon mutabilis*, which is also a social parasite – in this case of ants *Formica lemani*. *Microdon* specializes on a single host species and it shows extreme local host specificity –when *Microdon* eggs are introduced into *F. lemani* nests that are more than 3 km away from the natal nest, egg survival is reduced from *c*. 96% to 0% (Schönrogge et al. 2006). *Microdon* larvae feed on eggs and small larvae of ants. After two years, a larva pupates and ecloses to become an adult. Adults live *c*. 3–7 days above ground and female lays eggs at the edges of *F. lemani* nests. Female dispersal is extremely limited (<2 m) typically resulting in oviposition in the same natal nest over generations. This may be a response to the sharp increase in egg mortality over distance mentioned above. In comparison, *Maculinea arion* adults which have not such exceptional host type specificity fly over 100 m in their distribution range and oviposit throughout the site. I just show these two fascinating examples of species interaction as examples of how complex and specific such species interactions may be. Moreover, these examples reflect the relationship between species interaction, specialization and dispersal. Some interesting questions arise out of these systems, for example how will they respond to recent habitat disturbance and anthropogenic climate change, and can they survive such threats? More important, what can we do to conserve such amazing systems? One approach helping us understanding such systems and predicting their responses is framing the system in terms of a ‘metacommunity’.

1.2. Metacommunity approach

A metacommunity can be defined as “a set of local communities that are linked by dispersal of multiple potentially interacting species” (Wilson 1992; Leibold et al. 2004; Holyoak et al. 2005), while a community is defined as “the individuals of all species that potentially interact within a single patch or local area of habitat” (Holyoak et al. 2005). The metacommunity approach was created as a framework for explaining the dynamics of entire communities in spatially structured landscapes. This approach should provide insights how spatial integrated mechanism can determine patterns of distribution, abundance, species interaction, and diversity at local and regional (metacommunity) scale (Leibold et al. 2004; Holyoak et al. 2005). From these definitions, one can see that two elements playing a main role in the metacommunity are ‘species interaction’ and ‘dispersal’ (Leibold et al. 2004). At the local level, species in local community interact with each other. The interactions can be considered in different levels from pairwise interaction like conventional Lotka-Volterra models, trophic structure, or foodweb interactions. At regional level, dispersal connects local communities and can have many consequences, from colonization of empty sites to ‘rescue effect’ (Brown and Kodric-Brown 1977; Hanski 1999) or ‘mass effect’ (Shmida, and Wilson 1985; Mouquet and Loreau 2002, 2003) affecting species abundance, species interaction, community structure and dynamics (Holt et al. 2003; Leibold et al. 2004).

Evolution might affect metacommunity dynamics in many aspects, for example adaptation or maladaptation of species in landscape with heterogeneous resource would modify species compositions in local communities, while evolution of dispersal and habitat specialization modifies habitat connectivity (Urban and Skelly 2006). On the other hand, metacommunity dynamics might influence evolution of species within metacommunities, e.g. diverse communities and heterogeneous landscape might generate a complex selection mosaic for interacting species (Thompson 2005; Urban and Skelly 2006). For these reasons, an ‘evolving metacommunity’ approach that assumes (or allows for) genetically determined trait variation within species with an evolutionary process is important to provide explanations on how spatial variation and dispersal determines local adaptation, species sorting (differences in the local demography of species and the outcomes of local species’ interactions causing by heterogeneous local patches – Leibold et al. 2004) and spatial and temporal patterns of interspecific interaction (Urban and Skelly 2006; Urban et al. 2008, 2012). In addition, this approach should allow us to understand and predict how species or a community can ecologically and evolutionary respond to changing environments, such as global climate change (Urban et al. 2008, 2012).

Surprisingly, although the metacommunity and evolving metacommunity approach are established, the evolutionary relationship between two core elements, dispersal and interspecific interaction are not well understood. Indeed, most theoretical studies on dispersal evolution assume that target species do not interact with other species (Comins et al. 1980; Gandon and Rousset 1999; Travis and Dytham 1999; Travis et al. 1999; Perrin and Goudet 2001; Poethke et al. 2003, 2007). Only few studies did take species interaction into account – and those that did were limited to simple two species antagonistic interaction (Rohani and Ruxton 1999; French and Travis 2001; Briggs and Hoopes 2004; Lett et al. 2005; Green 2009; Poethke et al. 2010; Pillai et al. 2012). Therefore, there is still a lack of understanding of the dispersal evolution in both pairwise and multispecies system. For this reason, in this thesis, I will focus on how various principal types of species interaction affect dispersal evolution in more specious communities. Moreover, I will consider dispersal evolution in a widened context, exploring its concurrent evolution with habitat specialization (habitat niche width) under parasite pressure with spatial and temporal heterogeneity and climate change. In addition, I also focus on consequences of dispersal and its interaction with group tolerance on selection on group recognition and group formation.

1.3. Metapopulation and metacommunity dynamics

Metapopulation (or metacommunity) dynamics can be defined as spatial changes in the distributions or abundances of individuals or species (Holyoak et al. 2005). It is one of main issues in metapopulation as well as metacommunity ecology (Hanski 1998, 1999; Holyoak et al. 2005). These dynamics depend mainly on the details of recolonization, dispersal, and population growth (Hanski and Gaggiotti 2004). Holyoak and Ray (1999) actually list five key mechanisms driving these dynamics, i.e. (1) *extinction-recolonization dynamics*; (2) *rescue effects,* i.e. the reduction in local extinction rates by immigration (Brown and Kodricbrown 1977); (3) *population size effect* or mainland island effect – a smaller population is rescued by colonists from a larger population; (4) *source-sink dynamics,* i.e. rescue of populations in inferior habitats (sink populations) by immigrants from populations in superior habitats (source populations); (5) *habitat turnover* where patch destruction leads to extinction of local populations and patch creation produces new opportunities for colonization. These mechanisms can generate complex spatial pattern in species abundance of single or interacting species system even in homogeneous environment (Hassel and Wilson 1997; Tilman and Kareiva 1997; Hanski 1998).

Spatial and temporal heterogeneity (of landscapes) can influence metapopulation and metacommunity dynamics in many ways, especially in interacting species systems because both factors have many ecological and evolutionary consequences. As examples, such heterogeneity influences the evolution of dispersal (Comins et al. 1980; Hastings 1983; Travis 2001; Poethke et al. 2003, 2011) or may promote the stability of a host and parasite system (Hassell and Wilson 1997; Briggs and Hoopes 2004; Brockhurst et al. 2006). Moreover, spatial heterogeneity influences the evolution of transmission rate and virulence of parasites (Boots and Sasaki 1999; Haraguchi and Sasaki 2000; Thrall and Burdon 2002) and affects local adaptation between host and parasite (Thompson 1999*a*, 2005) and their genetic diversity (Chaianunporn and Hovestadt 2011).

1.4. Dispersal

Dispersal is a key ecological and evolutionary process that has influence not only on an individual’s fitness, but also population dynamics, species distribution, population genetics, and species diversity (Hanski 1999; Clobert et al. 2001; Bowler and Benton 2005). Moreover, it is a strategy for species to respond and survive under natural and anthropogenic disturbance, such as climate change or habitat loss and fragmentation (Parmesan et al. 1999; Hanski 2001; Thomas et al. 2001; Kokko and Lopez-Sepulcre 2006; Parmesan 2006; Phillips et al. 2010; Hof et al. 2011).

Dispersal is defined as “any movement of individuals or propagules with potential consequences for gene flow across space” (Ronce 2007). Although It was originally assumed that dispersal is a process independent of environmental conditions (Johnson and Gaines 1990), many theoretical as well as empirical studies show that dispersal can be driven by many ecological and evolutionary factors, such as population density (Travis et al. 1999; Poethke and Hovestadt 2002; Hovestadt et al. 2010), kin competition (Hamilton and May 1977; Comins et al. 1980; Gandon and Rousset 1999; Bach et al. 2006; Poethke et al. 2007), inbreeding avoidance (Gandon 1999; Perrin and Goudet 2001), population dynamics (Holt and McPeek 1996), spatio-temporal habitat variability (Comins et al. 1980; Travis and Dytham 1999; Travis 2001; Poethke et al. 2003). I schematically summarize the effects of these factors on dispersal evolution in Figure 1.2.

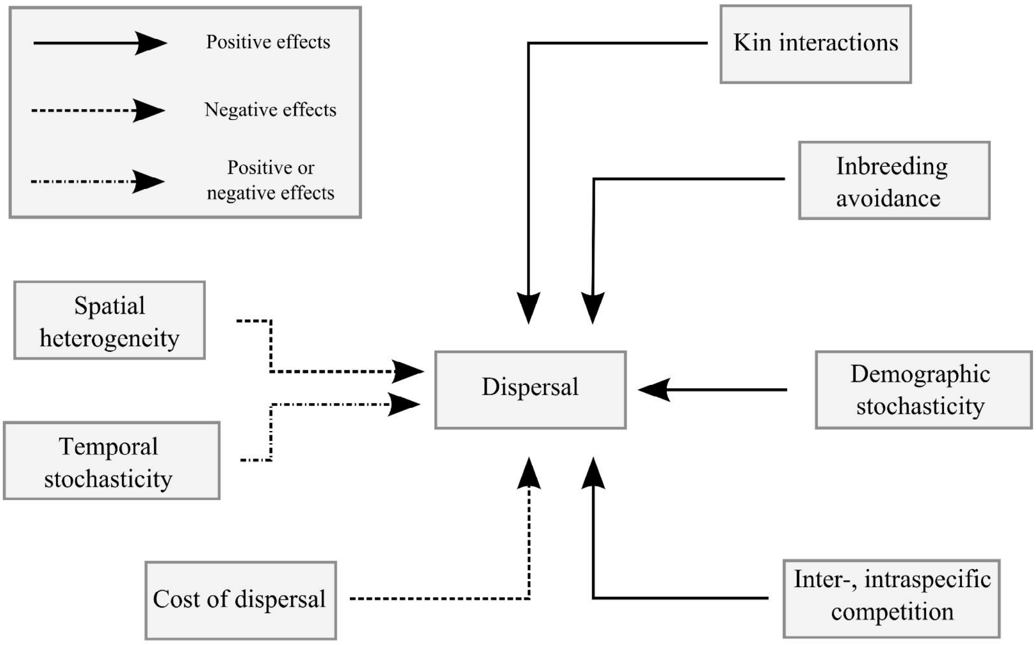

Figure 1.2: Schematic presentation of factors that affect dispersal evolution.

For a long time, researchers focus only on kin and intraspecific competition as a core factor determining dispersal evolution (Hamilton and May 1977; Comins et al. 1980; Gandon and Michalakis 1999; Ronce et al. 2000*a*; Lambin et al. 2001; Poethke et al. 2007). Nonetheless, there are many empirical studies highlighting that other types of (interspecific) interactions can influence dispersal too, such as antagonism (Heeb et al. 1999; Weisser et al. 1999; Boulinier et al. 2001; Sloggett and Weisser 2002; Kunert and Weisser 2003; Mondor et al. 2005) or mutualism (Leonardo and Mondor 2006; Mondor et al. 2008). The evolution of dispersal in systems of two interacting species is, however, only marginally investigated (Rohani and Ruxton 1999; French and Travis 2001; Briggs and Hoopes 2004; Lett et al. 2005; Green 2009; Poethke et al. 2010; Pillai et al. 2012). Dispersal evolution in complex (more specious) communities is even less examined, although this would be important for understanding the future ecological and evolutionary responses of communities to climate change (Urban et al. 2012).

In this thesis, I will investigate the dispersal evolution in different contexts, i.e. under pressure of different interaction types (commensalism, mutualism, and parasitism) and different community structure (pairwise and multispecies system). Moreover, I study effects of interrelationship between species interaction and spatial and temporal heterogeneity on evolution and interaction of dispersal with habitat specialization and habitat preference as dispersal can also have evolutionary consequences by interacting with (or feeding back on) the evolution of other traits. Lastly, I explore the consequences of dispersal coupling with group tolerance on group recognition and group formation

1.5. Consequences of interspecific interaction

Interspecific interaction may have multiple ecological and evolutionary consequences, e.g. coevolution (van Valen 1973; Janzen 1980), or behavioural modification such as decrease in activity, modification of responses to environmental stimuli, or the manipulation of moving behaviour of hosts (Poulin 1994; Thomas et al. 2002, 2005*a*). Interactions may further change genetic and species diversity (Frank 1993; Haldane 1992; Summers et al. 2003; Duffy et al. 2008; Duffy and Forde 2009; Yoder and Nuismer 2010; Chaianunporn and Hovestadt 2011) and species distribution (Richardson et al. 2000). Sometimes, species interactions lead to evolution of traits that are directly linked to their interaction. Examples can be morphological traits, such as the bill size of North American crossbills that specialize on the structure of lodgepine cones (Benkman 1999; Benkman et al. 2003), biochemical traits, such as the toxin in newts of genus *Taricha* and toxin resistance in the garter snake *Thamnophis sirtalis* (Brodie and Brodie 1999; Brodie et al. 2002) or behavioural traits, such as manipulation by a parasitic hairworm that cause an infected grasshopper to jump into water, where the adult parasite reproduces (Thomas et al. 2002). Moreover, prominent examples of evolution mediated by interspecific interaction can be found in resistance and virulence (May and Anderson 1983; Boots and Mealor 2007; Wild et al. 2009), dispersal ability (Weisser et al. 1999; Sloggett and Weisser 2002; Kunert and Weisser 2003; Mondor et al. 2005; Leonardo and Mondor 2006; Mondor et al. 2008), or habitat or resource preference (Singer et al. 2004; Diamond and Kingsolver 2010; Choutt et al. 2011).

In contrast to parasitism, relationships between mutualistic partners such as plants and their pollinators are seldom reciprocally specialized because specialization has high risk of mismatching between partners and spatial and temporal uncertainty (Anderson et al. 2005; Johnson and Steiner 2000). Nonetheless, there are some examples showing that a mutualistic interaction can also lead to coevolution of hosts' and mutualistists' trait, for example the 'mega-nosed' fly *Moegistorhynchus longirostris* which has an extreme long mouth part and pollinate plants in summer-flowering species of Iridaceae, Geraniaceae and Orchidaceae. Several species in these flowering plants have evolved long-tubed flower and are pollinated exclusively by this fly (Manning and Goldblatt 1997).

Dispersal is an important trait respectively strategy that responds to interspecific interaction because with dispersal an individual can avoid its undesirable antagonistic partners and/or follow its mutualistic partners. Therefore, it is expected that an individual should adjust its dispersal behaviour corresponding to presence/absence of partner species. Indeed, this behaviour is observed in many species, for example many aphid species can produce either developing a winged (dispersal morph) or unwinged morph according to presence of parasites, predators or mutualists (Weisser et al. 1999; Sloggett and Weisser 2002; Kunert and Weisser 2003; Mondor et al. 2005; Leonardo and Mondor 2006). Under predator or parasitoid pressure, aphids produce more winged offspring, which can colonize new plants (Weisser et al. 1999; Sloggett and Weisser 2002; Kunert and Weisser 2003; Mondor et al. 2005), whereas the presence of facultative bacterial symbiont *Candidatus Regiella insecticola* can reduce the proportion of winged offspring in the pea aphid *A. pisum* (Leonardo and Mondor 2006). However, how this selection pressure driven by species interaction acts and interacts with other selective force such as community structure, dispersal cost (or dispersal mortality) and environmental stochasticity is not well studied.

Multispecies interactions might results in different ecological and evolutionary outcomes than what would emerge under pairwise interactions (Thompson 1999*b*; Strauss and Irwin 2004; Thompson 2005). Moreover, multispecies models should be more realistic than single species or pairwise species models because organisms mostly interact simultaneously with many other species and rarely with just a single mutualistic or antagonistic species (the later may occur in highly specialized systems where guests live e.g. inside their host organism; e.g. wild primates and many of their endoparasites including viruses, protozoans and helminths – Pedersen et al. 2005). In addition, study of evolving multispecies metacommunity should provide a more realistic and more accurate view of change in species diversity in response to climate change (Urban et al. 2012). Nonetheless, it is also important to investigate single and pairwise species models as a building brick for understanding more complex metacommunity models. In this thesis, I will thus study and compare effects of different types of interspecific interaction and different community structure on dispersal evolution (see more details below). In chapter 2, I will focus on the effects of different interspecific interaction types on dispersal evolution and how the effects are influenced by other selective forces such as dispersal mortality and environmental stochasticity (extinction risk) and community structure (by comparison between pairwise and multi species systems).

1.6. Dispersal and habitat specialization

Dispersing individuals face another problem when living in heterogeneous landscape, as their fitness may vary between habitat types beyond simply survival–non-survival. Often scientists assume that in this habitat selection process, organisms have to trade-off spectrum of suitable habitats (niche width) with the maximum fitness in optimal habitat (Levin 1962, 1968; Wilson and Yoshimura 1994) as captured in the phrase “Jack of all trades, master of none”. Accordingly, organisms may be categorized along a spectrum ranging from highly specific habitat (or resource) specialists to habitat generalists (opportunists). While a specialist can use narrower range of habitats or resources, it can perform better in its optimal habitat than a generalist.

Indeed, dispersal and habitat specialization show close relationship with each other (Poisot et al. 2011). As a species evolves into a habitat specialist, apparent landscape heterogeneity increases from that species' perspective because fitness reduction associated with moving from optimum to suboptimum habitat is steeper for a specialist than a generalist. Theory has long established, however, that spatial heterogeneity selects against dispersal (Comins et al. 1980; Hastings 1983; Travis 2001; Poethke et al. 2003, 2011) because dispersal would move individuals from well-adapted to poorer habitats and thus reduce the fitness expectation of migrants: Habitat heterogeneity adds an implicit settlement cost to dispersers (Bonte et al. 2011). For this reason, one can expect that when the landscape surrounding an individual is heterogeneous, habitat specialists should perform limited dispersal, whereas a habitat generalist should be more dispersive. It is in turn likely and intuitive that dispersal can also affect the evolution of specialization (Brown and Pavlovic 1992; Day 2000; Ronce and Kirkpatrick 2001; Parvinen and Egas 2004; Nurmi and Parvinen 2008, 2011; Nurmi et al. 2008).

It is also likely that species interaction can modify habitat utilization of partner species because it can modify habitat quality and thus affect habitat specialization. For example, mutualists can promote habitat generalization since they facilitate expansion of host tolerance to environments (Richardson et al. 2000; Poisot et al. 2010). Natural enemies can affect habitat specialization, since they reduce fitness expectation in host's optimal habitat or resources and drive hosts to utilize suboptimal habitats that are free of enemies or to modify resource preference (Jeffries and Lawton 1984; Poisot et al. 2010; Chaianunporn and Hovestadt 2011; Choutt et al. 2011). This phenomenon is observed in many species. The bog fritillary butterfly *Boloria eunomia*, for example, frequently laid eggs in suboptimal habitats when parasite abundance was high in optimal habitats (Choutt et al. 2011). As another example, pressure from parasitoids can alter food plant preference in the generalist caterpillar *Grammia geneura* (Singer et al. 2004) and the tobacco hornworm *Manduca sexta* (Diamond and Kingsolver 2010). In chapter 3, I will study the evolution of dispersal and habitat specialization in more details. I will present how these two evolutionary traits are influenced by species interactions, trade-off between niche widening and fertility (cost of generalization), and landscape arrangement.

1.7. Adaptation to global climate change

It is reported and predicted that global climate change impacts behaviour, diversity, and distribution of many species (Hoegh-Guldberg 1999; Hughes 2000; Peñuelas and Filella 2001; Walther et al. 2002, 2005; Parmesan and Yohe 2003; Root et al. 2003; Badeck et al. 2004; Parmesan 2006; Thomas 2010; Corlett 2012). Indeed, in this context, dispersal is an ecological key attribute of species because (only) dispersing individuals could move along with changing climate leading to distribution range shift or range expansion (Hill et al. 1999; Parmesan et al. 1999; Thomas et al. 2001; Parmesan and Yohe 2003; Hickling et al. 2006; Parmesan 2006; Moritz et al. 2008). Nevertheless, dispersal is not the only possible way in which a species could responds to climate change. It could persist under the climate change in situ due to phenotypic plasticity in population e.g., acclimatization (the physiological adaptation of an animal or plant to changes in climate or environment) or developmental adjustments (Dawson et al. 2011), genetically adapt to the new climate by increasing tolerance (Skelly et al. 2007; Oliver and Palumbi 2011), or adjust preference (and abilities) to new local temperature regimes (Levitan 2003; Balanyá et al. 2006). Moreover, species may simply change their phenology (Peñuelas and Filella 2001; Badeck et al. 2004; Visser and Both 2005; Franks et al. 2007). One might argue that such evolutionary process cannot occur fast enough to track climate change. However, some studies highlight that evolution in traits like e.g. thermal tolerance or thermal preference can occur rapidly within few generations (Good 1993; Skelly and Freidenburg 2000; Balanyá et al. 2006; Skelly et al. 2007).

Clearly, all these possible responses are not mutually exclusive. A species can ‘follow’ two or more of these ‘strategies’ at the same time. In addition, the climate change might lead to modification of individuals’ surrounding in many aspects, such as vegetation height or habitat dryness (Allen et al. 2010; Elmendorf et al. 2012). For this reason, multidimensional responses might be more suitable than responses in a single trait. An example for such multidimensional responses includes range expansion and shift in host preference of the European butterfly *Aricia agestis*. During its range expansion, the *A. agestis* also rapidly expanded its niche width by shifting its host plant from genus *Helianthemum* to *Geranium* and *Erodium* species (Thomas et al. 2001). Further, the responses of a species sometimes are context specific, e.g. moose *Alces alces* that show different responses at different sites, i.e. they have persisted, undergone habitat shift by changing elevation and topography or migrated to other sites depending on the pattern of climate change and the capacity of populations (Dawson et al. 2011). These interactions between different types of evolutionary and ecological responses should be understood in order that we can assess the threat of climate change on each species and manage right conservation strategies.

As already discussed above (section *1.5. Consequences of interspecific interaction*), species interaction can affect evolution of some traits that are also important for adaptation to climate change, such as dispersal, habitat (or resource) preference, and habitat specialization (including temperature tolerance). In some cases, however, climate change might affect species interactions and result in massive effects on species distribution and diversity. Pounds et al. (2006), for example, propose that increasing temperature promoted growth of a pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*) causing outbreaks and leading to extinction of many amphibian species. Further, species interaction might have large implications for the (evolutionary) responses of species to climate change. An accounting for interactions may be important for correctly predicting (future) response to climate change. Unfortunately, there are only few studies focusing on the response of interacting species to such change (Berg et al. 2010; Urban et al. 2012).

As described here, responses to climate change of a species might be very complex because they relate with many traits and might be different under different conditions. For this reason, a theoretical framework is important for understanding this phenomenon. I thus will study the multidimensional evolutionary responses of a host species to climate change which consist of dispersal, temperature preference (optimal temperature) and temperature tolerance (niche width). Moreover, I compare these responses in different conditions, i.e. under interspecific interaction, different trade-off structure for generalization and different spatial landscape.

1.8. Dispersal and group formation

In some systems, certain ‘marker traits’ play an important role for the recognition and adoption of new members into groups respectively the reproductive success of group members. An example of such marker traits include bird song where singing the ‘right’ dialect may promote male reproductive success (Tomback and Baker 1984; Slabbekoorn and Smith 2002), while strangers singing ‘unfamiliar’ dialects suffer from reduced mating success. Another example is chemical profiles in social insects (Zinck et al. 2009; Meunier et al. 2011; Sturgis and Gordon 2012) that affect e.g. the adoption of new queens into colonies. Interestingly, there may be as such nothing specific about a certain dialect or a certain chemical profile – the fitness relevance primarily emerges because local groups reach a ‘consensus’ on how a proper group member should sing, smell, or look like and thus impose costs on rare phenotypes (positive frequency dependent fitness). Nonetheless, such traits might have other functions such as recognition and avoidance of (social) parasites (Gardner and West 2007; Martin et al. 2011).

According to the Hamilton’s rule, emergence of such traits in an altruism group is expected because it enables a group member to behave altruistically towards other group members, but reject non-group members or other species that will exploit the group (Hamilton 1964). Dawkins (1976) proposes this idea in his ‘green beard’ hypothesis that states that holders of the green beard gene could recognize other bearers of the same gene and target cooperative behaviour toward them. It has, however, been argued that – because of the complicated threefold assumption underlying the idea (bearing the trait, recognizing it, cooperating with it) – such genes were unlikely to emerge (Hamilton 1964; Dawkins 1976; Maynard Smith 1976; Grafen 1998). Further, for the classic green beard genes, the genetic model predicts that green beard genes would soon go to fixation (Wade and Beeman 1994; Gardner and West 2010), unless it has deleterious effects on the fecundity of the trait holder (e.g. in the red fire ant, *Solenopsis invicta*; Keller and Ross 1998). It is thus questionable, why traits, such as chemical profiles or certain song dialects, do not go fixation, and how variants of such trait may (regionally) coexist.

Moreover, groups do sometimes contain members that are genetically diverse. Genetic heterogeneity can influence the group interaction because a group member in such a group has to face two problems: if an individual is too restrictive, it will have a relatively high risk to reject a desirable recipients (a rejection error), whereas if an individual is too permissive, it will have a relatively high risk to accept undesirable recipients (an acceptance error). According to the “optimum acceptance threshold model” (Reeve 1989; Starks et al. 1998), it is expected that organism should evolve the optimal or evolutionarily stable acceptance threshold (degree of tolerance) which minimizes both a rejection error and an acceptance error. Reeve (1989) suggests that this threshold might be a function of the relative frequencies of interactions and/or the fitness consequences of accepting or rejecting desirable respectively undesirable recipients.

It is known that dispersal is a factor that can determine within and among group genetic diversity because dispersal leads to ‘mixing’ of individuals with different traits and of different kin (Gandon 1999; Gandon and Michalakis 2002; Lenormand 2002; Ronce 2007), or in the other words, the frequency of interactions between similar and dissimilar individuals. High dispersal rate can lead to homogenizing genetic variation at larger scale (Gandon 2002; Vogwill et al. 2011). Consequently, different dispersal rate should have different effects on (and should correlate with) group tolerance and trait recognition. Correspondingly, dispersal is considered to be one of the most important aspects determining the mode of colony founding and reproduction in social insects (Hölldobler and Wilson 1990; Keller 1993; Pedersen and Boomsma 1999; Seppä et al. 2004; Sundström et al. 2005; Berghoff et al. 2008; Helmkampf et al. 2008). Ants, for example, tend to form polygynous groups when the dispersal is limited, whereas monogyny tends to be associated with long range dispersal. Similarly, dispersal is one of factors that determines the divergence of dialects between bird populations (Wright and Dorin 2001; Colbeck et al. 2010). However, theoretical studies and quantitative analyses of relationship between dispersal and group recognition system (consensus) are still absence – especially on how the two may feedback on each other’s evolution. For this reason, in this thesis, I will investigate consequences of dispersal and group tolerance on group formation of a species which uses its recognition trait for adoption new individual into a group. This should provide us an outlook how the diversity of the recognition trait observed in nature is *per se* maintained.

1.9. Topics of this thesis

In the following chapters, I will focus on the roles of interspecific interaction on evolution of dispersal and habitat specialization (habitat niche width) by utilizing spatially explicit individual-based models. In this work, I will use the terms “host” and “guest” to refer to two partners involved in an interaction. A guest species is defined as a partner that always gains from the interaction with its host, while a host either receives a disadvantage (parasitism; +, -), is unaffected (commensalism; +, o), or receives a benefit (mutualism; +, +) from the interaction. Further, a guest requires the presence of its hosts for survival and reproduction, while a host can exist and reproduce without guests. This is an obvious ‘asymmetry’ occurring in most (specialised) host-parasite or predator-prey systems but may also occur in mutualistic systems where the two partners may not equally strongly depend on the interaction.

In chapter 2, I investigate effects of different types of interaction (commensalism, mutualism, and parasitism), and different intensity of interactions on dispersal evolution of hosts and guests. Moreover, since the multispecies interaction might produce other ecological and evolutionary outcomes than just pairwise interaction (Strauss and Irwin 2004), I further compare results from pairwise interaction systems (one host and one guest species, Figure 1.3A) with those from multispecies systems (two host and two specialized guest species, Figure 1.3B). Furthermore, I explore how two selective forces on dispersal evolution, namely dispersal mortality and external extinction risk, modulate the effects of species interaction.

In chapter 3, I explore effects of species interaction (here only one host and one guest species either with a parasitic or commensalic interaction – Figure 1.3A) on dispersal and habitat niche width evolution in heterogeneous landscape by varying the habitat attribute of each patch. I do not include a mutualistic interaction in this study as the results presented in chapter 2 show that in two species system, the effect of mutualism does not differ greatly from that of commensalism. The habitat attribute under investigation should reflect a continuous property of habitat, such as ambient habitat temperature, soil pH, or sodium concentration. Spatial heterogeneity adds another dimension to dispersal evolution, because it adds a dispersal cost for hosts as an implicit ‘settlement cost’ (Bonte et al. 2011) due to the risk of moving from the well-suited natal habitat to a less suitable habitat where host fitness is reduced. In my models, guest’s fitness is not directly affected by habitat attributes.

To carry out my studies, I adapt the model introduced in the chapter 2 by implementing landscape heterogeneity that affects the fitness of the host species only. I introduce two evolving host traits besides dispersal, namely ‘host habitat preference’ representing optimal habitat of a host and ‘habitat niche width’ determining the degree of habitat specialization (respectively its ‘tolerance’) of a host individual. I focus on consequences of guest search efficiency (affecting intensity of interaction and population dynamics), the cost of niche widening (generalization; determined by habitat–fertility trade-off), and external extinction risk on concurrent evolution of dispersal and habitat niche width.

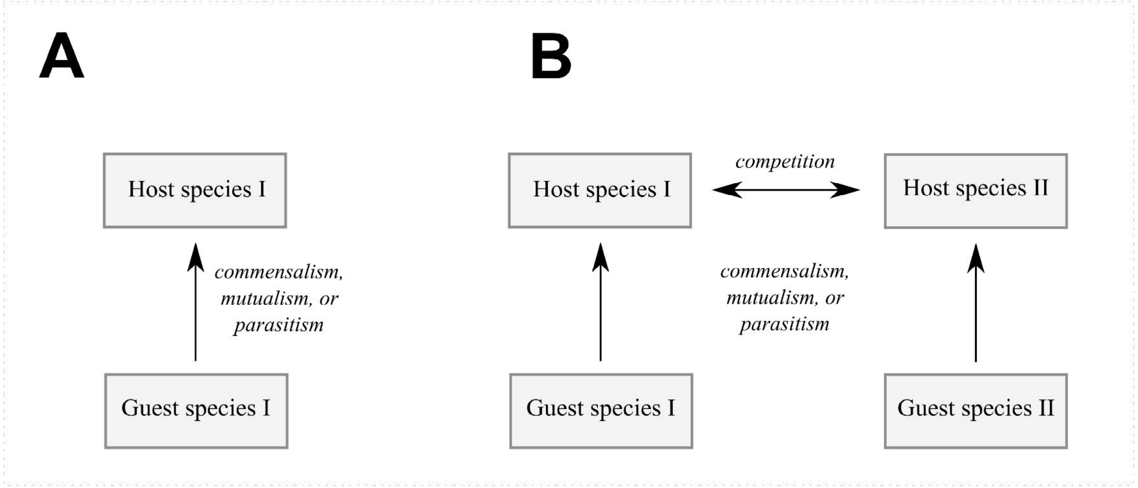

Figure 1.3: Schematic diagram representing species interactions in the studied systems: (A) two species system (one host and one guest species); (B) four species system (two host and two guest species).

In chapter 4, I introduce temporal dynamics of the habitat attribute (here we assume that it represents temperature) to investigate how climate change (increase in temperature) and parasitism (compared to commensalism) simultaneously influence evolutionary responses in host species. I assume three possible evolutionary responses of hosts to climate change, i.e. host individuals can move to a more suitable patch (selection on dispersal evolution), increase temperature tolerance (expansion of its niche width), or change temperature preference (local adaptation). Such a model of eco-evolutionary dynamics in a multispecies system with spatial context should provide a more realistic approach to predict future changes in response to climate change than simple single species models that often used to assess effects of climate change (Urban et al. 2012) because it is highlighted by many studies that biotic interactions are important drivers for a species’ response to the climate change (Hampe 2004; Brooker et al. 2007; Berg et al. 2010; Gilman et al. 2010; Urban et al. 2012). In addition, I already demonstrate in chapter 2 and 3 that parasitic interaction can determine dispersal and niche width evolution of hosts, two traits that play roles in response to the climate change.

In chapter 5 – somewhat separate from even though related to the other chapters – I utilize analytical as well as individual-based models to analyze effects of dispersal and group tolerance on group recognition system. Theoretical studies predict that such a group recognition trait should typically go to fixation (Wade and Beeman 1994; Gardner and West 2010) as the consequence of positive frequency-dependent selection (the more abundant a phenotype, the larger the benefit for its carrier). However, in real systems, we frequently observe diversity (even at small spatial scale) in such traits in different animal taxa (such as ants: Hölldobler and Wilson 1990; Vander Meer and Morel 1998; Meunier et al. 2011; in birds: Hausberger et al. 2008). Here, I use a simple model consisting of two groups with (potentially) two phenotypes of a ‘marker trait’ to explain under which conditions (dispersal and group tolerance) marker diversity might be maintained and local or regional coexistence of different phenotypes might be possible. I especially consider how dispersal affects coexistence but also on the existence of such recognition systems may feed back on the evolution of between group dispersal.

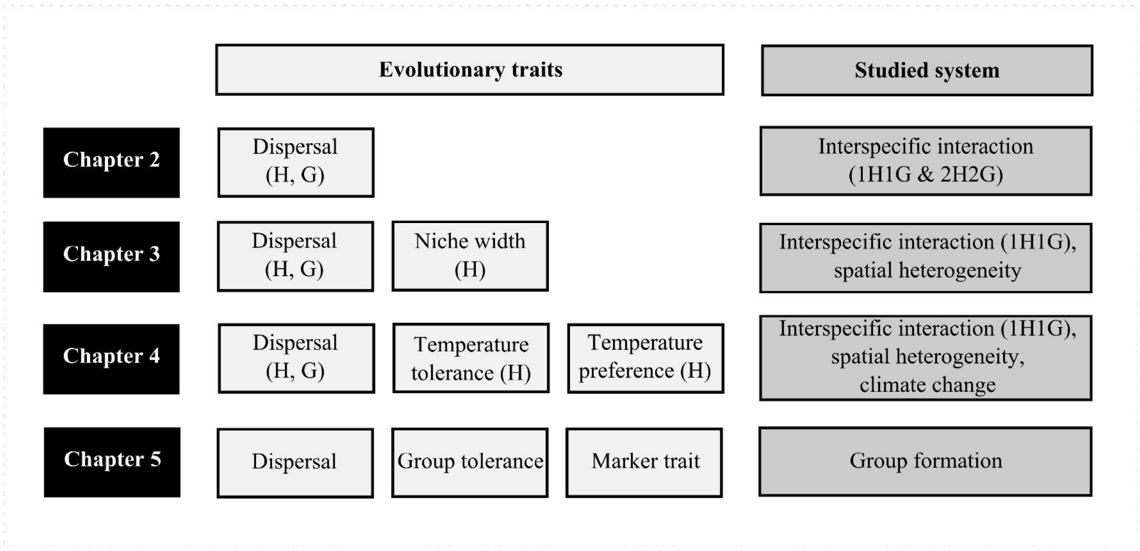

Figure 1.4: Schematic illustration contrasting the community structure under investigation in each chapter studied, as well as the traits allowed to evolve (H=host, G=guest; 1H1G=System consisting of one host and one guest species, 2H2G=System consisting of 2 host and 2 guest species).

I sum up and present the studied system from each chapter in Figure 1.4. In this figure, I show the connection respectively contrast between evolutionary traits and studied system in each chapter. The models in chapter 2–4 are based on a same individual-based metacommunity model and I build up the model by adding environmental (such as spatial and temporal heterogeneity) and trait elements (such as habitat niche width and temperature preference); therefore, the system of these three chapters show some similarity. This will also facilitate the future studies that focus on different aspects from what I explore in this thesis, for example evolutionary responses to climate change of multispecies system. In chapter 5, since I focus on the group recognition system, the model in this chapter is quite unique from the rest. However, it still resembles to the other models as presented in Figure 1.4 and group interaction should be analogue to the two-hosts-two-mutualists system in chapter 2.

In the last chapter, I summarize the role of interspecific interactions and them in combination with other selective forces on dispersal evolution. Moreover, I show how the prediction of multispecies system differs from that of single species system in the aspect of species’ response to global climate change. At last, I will present the future direction for further studies in aspect of ecological and evolution dynamics in metacommunity models.

Chapter 2

Evolution of dispersal in metacommunities of interacting species[1]

With Thomas Hovestadt

2.1. Introduction

Dispersal is an important strategy of organisms that plays a role in e.g. range expansion (Hill et al. 1999; Thomas et al. 2001; Walther et al. 2002; Hughes et al. 2003; Parmesan 2006) or their ability to cope with habitat loss and fragmentation (Hanski 2001). Understanding the ecological and evolutionary mechanisms underlying dispersal becomes increasingly important in light of anthropogenic climatic change and human-caused habitat destruction (Parmesan et al. 1999; Hanski 2001; Thomas et al. 2001; Parmesan and Yohe 2003; Parmesan 2006; Robinet and Roques 2010). Especially, for systems of interacting species, e.g. parasites and their hosts, predators and preys, herbivorous insects and their host plants, or pollinators and flowering plants, such environmental changes might have complex effects on individual fitness, population dynamics, and species distribution. They may lead to e.g. asynchrony of life cycles between partners in space (Schweiger et al. 2008; Kiers et al. 2010; Pelini et al. 2010) and time (Visser and Both 2005; Parmesan 2006; Berg et al. 2010). Ultimately, such a mismatch might lead to extinction of one or both partners.

It was originally assumed that dispersal is a process independent of environmental conditions (Johnson and Gaines 1990), but theoretical as well as empirical evidence suggest that the tendency of organisms to leave their natal patch can be condition-dependent (animals respond to external cues; see Bowler and Benton 2005) and phenotype-dependent (phenotypic trait adjusts dispersal propensity; Clobert et al. 2009). Moreover, several genetic and environmental factors are drivers of dispersal evolution (reviewed in Bowler and Benton 2005), e.g. kin selection (Hamilton

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and May 1977; Comins et al. 1980; Gandon and Rousset 1999; Bach et al. 2006; Poethke et al. 2007), inbreeding avoidance (Gandon 1999; Perrin and Goudet 2001), population dynamics (Holt and McPeek 1996), and spatio–temporal habitat variability (Comins et al. 1980; Travis and Dytham 1999; Travis 2001; Poethke et al. 2003).

Empirical studies suggest that interspecific interactions are also factors that influence dispersal related decisions, such as the production of dispersal morphs under predation pressure or with mutualistic partners (Weisser et al. 1999; Sloggett and Weisser 2002; Kunert and Weisser 2003; Mondor et al. 2005, 2008; Leonardo and Mondor 2006), or the avoidance of parasites (Heeb et al. 1999; Boulinier et al. 2001). In some cases, dispersal of one partner, such as a parasite or a mutualist, directly depends on the dispersal of its host that carries it away, because the species itself lacks the ability to move over large distances on its own (e.g. Perez-Tris and Bensch 2005; Bruyndonckx et al. 2009). In other instances, parasites manipulate host behaviours in order to facilitate their dispersal (Thomas et al. 2005).

Although an influence of species interactions on dispersal is expected and observed empirically, most theoretical studies on dispersal evolution assume that target species do not interact with other species (Comins et al. 1980; Gandon and Rousset 1999; Travis and Dytham 1999; Travis et al. 1999; Perrin and Goudet 2001; Poethke et al. 2003; 2007). Only few studies, did take species interaction into account – and those that did were limited to simple two species antagonistic interaction (Rohani and Ruxton 1999; French and Travis 2001; Briggs and Hoopes 2004; Lett et al. 2005; Green 2009; Poethke et al. 2010; Pillai et al. 2012). Many of these studies focus on the interplay between dispersal and the stability of host–parasite systems, and demonstrate that dispersal can stabilize or destabilize a host–parasite system depending on ecological factors (Rohani and Ruxton 1999; French and Travis 2001; reviewed in Briggs and Hoopes 2004; Lett et al. 2005). Some recent studies examine factors that can influence the dispersal evolution of two species involved in antagonistic interactions, and find that population growth rate of hosts, search efficiency of parasitoid (Green 2009), predation risk (Poethke et al. 2010), and strength of predation (Pillai et al. 2012) can affect dispersal evolution. Nonetheless, the effects of different types of interaction or the effects of more complex community organization on dispersal evolution have rarely been studied.

Here, we investigate effects of three types of interspecific interactions, namely parasitism, commensalism, and mutualism on dispersal evolution in a metacommunity context. For this purpose, we develop and utilize an individual-based model with a spatially explicit landscape. Moreover, we investigate how species richness of the community structure influences the evolution of dispersal probability by comparing simple (one host and one guest species referred as 1H1G) and complex communities (two host and two specialized guest species referred as 2H2G). Note that in this article, a guest species is defined as a partner that always gains from the interaction with its host, while the host either receives a disadvantage (parasitism; +,-), is unaffected (commensalism; +,o), or a benefit (mutualism; +,+) from the interaction. Further, reproduction of guests requires the presence of their hosts, while hosts can exist and reproduce without guests, like insect herbivores and their host plants. We hypothesize that interspecific interaction and community diversity play a critical role in determining the evolution of dispersal probabilities. However, we also expect that other factors already known to affect evolution of dispersal, such as dispersal mortality (e.g. due to habitat fragmentation) or external extinction can modify (or even override) the impact of interaction effects.

2.2. Model and simulation

We develop and utilize a spatially explicit, individual-based metacommunity model to simulate the community dynamics and the evolution of dispersal in host and guest species in a spatially explicit landscape. Using individual-based models (IBM) has benefits when evolutionary and ecological time scale cannot be separated and when the assumption of monomorphic ‘resident strategy’ is not appropriate (Waxman and Gavrilets 2005). Furthermore, IBMs account for the influence of kin competition by default (Bach et al. 2006; Poethke et al. 2007).

The landscape is modelled as a two-dimensional grid of identical habitat patches. To avoid edge effects, this grid is wrapped into a torus in both dimensions. Each habitat patch can support a community of species that can consist of one or two host and one or two specialized (see below) guest species. An individual is thus always characterized by its affiliation with a certain ‘guild’ (host or guest), and a certain species (relevant if we assume more than one species per guild), and by a trait coding for its dispersal probability. Hosts and guests are modelled as haploid organisms reproducing asexually; we thus ignore possible complications associated with sexual reproduction, such as inbreeding depression, or recombination. We assume that hosts and guests have a synchronized and simple annual life cycle with discrete generations. After reproduction, all adult individuals die, and newborn individuals (potentially) may disperse. After reaching a target patch, they reproduce.

Host reproduction: Without guests, a host individual of species *i* in patch *m* at time *t* produces a number of offspring drawn from a Poisson distribution with mean $\lambda_i(m,t)$ as described by the following equation adapted from the Beverton–Holt model (Beverton and Holt 1981):

$$\lambda_i(m,t) = \frac{\lambda_i(0)}{1 + \frac{(\lambda_i(0)-1)}{K_i} \cdot (H_i(m,t) + \beta_{ij} H_j(m,t))}, \tag{2.1}$$

where $\lambda_i(0)$ is the net growth rate and K_i the carrying capacity of patches for host species *i*, and β_{ij} is the competition coefficient representing the effect of host species *j* on host species *i*. $H_i(m,t)$ and $H_j(m,t)$ are the number of host species *i* and *j* in patch *m* at time step *t*, respectively. Accordingly, the number of host offspring in each patch is regulated by intraspecific as well as interspecific competition in scenarios with two competing host species.

Species interaction and guests' reproduction: In any simulation run, we allow for only one type of between-guild interaction (parasitism, mutualism, or commensalism). In systems with more than one guest species, all guest species are of the same interaction type, but each guest species is specialized on just one host species. The probability that an individual of host species H_i has an encounter with guest species P_i in patch *m* at time step *t* (encounter probability; $f(P_i(m,t))$) is calculated according to the Nicholson–Bailey equation (Nicholson and Bailey 1935) with a modified Holling's type II functional response (Holling 1959*a*, 1959*b*):

$$f(P_i(m,t)) = 1 - \exp\left(\frac{-a_i P_i(m,t)}{1 + a_i H_i(m,t)}\right), \tag{2.2}$$

where $H_i(m,t)$ and $P_i(m,t)$ are the number of host and guest species i in patch m at time t, and a_i is the per capita search efficiency of guests. In all simulations, a guest can interact with at most one host individual in its lifetime.

We assume that a guest encounter modifies the expected number of offspring for an 'infected' host from $\lambda_i(m,t)$ to $\rho_i\lambda_i(m,t)$, where ρ_i is defined by the type of interaction. We generally use ρ_i=0 for parasitism (i.e. infected hosts do not reproduce), ρ_i=1 for commensalism (no effect on host reproduction), and ρ_i=2 for mutualism, but also provide results for intermediate values of ρ_i in order to prove the generality of the results (see below). Note that by altering birth rates of hosts, guests implicitly affect the equilibrium density of the host population, because they do not change the mortality of hosts. Only guest individuals that encounter their appropriate host reproduce. The number of offspring produced by a successful guest is Poisson distributed with a mean value of ψ_i.

Dispersal: After reproduction, all adult hosts and guests die. Newborn hosts and guests decide to either disperse or remain in their natal patch (philopatry). An individual's decision to disperse depends on the dispersal probability d_h for hosts respectively d_p for guests. The trait determining the dispersal probability of each individual is constraint to $0 \leq d \leq 1$ and is inherited from its parent. Whether an individual disperses is decided by drawing a random number from the interval [0…1] – if the number is smaller than d the individual will disperse, otherwise it remains philopatric. In case of dispersal, an individual will move randomly to one of the eight neighbouring habitat patches (Moore neighbourhood; Gray 2003). Occasionally, this trait mutates with probability μ_h and μ_p for hosts and guests respectively (both fixed at 0.001) by drawing a random value from the uniform distribution [0…1].

Typically, we impose a dispersal cost on any dispersing individual, i.e. during dispersal, dispersing host or guest individuals die with probability c_h respectively c_p. In some scenarios, we set this cost to zero, however (see *Results*). After all (surviving) dispersers reach target patches, individuals mature and reproduce according to the rules specified above. In some scenarios, we further assume that local communities (host and guests) occasionally go extinct before reproduction with probability ε, due to e.g. external catastrophes.

Scenarios and parameter values: In this study, we focus on the effect of the species–interaction type on the evolution of dispersal probability in hosts and guests. For this purpose, we compare results for the three types of interaction as mentioned above. Moreover, we contrast dispersal evolution in simple communities (one host and one guest species; 1H1G system) with that in communities that consists of two host and two guest species (2H2G system). Note that in the 2H2G communities, direct interspecific competition only occurs between host species, but not between guest species, as each guest species is completely specialized on its single host. In order to prevent global loss of species in the 2H2G system, we assume that at each generation, newborn individuals occasionally mutate to the other species of the same guild with probabilities μ_h or μ_p for hosts or guests respectively, but retaining their original dispersal probability. With this mutation process and the fact that we consider the two host species in the system to be ecologically equivalent (see below), our system can be interpreted as two different strains within a species or as two ecologically similar species in the same functional group: Each host strain is “utilized” by one strain of guests, but not the other. For simplicity, we use the term “species” to describe these groups of individuals.

In order to simplify interactions in the system, we assume throughout that host species 1 and 2 are competitively equivalent ($\lambda_1(0)=\lambda_2(0)=5$; $K_1=K_2=K$; $\beta_{12}=\beta_{21}=1$). They would thus behave ‘neutrally’ (*sensu* Hubbell 2001) in the absence of guests, or if the interaction is commensal. As shown in several studies (e.g. Poethke et al. 2007; Green 2009), host carrying capacity K influences the evolution of dispersal due to its effect on demographic stochasticity and kin competition; however, a strong effect of kin competition is typically limited to lower K values. We ran preliminary simulations to test how K influences dispersal evolution. As expected, in the commensalism and mutualism scenario, K and thus demographic stochasticity only influence results as long as K is smaller than *c*. 200; the larger K, the lower the evolving dispersal probabilities (*Appendix I*, Figure 2.A1A and 2.A1B). We thus generally assume $K=500$ for those two scenarios. Interestingly, for the parasitism scenario, we observed an inverse effect of K, i.e. in larger populations, larger dispersal probabilities evolve. The rate of change becomes negligible at about $K\geq1000$ (*Appendix I*, Figure 2.A1C and 2.A1F). This interesting result warrants further exploration, which is beyond the scope of this study. Here we set $K=1000$ for all parasitism scenarios.

For guests, population size (carrying capacity) is implicitly controlled by the limited growth of host populations. We choose a low value of the mean number of offspring for guests species *i* (ψ_i=2) for two reasons. First, if ψ_i is too large, it may lead to collapse of the host population in the parasitism scenario. Second, iterations become computationally intensive in the mutualism scenario due to large number of hosts and guests establishing in the system. Further, the role of ψ clearly interacts with that of search efficiency or handling time as these parameters jointly define the growth of guest populations (see *Discussion*).

Since dispersal evolution is influenced by other forces than just the interaction type, we modulate in our simulations three additional factors affecting dispersal evolution: (i) Search efficiency of guests (a_i; see *eq.* 2.2), (ii) dispersal mortality of hosts and guests (c_h and c_p, respectively), and (iii) external extinction risk of local communities (ε). These factors have previously been shown to play a critical role in the evolution of optimal dispersal probabilities of organisms (Comins et al. 1980; Gandon and Rousset, 1999; Poethke et al. 2003; Bach et al. 2006; Green 2009).

We carry out simulations with values of a_i ranging from 0.005 to 0.05 in intervals of 0.003. Similar dispersal mortality of hosts and guests is always assumed; we vary the values of c_h and c_p from 0 to 0.26 in intervals of 0.02. We carried out additional simulations with non-identical dispersal mortalities for hosts and guests. As expected, the guild suffering from higher dispersal mortality evolves lower dispersal probabilities than the other guild, but the results presented here are not qualitatively affected by this modification. Three values of ε are used for the simulations, namely 0, 0.001 and 0.01 – results for the latter two values are provided only in *Appendix I*, Figure 2.A3–2.A4. Moreover, to test the generality of our results, we modulate, for a subset of simulation settings, the effect of guests on host fecundity (ρ_i) more gradually: While ρ_i=0 implies maximum damage by parasites (host castration) other values between 0 and 1 (commensalism) would imply weaker damage to hosts (partial fecundity reduction). In turn increasing ρ_i beyond 1 gradually increases the mutual benefit for hosts. We thus run simulations with $\rho_i \in [0, 0.05, \dots 2]$ at ε=0 and c_h=c_p=0.1. While ρ_i could principally grow to infinity, we consider a doubling (ρ_i=2) in host fertility already as a very large mutualistic effect and results suggest that behaviour does not change as p_i increases above 2. A summary of all model parameters and their standard values is provided in Table 1.

Table 2.1: Definition and ranges of values of parameters used

Symbol	*Description*	*Values*
a_i	per capita search efficiency of guest species *i*	$a_i \in [0.005, 0.008, ..0.05]$
$\lambda_i(0)$	net growth rate of host species *i*	5
ρ_i	effect of guests on host's fecundity for guest species *i*	0 (parasitism), 1 (commensalism), or 2 (mutualism)
K_i	patch capacity for host species *i*	1000 (parasitism), or 500 (commensalism and mutualism)
β_{ij}	competition coefficient of species *j* on species *i*	1
ψ_i	mean number of offspring for guest species *i*	2
μ_h and μ_p	mutation rates for hosts and guests	0.001
c_h	dispersal mortality of hosts	$c_h \in [0, 0.02, \ldots 0.26]$
c_p	dispersal mortality of guests	$c_p \in [0, 0.02, \ldots 0.26]$
ε	external extinction risk	0, 0.001, and 0.01
d_h	dispersal probability of hosts	evolving
d_p	dispersal probability of guests	evolving

Initial conditions: At the beginning of every simulation, all patches are initialized with *K* hosts. In 2H2G scenarios, we initialize hosts in a 'checkerboard pattern', i.e. each other patch contains *K* individuals of host species *i* respectively species *j*. The purpose of this checkerboard pattern is to increase heterogeneity in order to maintain diversity in mutualism scenarios; without such heterogeneity, a mutualistic 2H2G system would typically collapse into a 1H1G system due to positive frequency dependence that always generates a benefit for the more abundant species pair. In parasitism and commensalism scenarios, the spatial heterogeneity (checkerboard pattern) is maintained only transiently. We will return to the implications of this clearly very arbitrary setting in the *Discussion*. Simulations are always initialized with a small number of guests (10 of each guest species) in order to avoid the collapse of host population at the beginning of simulations. The value for the dispersal probability for every host and guest at the beginning is initialized with 0.01. Again, we initialize with low values to maintain the spatial heterogeneity initially created in the 2H2G systems. For the parasitism and commensalism scenario the initial values for dispersal probability play no role for the ultimate outcomes of dispersal evolution.

For the simulations, we create an elongated lattice landscape of dimension 128 x 8 patches. In comparison to a square landscape, this form promotes the emergence of clear spatial patterns at a lower total population size and thus saves computation time; the setting does not have a principal effect on our results. A single simulation runs over 4000 generations for the parasitism scenarios but only over 2000 generations for the commensalism and mutualism scenario. In the latter two scenarios, populations do not fluctuate as strongly as in the parasitism scenario and approach evolutionary equilibrium more quickly.

Analyses: In most simulations (parasitism with low search efficiency, commensalism and mutualism), evolving dispersal probabilities of hosts and guests converge to constant values after 1000 generations (*Appendix I*, Figure 2.A2A). However, in the parasitism scenarios with high parasite search efficiency (a_i) or in the 2H2G scenarios, host and parasite (meta) populations tend to fluctuate widely resulting in a perpetual oscillation of mean dispersal probabilities of hosts and parasites (*Appendix I*, Figure 2.A2B–2.A2F). Therefore, we average mean dispersal probabilities of hosts and guests over the last 100 generations of each simulation run for analysis.

To compare effect of population dynamics of hosts and guests on dispersal evolution, the encounter probability for hosts in one of the patches is calculated according to *eq.* 2.2. We use here the standard deviation of the arcsine-transformed encounter probability over time to capture the temporal dynamics of the system. It correlates well with the oscillation of host and guest populations: Low standard deviations indicate stable populations, while high deviations reflect strong population fluctuation. Note that we use the arcsine-transformation for the encounter probability because the latter cannot be normally distributed and its value is restricted to the range 0 to 1. This value is calculated for each scenario over the last 100 generations.

2.3. Results

1H1G: Commensalism and the effects of dispersal mortality and external extinction risk: For hosts, the 1H1G commensalism scenario can serve as a “reference case” because the interaction with guests is irrelevant to the hosts’ fitness and the evolving dispersal probabilities of hosts in this scenario are consequently not different from those evolving in a single species system. We first consider the impact of the other selective forces that can influence results in the commensalism scenario. Figure 2.1A shows that dispersal probability of hosts responds very sensitively to an increase in dispersal cost (dispersal mortality) falling from very high values if costs are null (d_h>0.5 at c_h and c_p=0) to very low values (d<0.02) if dispersal mortality becomes larger than 0.1. Search efficiency a_i of guests has no noticeable effect on the evolution of dispersal probabilities in hosts, however. Introduction of an external extinction risk (ε>0) generally leads to a rise in evolving dispersal probabilities (*Appendix I*, Figure 2.A3A–2.A3C). Both results – the influence of dispersal mortality and of external extinction risk on dispersal probabilities – are neither new nor surprising (see *Discussion*). However, we provide them here as reference so that we can better understand how species interactions modify their impact.

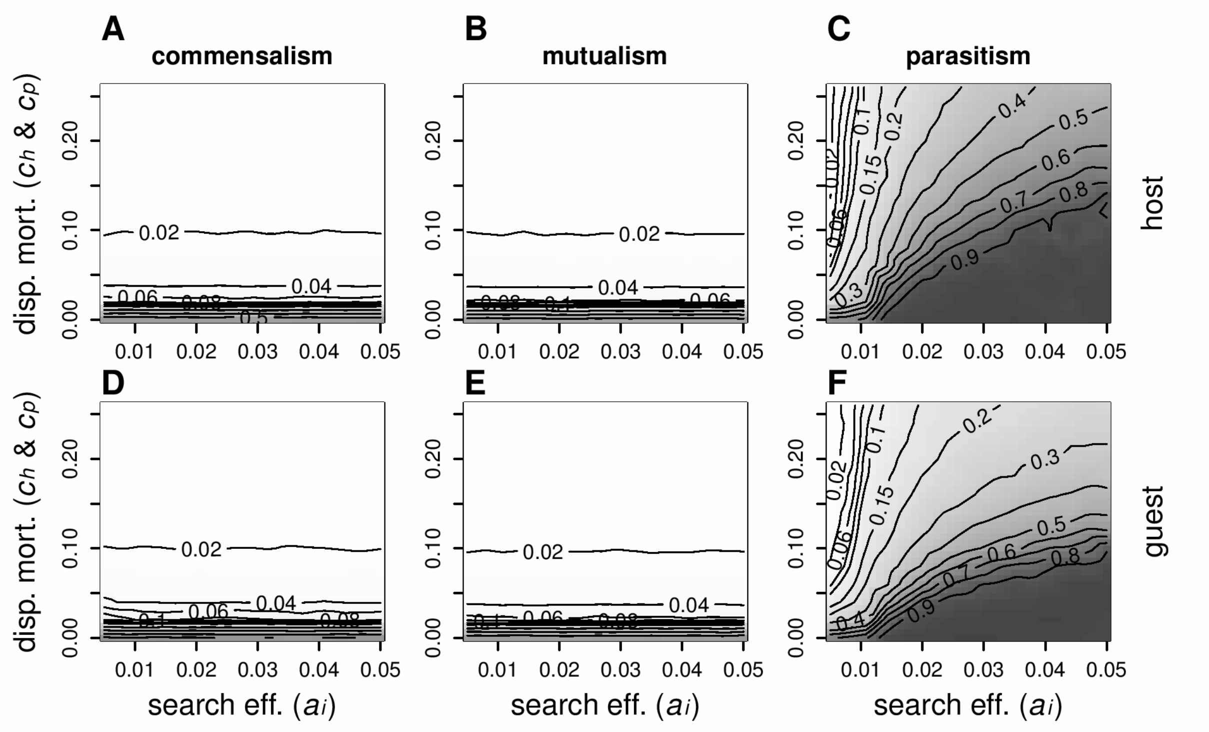

Figure 2.1: Effect of interaction type, guest search efficiency (a_i) and dispersal mortality of hosts and guests (c_h and c_p) on the evolution of mean dispersal probabilities in the one host one guest species (1H1G) scenarios: (A and D) commensalism; (B and E) mutualism; (C and E) parasitism. The upper row (A–C) shows results for hosts and the lower (D–F) for guests. Different gray tones and contour lines represent the evolving dispersal probabilities, averaged over the last 100 generations simulated (in total 2000 generations for commensalism and mutualism, and 4000 generations for parasitism). External extinction risk ε=0; c_h and c_p are always identical.

1H1G: Comparison between three interaction types: Results for the mutualism scenario are hardly different from those for the commensalism scenario with slightly lower dispersal probabilities evolving under corresponding conditions (Figure 2.1B). In contrast, in the parasitism scenario, we witness the evolution of much larger dispersal probabilities of hosts, especially if search efficiency of guests (a_i) becomes large (see below, Figure 2.1C). Dispersal mortality of hosts and guests (c_h and c_p) affects evolution of dispersal probability in hosts in the mutualism and parasitism scenarios principally in the same way as in the commensalism scenario, i.e. an increase in the cost of dispersal (dispersal mortality) selects for lower dispersal probabilities (Figure 2.1B and 2.1C). Introducing an external extinction risk has the same effect in the mutualism (*Appendix I,* Figure 2.A3D–2.A3F) as in the commensalism scenario. It becomes more evident, however, that generally slightly lower dispersal probabilities evolve in hosts under mutualism than under commensalism. In contrast, ε has very little additional effect on dispersal evolution in the parasitism scenario, except if parasite's search efficiency a_i is very small (*Appendix I*, Figure 2.A3G–2.A3I).

1H1G: Effects of search efficiency a_i: To understand the different effects of guest search efficiency, a_i, in the scenarios with different interaction types, it is illuminating to compare its effect on local population dynamics and hosts' encounter probability with guests. In Figure 2.2, we provide graphs of the standard deviation in encounter probability and dispersal probabilities plotted over a_i as well as two examples (one for small (a_i=0.005) and one for large search efficiency values (a_i=0.05) for each interaction type) showing the fluctuation of local population size and encounter probability in time for each interaction type. In the commensalism as well as the mutualism scenarios, an increase in search efficiency noticeably influences the temporal dynamics in neither population size nor encounter (the standard deviation of this value remains constant), nor does it affect the evolution of the dispersal probability in hosts (Figure 2.2A and 2.2B). In the parasitism scenario, on the other hand, the spatio-temporal dynamics in population size, standard deviation of encounter probability, as well as dispersal probability all increase with increasing search efficiency (Figure 2.2C1). Indeed, with large a_i values, local host and parasite populations and local encounter probability start to fluctuate widely (see Figure 2.2C3) introducing very large spatio-temporal variability into the metacommunity.

1H1G: Comparison between hosts' and guests' dispersal probability: Principally, the evolution of dispersal probability of guests responds to all factors (search efficiency, dispersal mortality and external extinction risk) in a similar way as in their hosts; consequently a strong correlation between evolving dispersal probabilities in hosts and guests emerges (Spearman rank correlation $r_S \geq 0.99$ in all three interaction scenarios; compare Figure 2.1A–2.1C with 2.1D–2.1F). However, dispersal probabilities of guests tend to be lower than those of their hosts in corresponding scenarios. The lower dispersal probabilities evolving are not caused by a difference in the adaptive potential of guests due to the smaller population size of guests compared to that of their hosts. This is confirmed by Figure 2.A2 (*Appendix I*), which demonstrates that dispersal probabilities of hosts and guests reach stable states long before data are evaluated for analysis and presentation.

2H2G: Comparison between three interaction types: Moving from a two species (1H1G) to a four species (2H2G) system introduces aspects of frequency-dependent selection in the case of mutualisms as well as parasitism (more on this below and in *Discussion*). In the commensalism scenarios, however, such frequency-dependent effects do not occur from the hosts' perspective. Consequently, evolving dispersal probabilities of hosts are similar in corresponding 1H1G and 2H2G scenarios (compare Figure 2.A3A–2.A3C and 2.A4A–2.A4C, *Appendix I*).

Matters appear more complicated, however, in the case of parasitism and mutualism (Figure 2.3). In the mutualism scenarios, even lower dispersal probabilities evolve in hosts as well as guests than in the corresponding 1H1G scenarios (compare Figure 2.3A with Figure 2.3B). Further, a dependence of dispersal evolution on guest search efficiency emerges that is not present in the 1H1G scenarios; with large a_i values (and low dispersal mortality) results tend to become similar to those for the 1H1G scenario. Further, with the introduction of external extinction risk results for the 2H2G scenario become generally more similar to those for the 1H1G case (compare Figure 2.A3D–2.A3F and 2.A4D–2.A4F, *Appendix I*).

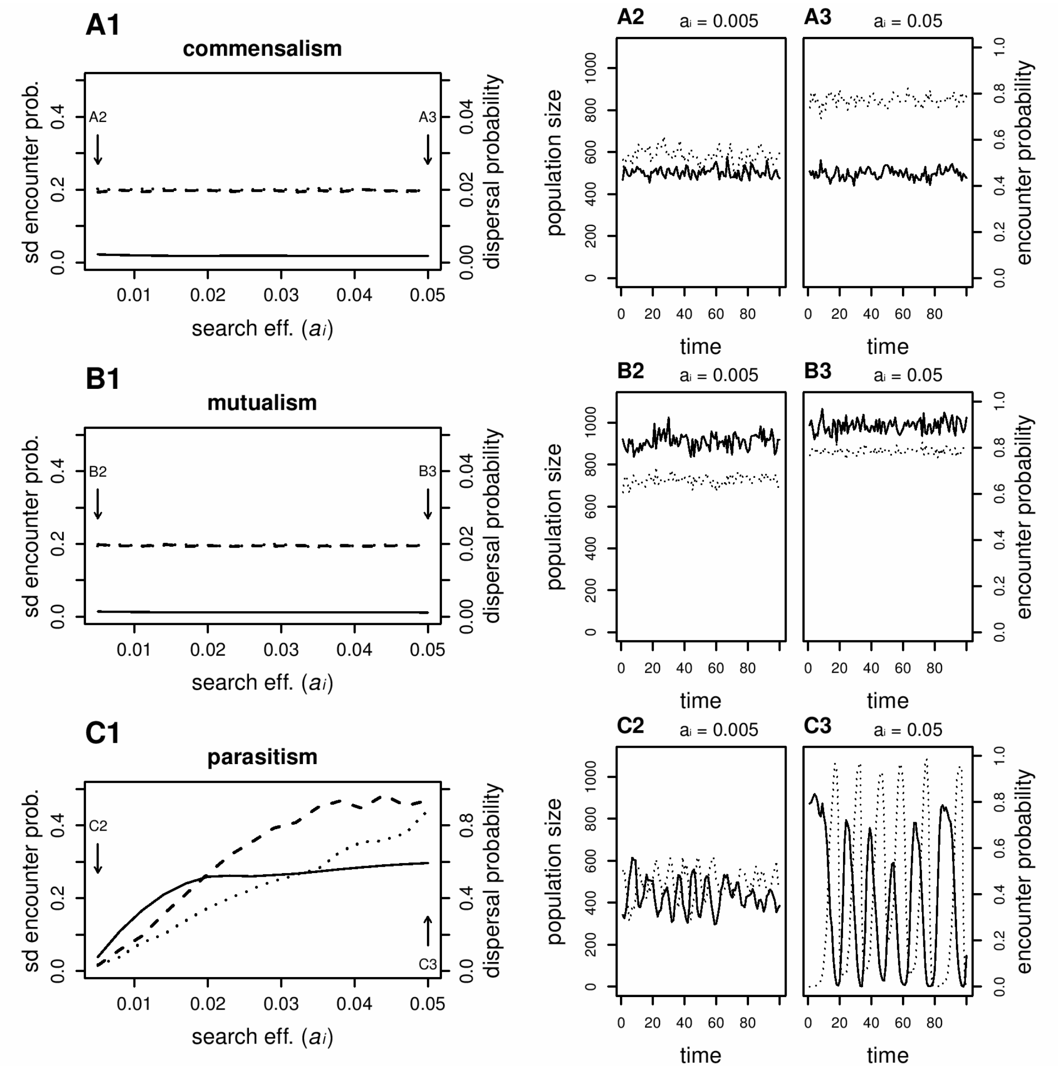

Figure 2.2: Effect of guests search efficiency (a_i) on temporal variability in host–guest encounters, host population dynamics, and evolving mean dispersal probabilities in 1H1G scenarios: (A) commensalism, (B) mutualism, (C) parasitism. In (A1–C1), the solid line gives the standard deviation of arcsine-transformed probability that a hosts encounters a guest (see *Model and simulation* for details), the dashed line the evolved average host dispersal probabilities and the dotted line the dispersal probabilities for guests. Values are averaged over the last 100 generations simulated. Note the different scales for dispersal probability in (A1), (B1) and (C1). Panels (A2–C2) show examples for local host population dynamics (solid lines) and the expected encounter probabilities (dotted lines) over time for scenarios with low guest searching efficiency (a_i=0.005). Panels (A3–C3) provide similar data for scenarios with high efficiency (a_i=0.05). External extinction risk ε=0; dispersal mortality c_h=c_p=0.1.

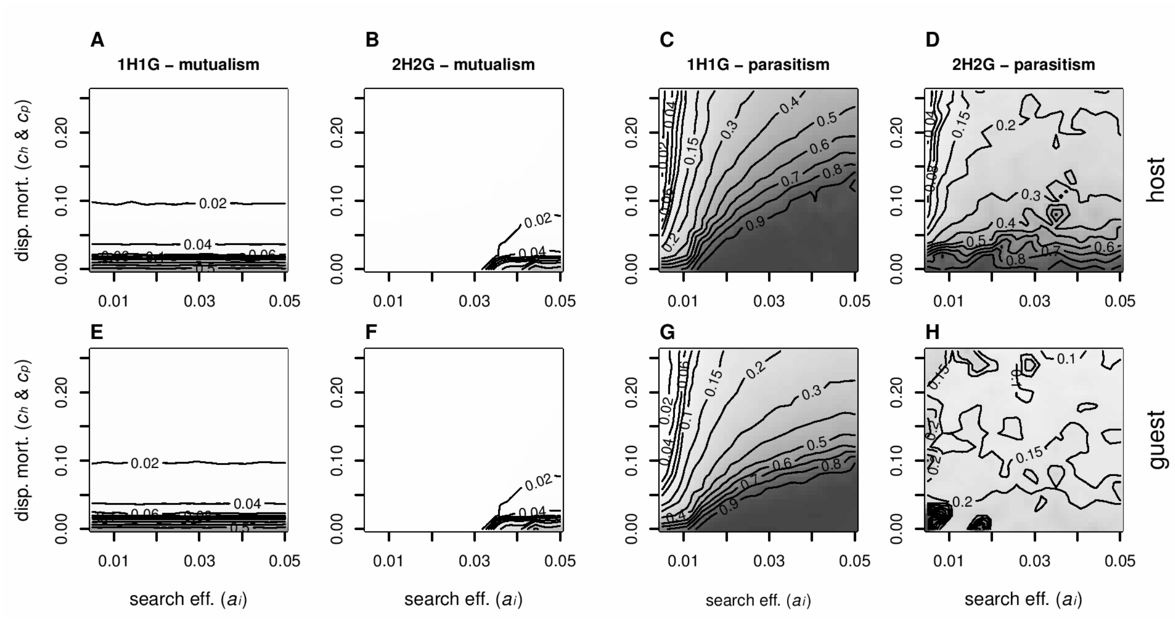

Figure 2.3: Effect of interaction type, guest search efficiency (a_i), and dispersal mortality of hosts and guests (c_h and c_p) on the evolution of mean dispersal probability in 1H1G compared to 2H2G systems. The upper row (A–D) shows results for hosts and the lower (E–H) for guests: (A and E) 1H1G Mutualism; (B and F) 2H2G – Mutualism; (C and G) 1H1G – Parasitism; (D and H) 2H2G – Parasitism. Different gray tones and contour lines represent dispersal probabilities, averaged over the last 100 generations simulated (2000 generations for mutualism, and 4000 generations for parasitism). External extinction risk ε=0; c_h and c_p are always identical. Results for 2H2G commensalism scenarios are very similar to those for 1H1G, and are not shown.

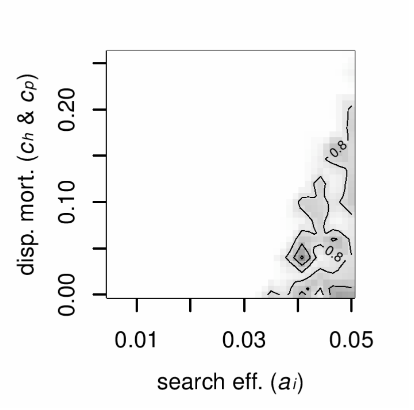

Figure 2.4: Emerging imbalance (from initial 1:1 ratio) in global host abundance in the 2H2G mutualism scenario in dependence of guest search efficiency (a_i) and dispersal mortality for hosts and guests (c_h and c_p). Gray colours and contour lines represent the global proportion (across metacommunity) of the rarer of the two host species ($H_{rare}/(H_{rare}+H_{abundant})$) averaged over the last 100 generations simulated. In the white area, the proportion of two host species is very close to 1:1. External extinction risk ε=0; c_h and c_p are always identical.

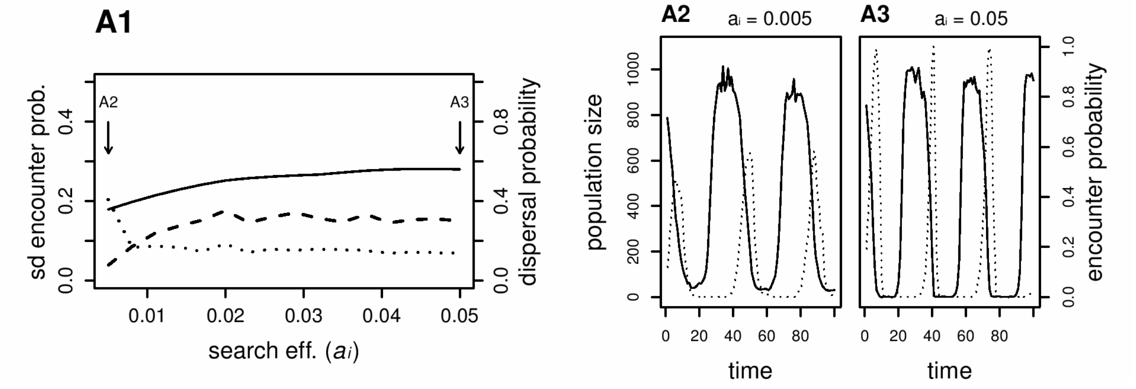

Figure 2.5: Effect of guest search efficiency (a_i) on temporal variability in host–guest encounters, host population dynamics, and evolving mean dispersal probabilities in parasitic 2H2G scenarios: (A1) Solid line gives the standard deviation of the arcsine-transformed probabilities that a hosts encounters a guest, the dashed line the evolved average host dispersal probabilities, and the dotted line the dispersal probabilities for guests. Values are averaged over the last 100 generations simulated. (A2) Example for local host population dynamics (solid lines) and the expected encounter probabilities (dotted lines) over time for a scenario with low guest searching efficiency (a_i=0.005). (A3) Similar example for a scenario with high efficiency (a_i=0.05). Note that dynamics of only one host species is shown. External extinction risk ε=0; dispersal mortality c_h=c_p=0.1.

In the 2H2G parasitism scenarios, we also observe that mean dispersal probabilities evolving in both guilds are generally lower than in the 1H1G scenarios, except if dispersal mortality and/or search efficiency are very low (compare Figure 2.3C with Figure 2.3D). Despite this general decline, larger dispersal probabilities evolve under parasitism than either under commensalism or mutualism in the 2H2G scenarios (compare Figure 2.A4G–2.A4I with Figure 2.A4A–2.A4F, *Appendix I*). The influence of dispersal mortality and search efficiency on evolving dispersal probability both tend to become weaker in the 2H2G compared to the 1H1G scenario – especially for the dispersal of guests. The different evolutionary response in host and guests breaks the tight correlation between host and guest dispersal probability observed in all other scenarios (r_S<0.5 whereas in other scenarios, r_S>0.99). Like in the 1H1G scenarios, however, external extinction risk does not affect evolving dispersal probabilities greatly (in the range of values tested) except under parameter combinations (high dispersal mortality risk, low search efficiency) where very low dispersal probabilities evolve without external extinction (compare Figure 2.A3G–2.A3I with Figure 2.A4G–2.A4I, *Appendix I*).

Comparing 1H1G with 2H2G for mutualism and parasitism: The differences between the 1H1G and 2H2G scenarios emerging for the mutualism and parasitism scenarios warrant a more detailed investigation. In the case of mutualism, the interaction imposes obvious positive frequency dependence for hosts as well as guests: Both partners will perform better the more abundant their respective partner. This makes it very difficult for immigrants of the other pair to establish in such communities; with the ‘checkerboard pattern’ (see *Model and simulation*) implemented at initialization, we thus impose and added cost for dispersing hosts and guests as they have a 50% risk of immigrating into a patch dominated by the other host–guest pair. This added risk selects for very low dispersal probabilities and thus stabilizes the global coexistence of the two H–G pairs. However, if other factors like an external extinction risk promote evolution of higher dispersal probabilities the system becomes globally unstable and sooner or later one of the H–G pairs will start to dominate at large scale ultimately transferring the 2H2G into a 1H1G system (that is why we had to initialize simulations with low dispersal probabilities). A comparison of Figure 2.4 with Figure 2.3B shows that noticeable dispersal probabilities tend to emerge in the 2H2G mutualism scenario just then when the system globally deviates from the 1:1 ratio of the two host types imposed at initialization, i.e. when the original checkerboard pattern becomes destroyed. At that moment the abovementioned risk of immigrating into patches dominated by the other host species becomes smaller for the more abundant species (pair), making dispersal a more valid option. In Figure 2.A5 (*Appendix I*), we provide evidence that the ‘grain’ of the initials spatial pattern implemented has indeed a great impact on this balance (see more details in *Discussion*). If we initialize simulations with one H–G pair on one side of the landscape and the other pair on the other side dispersal probabilities very similar to the 1H1G scenario evolve under all conditions.

In the parasitism scenario, search efficiency of guests does not modulate dispersal evolution of hosts and guests in 2H2G as strongly as in 1H1G system – noticeable dispersal probabilities in hosts evolve even if search efficiency of parasites is low (compare Figure 2.3C with Figure 2.3D). One obvious difference between the 1H1G and the 2H2G scenario is that the standard deviation in host encounter probability (with parasites) remains high even at low a_i values (compare Figure 2.5A with Figure 2.2C). To understand this we need to recognize that under parasitism, frequency-dependence acts in a different way than in the mutualism scenario. Parasites will still flourish most where their host species is most abundant (positive frequency dependence), but hosts will typically achieve highest fitness where they are rare (negative frequency dependence). Consequently, local host and parasite populations in 2H2G system fluctuate widely even at low parasite search efficiency (Figure 2.5A2 and 2.5A3). Indeed, local host populations may experience periods of considerable length where they are completely free of parasitism.

Influences of strength of the species interaction (ρ_i): The effect of guests on hosts' fecundity (ρ_i) is one of the factors that can influence our results. In Figure 2.6, we present results for simulations where we gradually change parameter ρ_i, i.e. move more gradually from the most extreme negative effect of parasitism on hosts (no reproduction of hosts) to the positive effect of mutualism. In the 1H1G scenario, we see a drastic decline in evolving host dispersal probabilities (from d_h=0.8 to d_h=0.02 where a_i=0.05) as we move from complete (ρ_i=0) to just a more moderate version of parasitism (ρ_i=0.5; =50% fertility reduction for hosts). Beyond that point a further reduction in dispersal probabilities is not observable. This pattern corresponds well with a similar decline in the variance in local host encounter probability (with guests) and population dynamics (Figure 2.6A and 2.6B). In the 2H2G scenarios, the pattern is principally similar but the decline is much more shallow (Figure 2.6C and 2.6D). With more moderate types of parasitism (i.e. ρ_i>c. 0.2), we thus observe the evolution of higher dispersal probabilities in the 2H2G compared to the 1H1G scenario.

2.4. Discussion

Avoidance of local (resource) competition, bet-hedging, and reduction of kin competition have long been identified as fundamental factors promoting the evolution of dispersal (Hamilton and May 1977; Comins et al. 1980; Gandon and Michalakis 1999; Ronce et al. 2000*a*; Poethke et al. 2007); we ignore here inbreeding avoidance as another important mechanisms (Gandon 1999; Bowler and Benton 2005; Gros et al. 2008) as it does, by definition, not play a role in our simulation experiments. On the other hand, it is also known that spatial heterogeneity is as such selecting against dispersal, as individuals would typically move from favourable to unfavourable habitats (Hastings 1983; Poethke et al. 2011). Our simulation results suggest a potentially large effect of species interactions for the evolution of dispersal strategies. However, before pursuing this issue further, we first want to explain results for the 'reference' commensalism scenario in light of these general principles.

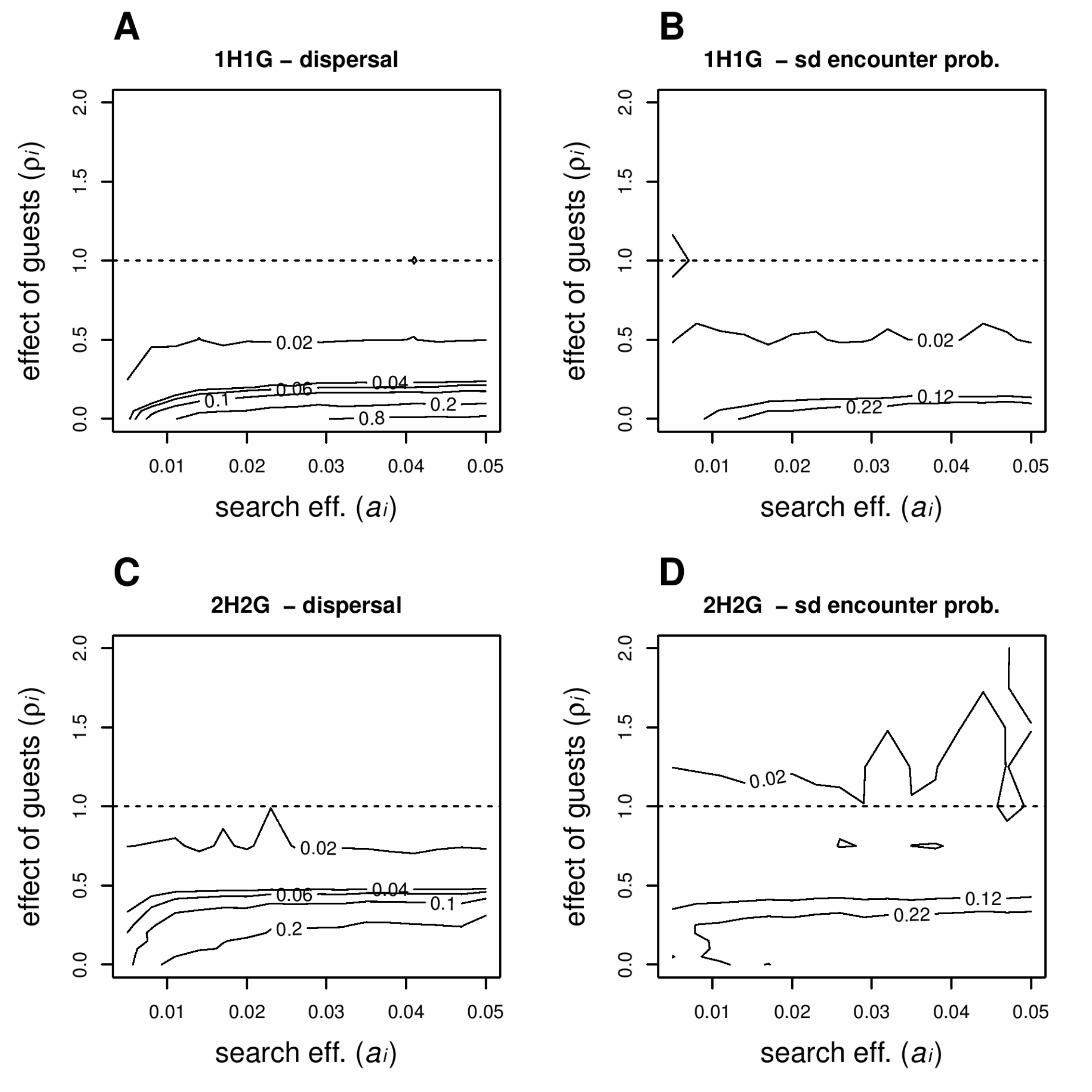

Figure 2.6: Influence of the effect of guests on host fecundity (ρ_i) and guest search efficiency (a_i) on dispersal evolution and host encounter probability in 1H1G (A and B) and 2H2G (C and D) scenarios. Contour lines in (A and C) represent evolving host dispersal probabilities. Contour lines in (B and D) specify the standard deviation of arcsine-transformed encounter probabilities of hosts with their guests (also indicative of population dynamics) emerging in the 1H1G and 2H2G systems. Note that according to our definition (see *Model and simulation*), the interaction with $0 \leq \rho_i < 1$ is parasitism, $\rho_i = 1$ is commensalism (dashed lines), and $\rho_i > 1$ is mutualism. External extinction risk $\varepsilon = 0$; dispersal mortality $c_h = c_p = 0.1$.

Commensalism and dispersal evolution: In the commensalism scenarios host–guest interactions are irrelevant for the hosts' fitness and guest search efficiency consequently plays no role for the evolution of dispersal in hosts. Due to the assumption of ecological equivalence the effect of intra- and interspecific competition within respectively between host species is identical – from the hosts' perspective the conditions in corresponding 1H1G and 2H2G are thus also identical (and spatially homogeneous) and dispersal evolves to similar levels in either case.

In our reference scenario with large populations, no environmental stochasticity, and no external extinction, local populations are extremely stable (apart from some demographic stochasticity), and dispersing provides little ecological benefit in terms of competition reduction, simply because the intensity of resource competition is the same everywhere. As such this promotes the evolution of very low dispersal probabilities as soon as dispersal is associated with even small costs. However, low dispersal also leads to the emergence of kin structure (individuals within local populations are more closely related than among populations) so that avoidance of kin competition becomes an issue (Hamilton and May 1977). When other ecological circumstances generally disfavour dispersal, kin competition may thus become the prime ‘motivation’ underlying dispersal (Poethke et al. 2007) assuring minimum dispersal even under extremely unfavourable conditions as in the commensalism scenario without dispersal cost. We once more want to point out that individual-based simulations account for kin competition by default (Bach et al. 2006; Poethke et al. 2007). With the introduction of external extinction risk, dispersal is ecologically favored, however, as it opens the opportunity to colonize empty habitats and requires a strategy of bet-hedging (Ronce 2007). These results reiterate previous findings and they can readily be explained in light of the general principles outlined in the *Introduction* and the first paragraph of the *Discussion*. The reasoning applied is not new but recapitulating it may help to understand in the following the implications of other types of species interactions for the evolution of dispersal.

Effects of mutualism on dispersal evolution: Evolved dispersal probabilities were nearly identical in the 1H1G commensalism and mutualism scenarios. This is not surprising if we recognize that local population dynamics and the probability of host–guest encounter are temporally stable in both scenarios. Like in the commensalism scenario, kin competition is thus the primary driver of dispersal evolution and like in that scenario, introduction of external extinction leads to selection of higher dispersal probabilities. The very slightly lower dispersal probabilities evolving under mutualism can be traced to the larger population sizes forming with this type of interaction – this reduces even further the role of demographic stochasticity and slows down the emergence of tight kin structure.

The similarity of results vanishes, however, if we compare results for the 2H2G scenarios. The specific procedure chosen at initialization introduces a spatial heterogeneity into the 2H2G scenarios that is completely irrelevant for hosts in the commensalism but not in the mutualism scenario. The positive frequency dependence emerging under mutualism makes it very hard to establish as a rare type (and immigrant) in a community dominated by the other host–guest pair. This implies an added "settlement cost" (Bonte et al. 2011) for potential migrants promoting the evolution of very low dispersal probabilities. This evolutionary feedback effect may stabilize regional coexistence of different host–mutualist pairs once a heterogeneous distribution has established.

However, if the evolution of dispersal is promoted for other reason, e.g. by external extinction risk or other sources of environmental variability, a multispecies metacommunity tends to become increasingly dominated by one host–mutualist pair because the positive frequency dependence plays out at larger spatial scales. This is in agreement with more general prediction that mutualistic interactions can lead to loss in diversity (May 1973; Vandermeer and Boucher 1978; Law and Koptur 1986; Bever 1999; Benadi et al. 2012). Coexistence of several host species and their specialized mutualistic partners is thus always threatened.

In Figure A2.5 (*Appendix I*), we show how alternative initial spatial arrangement influences the dispersal evolution. We compare our 'fine grain' checkerboard with a 'coarse grain' checkerboard (4 squares pattern that is similar to the checkerboard, but each square of the checkerboard contains 2x2 patches of same host – mutualist species pair) and a 'left–right' pattern where each species pair populates one side of the landscape. In the coarse grain and left–right setting, higher dispersal probabilities may evolve even in the mutualism scenario because dispersing hosts would typically immigrate into populations dominated by the same host species. Further, while the three arrangement patterns give different results in the scenarios without dispersal mortality, all results converge when only a small amount of dispersal mortality is introduced. Moreover, in all spatial arrangement, all host–mutualist pairs are maintained, but in some cases, they form large clusters – presumably of dimensions larger than typical dispersal distances, and thus the higher dispersal probabilities are promoted in these cases.

Clearly, our simulation does not explore how spatial heterogeneity in host–mutualist distribution could emerge in the first place. It is beyond the scope of this study to investigate this issue, but such heterogeneity might develop for various reasons, e.g. low connectivity, strong random fluctuations, or different selective pressures in different local sites. Here we only demonstrate how mutualistic interactions may stabilize such heterogeneity once emerged due to the evolution of low dispersal.

Effect of parasitism on dispersal evolution: In most of our scenarios, parasitism induced the evolution of much higher dispersal probabilities than either commensalism or mutualism except if parasite search efficiency was very low. This corresponds to the results of Green (2009) who also shows that high search efficiency of parasitoids may promote dispersal. This may be due to several mutually interdependent effects: (1) Parasitism (like predation) may induce strong oscillations in populations of hosts and guests. Such oscillations, in turn, create massive spatio-temporal variability in fitness expectations thus promoting the evolution of dispersal (Karlson and Taylor 1995; Holt and McPeek 1996; Ronce et al. 2000*b*; Gros et al. 2008). (2) The strong oscillations induced by parasitism may often lead to local population extinction, which both generated empty sites for dispersers to colonize and makes a bet-hedging strategy advantageous. For these reasons, high dispersal probability of hosts evolves, even when dispersal is costly. Our simulations suggest that it is indeed the impact of parasitism on population dynamics and thus spatio-temporal variability that primarily promotes the evolution of much higher dispersal. If we choose parameter combinations that do not lead to such oscillations evolving dispersal probabilities are not very different than those emerging under the other two interaction types. Note that we control the emergence of population oscillation by modifying search efficiency (a_i) and the effect of parasites (ρ_i) on their hosts while we keep parasite fecundity (ψ_i), and handling time constant. However, a modification of those parameters would also affect the emergence of population oscillations, as it is the combined effect of these parameters that determines the summary reproduction of guests and the damage done to the host population.

In the 2H2G parasitism scenario, however, an additional effect contributes to the evolution of high dispersal probabilities in hosts even if the effect of parasites on hosts is rather small. Parasitism imposes negative frequency-dependent selection on hosts as the more abundant host species carries a much larger risk of encounter with its parasite, at least over time. This in turn promotes perpetual turn-over of host populations (and global coexistence) and host dispersal because hosts can profit by immigrating into a patch dominated by the other host species. Local host populations may even completely avoid parasitism for considerable time periods under such conditions. Simply speaking, we again recognize the establishment of strong spatio-temporal variability in host fitness expectations. In fact, the host's parasitism load in the 2H2G became considerably smaller than in the corresponding 1H1G scenarios, which explains, in contrast to the explanation for the mutualism scenarios, the evolution of lower host dispersal probabilities in 2H2G scenarios.

Comparison between hosts' and guests' dispersal: In almost all of our simulation scenarios, hosts evolve (slightly) higher dispersal probabilities than their guests. However, the response to changing simulation parameters is usually highly correlated in hosts and guest. This result can be explained by an inherent asymmetry in the assumptions of our model, and a resulting asymmetry in the landscape structure as seen from the perspective of hosts compared to guests. We assume that hosts have the ability to colonize any empty patch available, because they can reproduce in the absence of their guest. Indeed immigrating into an empty patch is especially beneficial for hosts, because empty sites are free of inter- and intraspecific competition, and in the case of parasitism, also free of parasites. In contrast, a patch is unsuitable for guests as long as their host has not established a population there; this always adds an implicit dispersal cost for guests compared to their hosts. This difference does not count much as long as host populations are very stable (commensalism and mutualism), but becomes important when host populations may go extinct either due to internal (parasitism) or external reasons.

This discrepancy is further enhanced in the 2H2G scenarios, because guests have low fitness expectations in patches dominated by the wrong host. In the mutualism scenario, this argument similarly applies to hosts as the positive frequency dependence (with respect to host abundance) applies to hosts and their mutualistic partners in the same way. For this reason, we still found a close correlation in the evolutionary response of guests and their hosts 2H2G scenarios. However, in the 2H2G parasitism scenario, matters change as it pays for a host individual to immigrate into a community where its species is rare while a parasite is better off where its host is abundant. This promotes the evolution of much higher dispersal probabilities in host than in their parasites.

It should be noted that in the 2H2G system, we assume extreme specialization of guests i.e. they can utilize only one host species. However, if this assumption would be relaxed, and guests were able to reproduce on more than one host type (not necessarily with equal success), the difference between the 1H1G and the 2H2G scenario should be reduced, because the frequency dependent selection pressure on guests exerted in the 2H2G system would become weaker. At its extreme the two scenarios should converge if a guest would utilize both guest species equally well.

Empirical examples: Some example supporting our results come from aphid species that exhibit phenotype plasticity, either developing a winged (dispersal morph) or unwinged morph (Weisser et al. 1999; Mondor et al. 2005). Under predator or parasitoid attack, the pea aphid *Acyrthosiphon pisum* and the cotton aphid *Aphis gossypii* produce more winged offspring, which are then able to colonize new plants (Weisser et al. 1999; Sloggett and Weisser 2002; Kunert and Weisser 2003; Mondor et al. 2005). In contrast, the facultative bacterial symbiont *Candidatus Regiella insecticola* can reduce the proportion of winged offspring in the pea aphid *A. pisum* (Leonardo and Mondor 2006). Moreover, aphids that are tended and defended by ants (myrmecophilous aphids – defensive mutualistic association) disperse less readily than non-myrmecophilous species (Nault et al. 1976). Although, in this study, we do not consider phenotypic plasticity explicitly, these studies show that animals modify their dispersal morph according to the presence of mutualistic or antagonistic partners in agreement with our findings here. Phenotypic plasticity itself may be an adaptive strategy allowing a flexible response to the presence of interacting species.

2.5. Conclusion

When the evolution of dispersal is considered, ecologists tend to focus only on a single species and not on the possible affects of interaction with other species. Here we demonstrate some possible implications of interspecific interaction for the evolution of dispersal. (1) Parasitism may promote dispersal because it may induce strong spatio-temporal dynamics in population densities. Mutualism leads to local stability and may stabilize spatial heterogeneity thus selecting against dispersal. (2) Especially in more species rich communities, frequency-dependent selection may play an important role for the evolution of dispersal. (3) Species diversity may promote – for quite different reasons in mutualistic compared to parasitic systems – evolution of lower dispersal probabilities in hosts as well as guest species. We thus suggest that for a full understanding of the mechanism driving the evolution of dispersal, the effect of interspecific interactions between organisms should be taken into account.

2.6. Appendix I: Supplementary figures

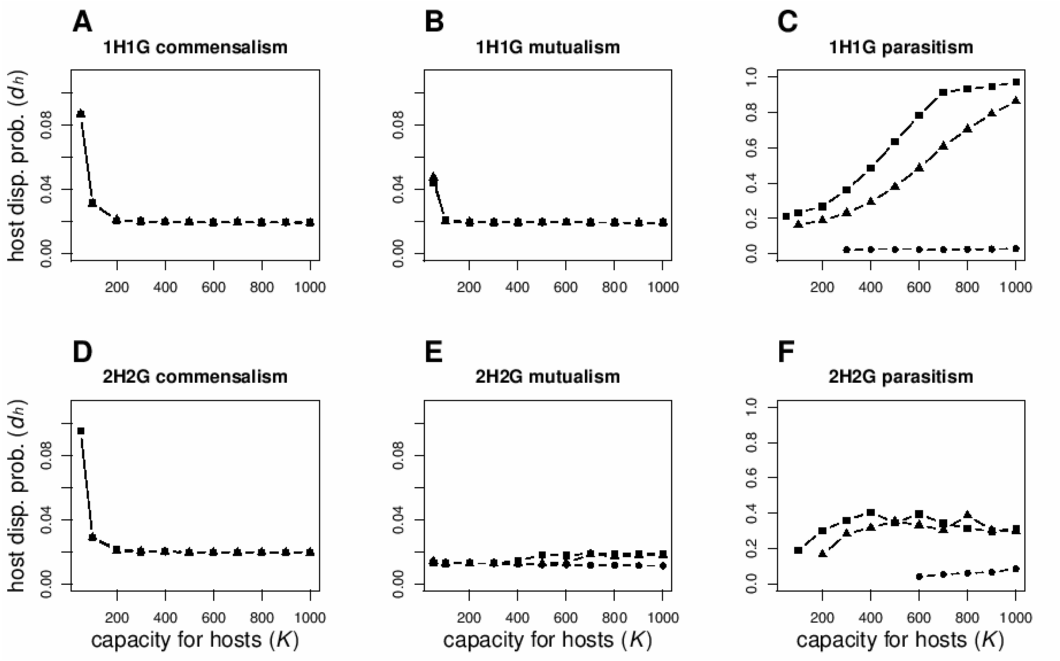

Figure 2.A1: Influence of patch carrying capacity K for hosts on the evolution of host dispersal in the commensalism (A and D), mutualism (B and E), and parasitism (C and F) scenarios; the upper row is for 1H1G, and the bottom row for 2H2G scenarios. In each panel, the three different lines show the evolved mean host dispersal probabilities (d_h) for three different search efficiencies of guests (a_i) plotted over K: Circles are for a_i=0.005, triangles for a_i=0.032, and squares for a_i=0.05. Note the different scaling of y-axis between the parasitism scenarios and the others. External extinction risk ε=0; dispersal mortality c_h=c_p=0.1.

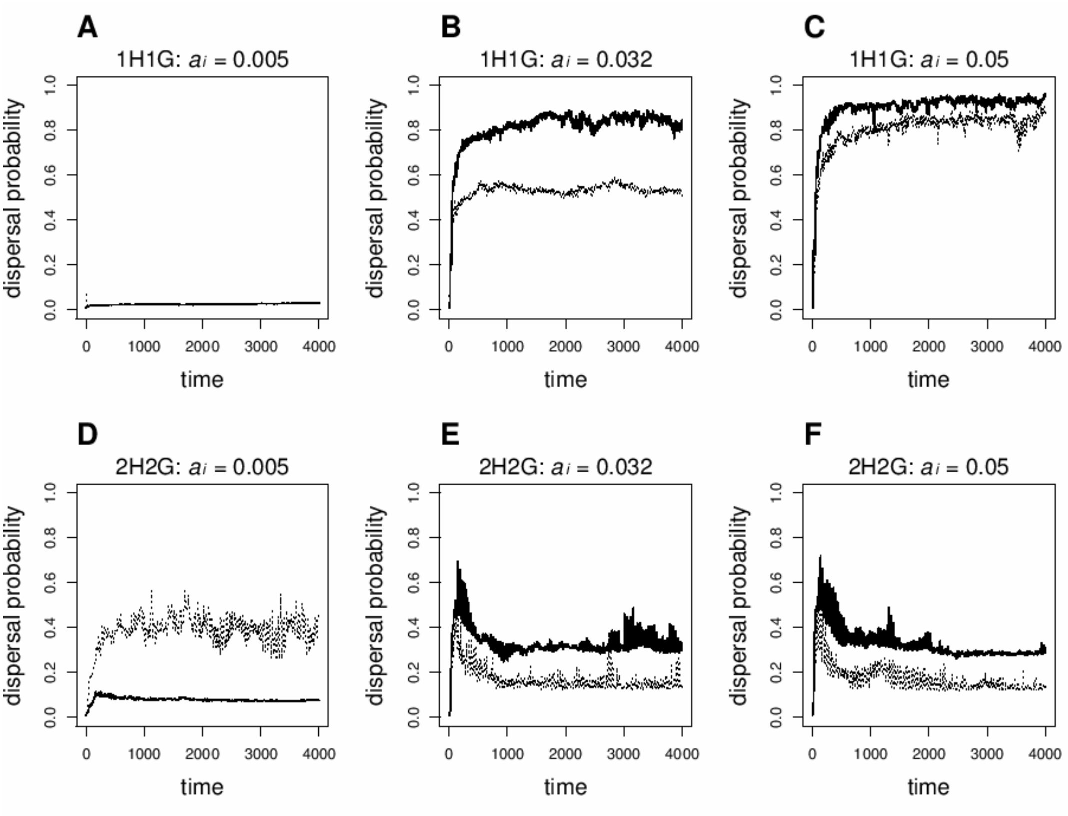

Figure 2.A2: Temporal dynamics of dispersal evolution in parasitic systems. Mean dispersal probabilities of hosts (d_h – solid lines) and parasites (d_p – dotted lines) for the 1H1G (upper row) and 2H2G systems (bottom row) are plotted over simulation time. Panels show results for different values for parasite (guest) search efficiency (a_i), i.e. (A and D) a_i=0.005, (B and E) a_i=0.032, and (C and F) a_i=0.05. External extinction risk ε=0; dispersal mortality c_h=c_p=0.1.

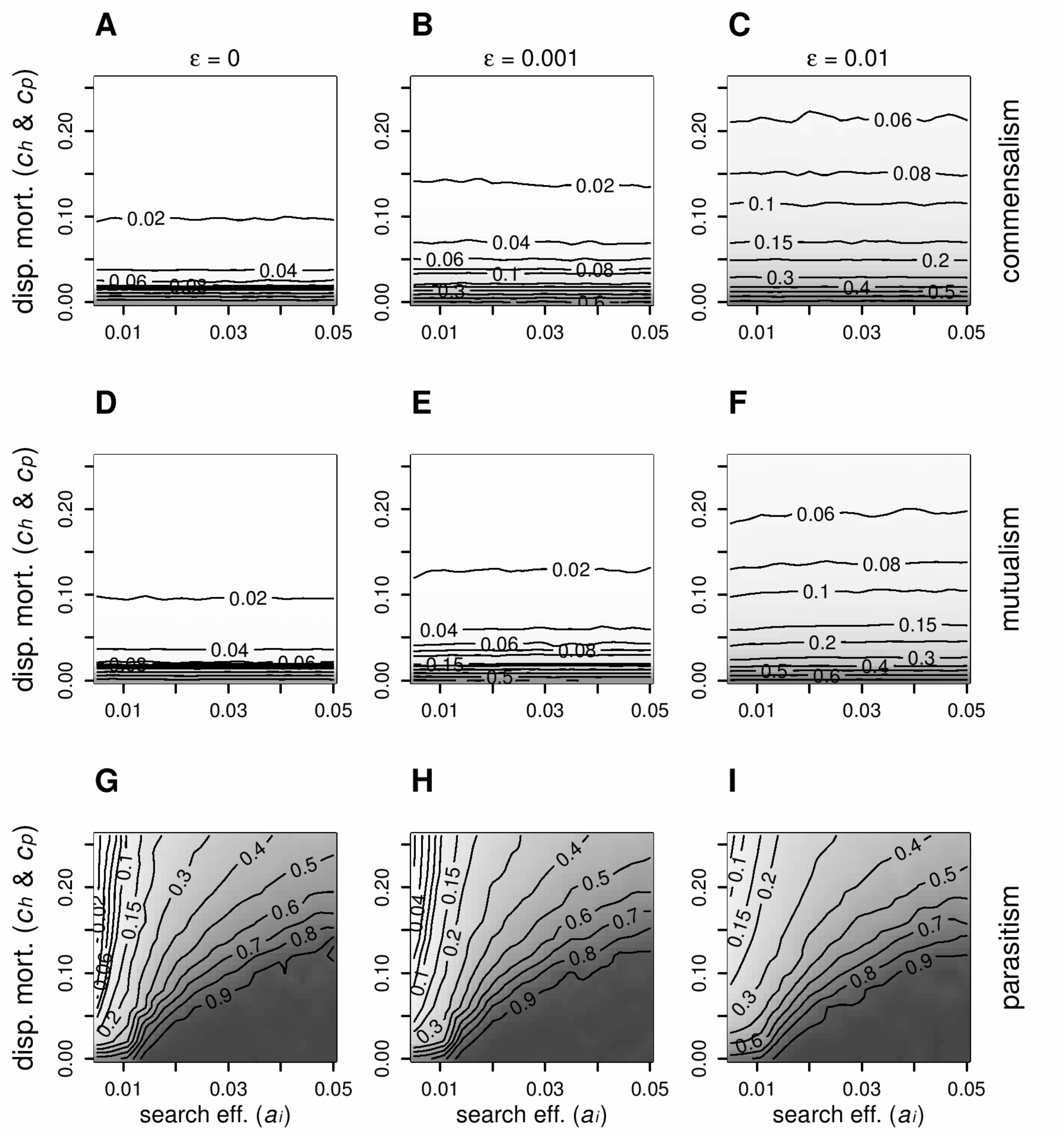

Figure 2.A3: Effect of external extinction risk (ε; different columns), guests' search efficiency (a_i; x-axis), and dispersal mortality of hosts and guests (c_h and c_p; y-axis) on the evolution of host dispersal in the different 1H1G scenarios: (A–C) commensalism, (D–F) mutualism, and (G–I) parasitism. Different gray tones and contour lines represent mean evolved emigration probability averaged over the last 100 generations simulated (in total 2000 generations for commensalism and mutualism, and 4000 generations for parasitism). Dispersal mortality c_h and c_p are always identical: (A, D and G) ε=0, (B, E and H) ε=0.001, (C, F and I) ε=0.01.

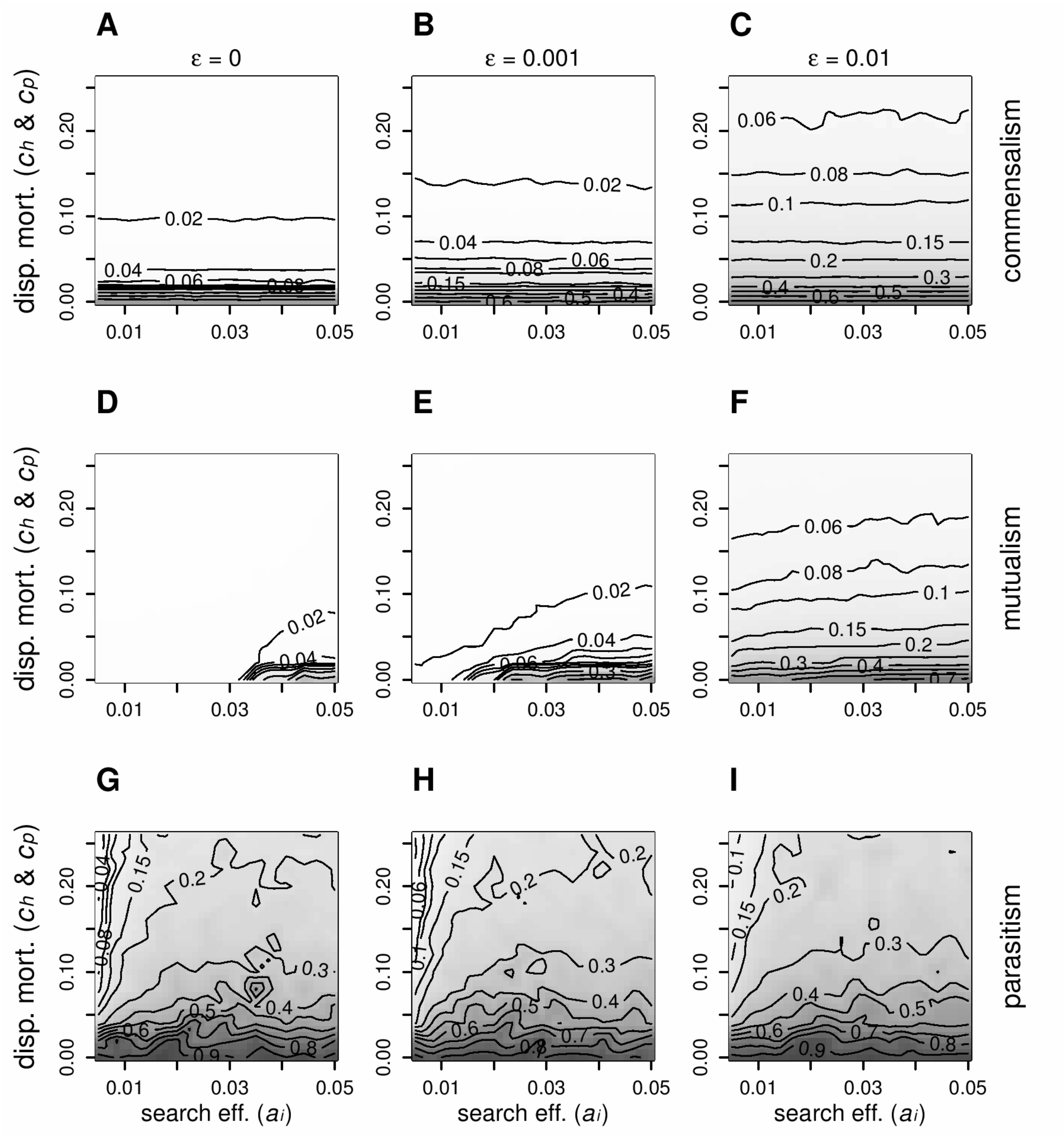

Figure 2.A4: Effect of external extinction risk (ε; different columns), guests' search efficiency (a_i; x-axis), and dispersal mortality of hosts and guests (c_h and c_p; y-axis) on the evolution of host dispersal in the different 2H2G scenarios: (A–C) commensalism, (D–F) mutualism, and (G–I) parasitism. Different gray tones and contour lines represent mean evolved emigration probability averaged over the last 100 generations simulated (in total 2000 generations for commensalism and mutualism, and 4000 generations for parasitism). Dispersal mortality c_h and c_p are always identical: (A, D and G) ε=0, (B, E and H) ε=0.001, (C, F and I) ε=0.01.

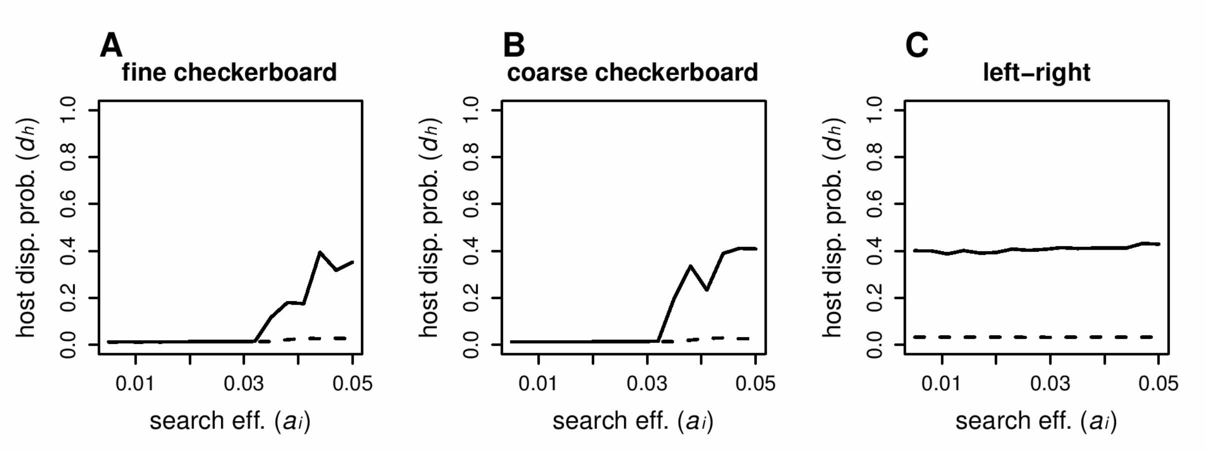

Figure 2.A5: Effect of initial spatial arrangement of host populations in mutualistic 2H2G systems on the evolution of host dispersal. Evolving mean dispersal probabilities of hosts are plotted over search efficiencies of guests (a_i). Solid lines represent results for scenarios with dispersal mortality c_h=c_p=0, dashed lines for scenarios with c_h=c_p=0.04: (A) 'Fine checkerboard' (small scale spatial heterogeneity) as described in *Model and simulation* section and used for generating the results in main text; (B) 'Coarse checkerboard' similar to the fine checkerboard, but with blocks of 2x2 patches initialized with the same host species; (C) 'Left–right' pattern where each host species initially populates patches on one side of the landscape. External extinction risk ε=0.

Chapter 3

Concurrent evolution of random dispersal and habitat niche width in host-parasitoid systems[1]

With Thomas Hovestadt

3.1. Introduction

Dispersal is an ecological process with far reaching consequences for population dynamics, metapopulation persistence, or the formation of communities (Briggs and Hoopes 2004; Bowler and Benton 2005; Cadotte 2006; Ronce 2007; Filotas et al. 2010; Stone et al 2012). More specifically, in light of changing climate and increasing habitat fragmentation, dispersal will be a key to species persistence (Parmesan et al. 1999; Hanski 2001; Thomas et al. 2001; Kokko and Lopez-Sepulcre 2006; Parmesan 2006; Phillips et al. 2010, Hof et al. 2011). This especially holds whenever environmental change proceeds too fast or populations are too small – therefore lacking necessary genetic variability – for an adequate adaptive response to occur (Jump and Peñuelas 2005).

Dispersal, however, is itself an important life-history attribute (rather a suite of attributes) governed by many selective pressures, including kin competition (Hamilton and May 1977; Comins et al. 1980; Gandon and Rousset 1999; Bach et al. 2006; Poethke et al. 2007), inbreeding avoidance (Gandon 1999; Perrin and Goudet 2001), population dynamics (Holt and McPeek 1996), spatio-temporal habitat variability (Comins et al. 1980; Travis and Dytham 1999; Travis 2001; Poethke et al. 2003), or intra- and interspecific competition (Hamilton and May 1977; Comins et al. 1980; Gandon and Michalakis 1999; Poethke and Hovestadt 2002; Poethke et al. 2007). Many recent studies show that other types of species interactions like predation, parasitism, or mutualism also influence dispersal evolution (Weisser et al. 1999; French and Travis 2001; Sloggett and Weisser 2002; Kunert and Weisser 2003; Mondor et al. 2005; Green

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2009; Poethke et al. 2010; Chaianunporn and Hovestadt 2012*a*). For a proper understanding of dispersal evolution, we further have to keep in mind that dispersal may have strong (feedback) effects on the very conditions affecting its evolution (Poethke et al. 2003).

Theory has long established that spatial heterogeneity, as such, selects against dispersal (Comins et al. 1980; Hastings 1983; Travis 2001; Poethke et al. 2003, 2011) because dispersal would move individuals from good to poorer habitats and thus reduce the fitness expectation of migrants. Further, whenever landscapes are heterogeneous, organisms are typically not well adapted to all habitat conditions, i.e. they are specialized to certain habitat attributes (defining their ‘habitat niche’). A multitude of studies already investigated factors that affect the evolution of habitat niche width, such as potential trade-offs associated with niche broadening (Egas et al. 2004; Parvinen and Egas 2004; Abrams 2006b; Nurmi and Parvinen 2011), growth rate (Nurmi and Parvinen 2008; Nurmi et al. 2008), catastrophe probability (Kisdi 2002; Nurmi and Parvinen 2008, 2011; Nurmi et al. 2008), temporal variability of resources (Abrams 2006b), environmental heterogeneity (Kisdi 2002; Nurmi and Parvinen 2008), and dispersal probability (Brown and Pavlovic 1992; Day 2000; Ronce and Kirkpatrick 2001; Parvinen and Egas 2004; Nurmi and Parvinen 2008, 2011; Nurmi et al. 2008). Different species or populations show indeed different levels of specialization (niche width), i.e. species can be habitat specialists or generalists. For example, species of the Dipteran suborder Schizophora show different degrees of specialization to specific climate and temperature (Rohan et al. 2007), or sub-Antarctic weevils (*Ectemnorhinus* group) show between species variation in temperature tolerance as well as among populations within species (Klok and Chown 2003).

It is important to acknowledge that ‘perceived’ landscape heterogeneity depends on a species’ habitat niche width (or its tolerance to varying conditions) – from the perspective of a habitat generalist, the world is more homogeneous (the fitness landscape is more uniform) than from that of a specialist. Consequently, an interaction in the evolution of dispersal (propensity) and habitat niche width is expected, i.e. habitat generalists should – everything else being equal – disperse more readily than habitat specialists (Brown and Pavlovic 1992; Day 2000; Parvinen and Egas 2004).

Species interaction and spatial heterogeneity are thus an example of two forces that may exert selection on dispersal evolution in opposing directions. While antagonistic interactions, such as host-parasitoid interaction, can promote evolution of substantial dispersal due to negative frequency-dependent selection (Chaianunporn and Hovestadt 2012*a*), spatial heterogeneity selects against it. It is also expected that the habitat niche width of hosts should evolve corresponding to the dispersal evolution, because dispersal frequency affects the number of different habitat types which a lineage is exposed to. However, how should habitat niche width and dispersal concurrently respond to such opposing selective forces?

To answer this question, we develop a spatially explicit individual-based metacommunity model with heterogeneity among habitat patches within the model in order to investigate the effect of host-parasitoid interaction – compared to commensalistic interactions – on the interplay between the evolution of dispersal and habitat niche width. As an important added attribute we compare evolutionary outcomes for scenarios assuming different trade-offs associated with increasing niche width, i.e. different reductions in fertility for a habitat generalist in optimal habitat compared to the fertility of a more specialized individual. We further contrast our results with those from a homogeneous landscape. Note that dispersal costs already emerge due to habitat heterogeneity; therefore, we do not assume dispersal cost explicitly (more on this in *Discussion*). Finally, we determine how landscape arrangement (random and clustered arrangement) affects the interplay of the two traits' evolution.

3.2. Model and simulation

Simulation landscape: We adapt and utilize a spatially explicit, individual-based metacommunity model previously presented by Chaianunporn and Hovestadt (2012*a*). We expand the model by implementing landscape heterogeneity that affects the fertility of the host species only (see below). For computational reasons, we create spatially explicit lattice landscape of dimension 128 x 8 grid cells (patches): In comparison to a square landscape, such an elongated shape promotes the emergence of clear spatial patterns at a lower number of patches and total population size and thus saves computation time. Each cell is characterized by a continuous number indicating a habitat attribute (H_m – for habitat type of patch m). Studies addressing the coexistence of habitat generalists and specialists often assume habitat patches of two or more discrete resource types (Levins 1962; Egas et al. 2004; Abrams 2006a and b; Rueffler et al. 2007; Nurmi et al. 2008; Nurmi and Parvinen 2008, 2011). However, here we consider habitat attributes, e.g. habitat mean temperature, with a continuous distribution as is often assumed in models on ecological character displacement and speciation (Dieckmann and Doebeli 1999; Day 2000, 2001; Wilson and Richards 2000; Egas et al. 2005; Heinz et al. 2009). We generate two types of landscapes only different with respect to their spatial structure. We use the fractional Brownian motion method of the function "SpectralSynthesis" provided by the package "ecomodtools" implemented in the statistical computing platform R (Chipperfield et al. 2011) to generate an autocorrelated (fractal) landscape; in such a landscape similar habitats tend to be aggregated (Figure 3.1A). By using a Hurst exponent of 1 in both dimensions, we generate landscapes with habitat attributes between -1 and 1. The fractal method used makes sure that habitat attributes correlate periodically in the both dimensions, i.e. wrapped edges 'match' in x- and y dimension even in our elongated landscape (see an example in Figure 3.1A). From these landscapes, we derive uncorrelated but otherwise identical landscapes by simply re-shuffling (randomizing) the position of individual habitat cells (Figure 3.1B). From now on, we will call the first landscape type "clustered landscape" and the second landscape "random landscape". The grid of the landscapes is wrapped into a torus in both dimensions (a typical step taken is such simulations). Although this assumption might not be realistic, it helps us to eliminate specific edge effects we do not want to explore here in detail.

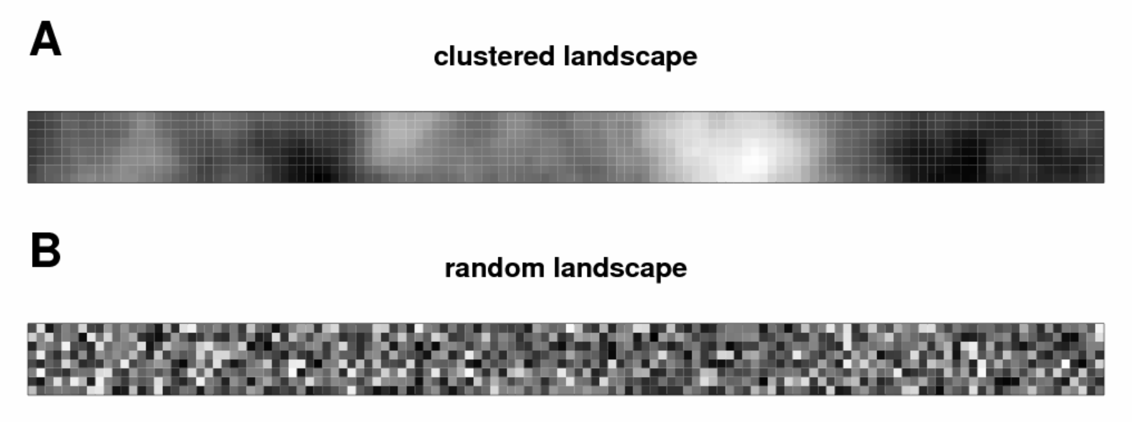

Figure 3.1: Examples for the two landscape types used in this study. (A) Random landscape; (B) Clustered (fractal) landscape. Grey tone indicates value of habitat attribute *H*. Both landscapes contain the same set of habitat cells, i.e. cells with identical values of *H*: The random landscape was simply generated by reshuffling the spatial coordinates of grid cells from landscape B).

Species community: Each habitat cell can support a community of a single host species and a single guest species (commensal or parasitoid). We assume that hosts and guests have a synchronized annual life cycle with discrete generations. The order of the life cycle of both species is as follows: After birth of hosts and guests, both species perform either natal dispersal to a new target patch or stay in their natal patch. We assume that species interaction occurs after the dispersal phase. Hosts and guests reproduce, and their fertilities are determined according to the interaction. After reproduction, all adult host and guest individuals die, and newborn individuals perform dispersal.

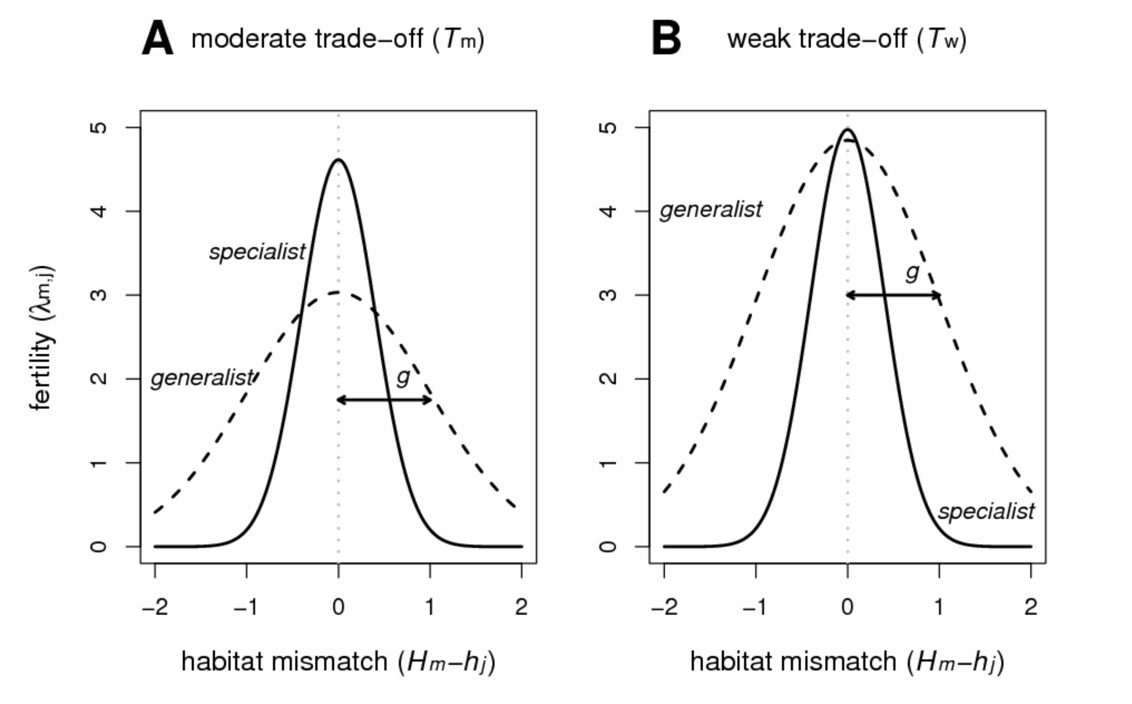

Figure 3.2: Effect of habitat–fertility trade-off (T) on mean fertility ($\lambda_{j,m}$) of habitat specialist (narrow habitat niche, g=0.4, full line) and habitat generalist (wide habitat niche, g=1; hatched line) in dependence of habitat mismatch. Habitat mismatch is calculated as the difference between the individual's optimum habitat h_j and the habitat attribute H_m. Habitat–fertility trade-off (T) controls the fertility disadvantage for more generalized compared to specialized individuals in the most favoured habitat (see methods, *eq.* 3.1). Here, we show fertility curves for two values of T, i.e. (A) moderate trade-off (T_m; c=1) and (B) weak trade-off (T_w; c=4).

Hosts and guests are both haploid organisms reproducing asexually. Guests cannot survive and reproduce in absence of hosts, but hosts can survive and reproduce without guest; guests thus always benefit from the interaction with their host. Here, we consider only two possible types of species interaction, i.e. 'antagonism' (host-parasitoid) where guests castrate their hosts, and ‘commensalism’ where guests do not affect the fitness of their hosts (see details below).

Host species: In our model, host reproduction generally depends on habitat type and competition. Each host individual j is characterized by heritable and evolvable traits h_j and g_j where the first defines the individual’s optimal habitat and the second its habitat niche width. The fertility of host individual j in habitat m is estimated according to a Gaussian distribution as:

$$\text{(3.1)} \quad \lambda_{m,j} = T\lambda_0 e^{-(\frac{(H_m - h_j)^2}{2g_j^2})}$$

$$\text{with } T = e^{-(\frac{g_j^2}{2c^2})},$$

where λ_0 the maximum fertility in optimum habitat, and c is a parameter controlling the habitat-fertility trade-off T. The fertility of any host individual is thus controlled by the match between the actual habitat attribute of the patch (H_m), and the host’s most preferred (optimal) habitat (h_j), and the host’s niche width (g_j). By the term T, we introduce a trade-off (general fertility reduction) imposing a ‘sanction’ on individuals that evolve a greater niche width as otherwise selection would always favour habitat generalists. Accordingly, more generalist individuals cannot produce as many offspring in optimal habitat more than specialized ones. The smaller the value of c is, the stronger the trade-off becomes (compare Figure 3.2A and 3.2B). With parameter c, we can thus control the degree of generalization evolving in the system by modifying the ‘cost’ for being a generalist.

The expected number of offspring surviving to reproduction for each host individual depends on local competition and is estimated according to the Beverton-Holt model (Beverton and Holt 1981):

$$\text{(3.2)} \quad \lambda_{m,j,t} = \lambda_{m,j} s$$

$$\text{with} \quad s = \frac{1}{1 + (\frac{\lambda_0 - 1}{K}) N_{H,m,t}},$$

where K defines patch capacity for hosts and $N_{\mathrm{H,m,t}}$ is the number of hosts in patch m at time t. Although attacked hosts do not reproduce in the host-parasitoid scenario (see below), we assume that they are only killed at the end of their development. They thus still compete with other individuals as is the case in many host species infected by parasitoids. For this reason, $N_{\mathrm{H,m,t}}$ is not discounted by the number of infected hosts. In our stochastic simulations, each non-infected host individual j in patch m thus finally produces a Poisson distributed number of surviving offspring with mean $\lambda_{\mathrm{m,j,t}}$. Note that according to this model, realized equilibrium density would depend on how well individuals are adapted to the habitat, and how tolerant they are – habitat generalists cannot reach the same densities than specialists even in an optimal habitat.

Host-guest interaction: We assume that within any habitat patch, the probability $p_{\mathrm{m,t}}$ that a host in patch m at time t encounters (and interacts with) at least one guest individual follows the Nicholson-Bailey equation (Nicholson and Bailey 1935) with Holling's type II functional response (Holling 1959*a*, 1959*b*), i.e.

$$(3.3) \qquad p_{m,t} = 1 - e^{-\frac{aN_{G,m,t}}{1+aN_{H,m,t}}},$$

where $N_{\mathrm{G,m,t}}$ and $N_{\mathrm{H,m,t}}$ are the number of guests respectively hosts within patch m at time t, and a the per capita search efficiency of guests. We (implicitly) assume that the guests' handling time is one, which implies that a guest interacts at most with a single host in its lifetime. Note that the exponential term of *eq.* 3.3 provides the probability of a host to not interact with guests.

As neither the individual attributes of hosts nor guests affect encounter probability except the search efficiency of guests, we use *eq.* 3.3 to first estimate the total number of encounters in the population and then randomly select the corresponding number of guests and hosts, respectively, from the total population as being involved in an encounter. Guests that encounter hosts always reproduce successfully with the number of offspring drawn from a Poisson distribution with mean ψ. Note that the guest population is implicitly density-regulated by the availability of hosts. Fertility of a host involved in an antagonistic interaction is reduced to 0 if the interaction is antagonistic (i.e. infected hosts do not reproduce), but is unaffected in the case of commensalism.

Dispersal: All adult hosts and guests die after reproduction. Newborn hosts and guests decide to disperse or stay in their natal patch. For each individual, this decision is determined by an inherited dispersal trait (d_h and d_g for hosts and guests respectively) that determines the individual's probability to emigrate; d_h and d_g always take values between 0 and 1. We will use the terms "dispersal trait" and "dispersal probability" synonymously. If an individual decides to disperse, it moves randomly to one of the eight neighbouring patches (Moore neighbourhood; Gray 2003) irrespective of the habitat type of the target cells. After dispersal, both hosts and guests interact and reproduce as explained above.

Evolution: We assume three evolving traits, namely the habitat type a host individual is best adapted to (h - optimal habitat), a host's niche width (g), and the dispersal trait (d), i.e. the dispersal probability (the first two are relevant for hosts only; dispersal evolves in hosts and guests). These traits are typically inherited from the parent, but they can mutate occasionally with mutation probability μ_h and μ_g for hosts and guests respectively (both fixed at 0.001). This value should reflect natural mutation rate and not be too large to prevent establishment of a clear optimal strategy. At the same time, with a too low mutation rate, evolving traits could not reach a stable state due to lacking variation within reasonable time spans. Mutations of traits occur independently. The mutation process of three traits is similar, *i.e.* a random value from the uniform interval between -0.05 and 0.05 is added to the trait value. The dispersal probabilities generated by the mutation process are limited to the range 0 to 1. The habitat niche width is limited between 0.1 and infinity (very low habitat niche width is not allowed for in simulations for technical reasons). Setting a lower limit to niche width also reflects the fact that natural habitats will never be completely stable over time so that a minimum niche width is mandatory for long-term survival.

Simulation scenarios and analyses: Our primary interest is to understand how the type of host–guest interaction affects the concurrent evolution of hosts' dispersal trait (and that of guests) and its habitat niche width (as we keep mean habitat values constant throughout, evolution of the optimum habitat trait (or local adaptation) is of less interest here). For this purpose, we compare the evolution of dispersal and niche width in the antagonistic system with that in the commensalistic system. In a previous study (Chaianunporn and Hovestadt 2012*a*), we have already shown that search efficiency of guests plays a crucial role for dispersal evolution in hosts and parasitoids, because it determines the population dynamics and the proportion of infected hosts. By adjusting the trade-off parameter *c*, we can manipulate the evolution of the niche width *g* of hosts in order to vary the strength of the selection imposed by landscape heterogeneity. We further assume that with nearest neighbour dispersal, the landscape structure could affect the evolution of dispersal. More specifically, we expect that in clustered landscapes the selection pressure imposed by habitat mismatch on dispersing individuals is lower than in the random landscape, and that thus evolution of dispersal is promoted in the former. In summary, we consider four additional factors apart from the interaction type likely to quantitatively affect evolution of dispersal and niche width, *i.e.* search efficiency of guests, habitat structure (random landscape vs. clustered landscape), the cost for generalization, i.e. the magnitude of the habitat–fertility trade-off *T*, and finally external extinction risk (see next paragraph).

We carry out simulations with different values for search efficiency (a) modified between 0.005 and 0.05 in intervals of 0.005. In this search efficiency range, the populations of hosts and guests do not go extinct due to strong dynamics or too low search efficiency of guests. Moreover, this range of values covers a spectrum of possible consequences for population dynamics of hosts and parasitoids from stable dynamics to strong fluctuation. Three different values for the trade-off parameter are implemented, i.e. a “strong trade-off” (T_s; c=0.25), a “moderate trade-off” (T_m; c=1), and “a weak trade-off” (T_w; c=4). We choose these three trade-off values as in preliminary simulations they lead to distinctly different results. In some simulations, we assume that before any reproduction commences, local communities may go extinct with external extinction risk ε=0.01 due to the impact of e.g. some environmental catastrophes (the results represented in the main text are for scenarios with ε=0, results for ε=0.01 are shown in *Appendix I*). All simulations are carried out on the two landscapes types generated. A summary of all model parameters and their standard values can be found in Table 1.

Each simulation run is iterated over 4000 generations. Patches are initialized with K host individuals and a small number of guests (10 individuals) in order to avoid the collapse of host population at the beginning of the simulation. We assign lower K=500 values in commensalism scenarios than in the antagonism scenario (K=1000) to account for the fact that parasitoids reduces host equilibrium population size. We choose these two carrying capacity values because if the values are lower, stochasticity can play an importance role for the evolution of dispersal probabilities (Chaianunporn and Hovestadt 2012*a*). Dispersal traits of hosts and guests are initialized by drawing random values from the uniform interval [0 … 1] for each individual. Optimum habitat traits of hosts are initialized by drawing from the uniform interval [-1 … 1] (the same range as the range of the habitat type). The trait for habitat niche width is initialized with a random value between 0.1 (minimal value of the niche width trait) and 1.1.

For graphical presentation, we estimate for each simulation run the means of the dispersal trait (in hosts and guests), and host niche width across the whole metacommunity over the last 100 generations. We carry out 5 replicate simulation runs for each parameter combinations, and the mean and standard deviation of 5 replications are calculated and demonstrated in the figures. For the dispersal traits, we compare the results with the results in the homogeneous landscape, which come from Chaianunporn and Hovestadt (2012*a*). Since our previous study shows that the dispersal evolution can be explained mostly by population dynamics, we analyse temporal global and local dynamics by determining the global population size of hosts and the encounter probability between hosts and guests ($p_{m,t}$; *eq.* 3.3) in each system.

Table 3.1: Definition and ranges of values of parameters used

Symbol	*Description*	*Values*
H_m	habitat attribute of patch *m*	$H_m \in [-1,1]$
ε	external extinction risk	0, 0.01
c	control parameter for habitat–fertility trade-off *T* (see *eq.* 1 and details in *Model and Simulation*)	$c \in [0.25, 1, 4]$ corresponding to [T_s, T_m, T_w]
K	patch capacity for hosts	1000 (antagonism), or 500 (commensalism)
λ_0	intrinsic host growth rate	5
a	per capita search efficiency of a guest	$a \in [0.005, 0.010, ..0.05]$
ψ	mean number of offspring of a guest	2
μ_h *and* μ_g	mutation rate of hosts and guests	0.001
h	host habitat trait (optimum habitat)	evolving
g	habitat niche width trait of hosts	evolving
d_h	dispersal probability of hosts	evolving
d_g	dispersal probability of guests	evolving

3.3. Results

Effect of species interaction: The effect of species interaction type and guest search efficiency (a) on dispersal evolution is not fundamentally different in homogeneous (Figure 3.3; open circle lines) and heterogeneous landscape (Figure 3.3; closed symbol lines): If search efficiency is high enough, antagonism strongly promotes the evolution of dispersal of both hosts and parasitoids whereas commensalism does not. The importance of the search efficiency in antagonistic interactions can be traced to its effect on the dynamics of the host–parasitoid system (Figure 3.4). If a is small, local host populations remain stable and infection risk (encounter probability) for hosts across the landscape is quite similar – there is thus little opportunity to evade parasitoids by dispersal: At the smallest a value (a=0.005), the system is very stable, so that the results do not differ from the results in the commensalism scenario (Figure 3.4; upper row). As a becomes larger, the system starts to develop the classical predator–prey cycles that introduce massive spatio–temporal heterogeneity at the landscape level and thus a great incentive for both partners to disperse (Figure 3.4; lower row). In contrast, with commensalism, search efficiency has no effect on host population dynamics and thus no relevance for the evolution of dispersal either – for this reason we only show results for a single value of a (a=0.05) for the commensalism scenarios in our figures (Figure 3.3).

Effect of habitat heterogeneity: Our results demonstrate that the introduction of habitat heterogeneity generally leads to the evolution of lower dispersal probabilities in hosts than in homogeneous landscape – how much lower depends on the magnitude of the habitat–fertility trade-off (T; Figure 3.3); The stronger the cost for generalism, the lower the dispersal probability. This is expected, as habitat heterogeneity introduces an added cost for dispersing individuals due to the risk of immigrating into mismatching habitats. Under conditions where host populations are stable, e.g. in antagonism with low search efficiency (Figure 3.4, upper row), or in commensalism, the incentive to disperse is thus generally low even when the cost (trade-off) for being a generalist is very small. In antagonism with high search efficiency, a strong trade-off decreases dispersal probabilities of hosts and guests, because it reduces local population dynamics (Figure 3.4, lower row). Nevertheless, large dispersal probabilities similar to those observed in homogeneous landscapes may evolve if the trade-off is weak (Figure 3.3A and 3.3B).

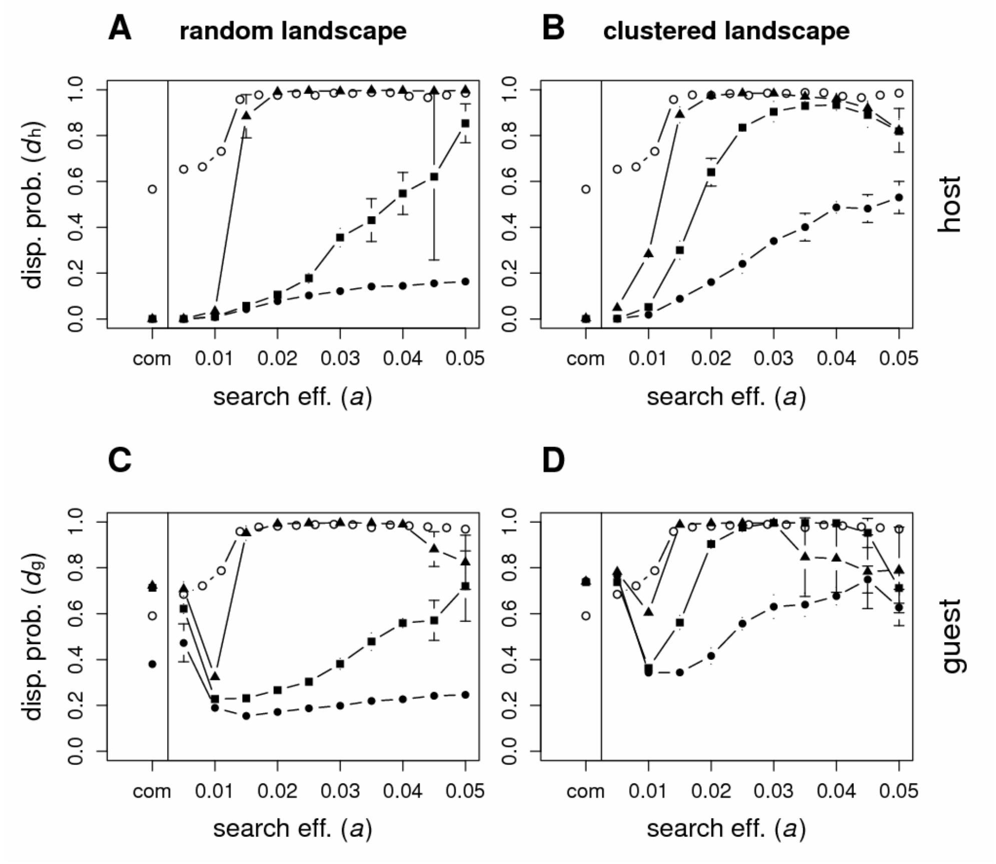

Figure 3.3: Comparison of evolving dispersal probabilities of hosts (d_h; upper panels) and guests (d_g; lower panels) in homogeneous (open circle) and heterogeneous landscapes (closed symbols). Different symbols represent results for different habitat–fertility trade-offs (T; see *eq.* 3.1): strong trade-off (circles: T_s; c=0.25), moderate trade-off (squares: T_m; c=1), and weak trade-off (triangles: T_w; c=4). The points on the left side ("com") represent results for the commensalism scenario at a=0.05, since they are not affected by the magnitude of a. (A) Dispersal probability of hosts (d_h) in random and (B) in clustered landscape. (C) Dispersal probability of guests (d_g) in random and (D) clustered landscape.

Note that reproduction of guests is as such independent of the habitat type and landscape heterogeneity. Consequently, we observe the evolution of higher dispersal probabilities in guests compared to hosts (Figure 3.3C and 3.3D) while this is opposite in homogeneous landscapes (see Chaianunporn and Hovestadt 2012*a*). Nonetheless, evolving dispersal probabilities for guests are also lower in the heterogeneous than in homogeneous landscapes, especially when the trade-off is strong – a result that is initially puzzling. However, in heterogeneous landscapes, host population density is not uniform across the landscape due to the distribution of the habitat types, *i.e.* in more extreme habitats, host populations are generally smaller than those in habitats with intermediate attributes – more so the stronger the habitat–fertility trade-off. This feature introduces spatial heterogeneity also from the guests' perspective (here rather in terms of local host population size than habitat quality). The effect is larger in random (Figure 3.3C) than in clustered landscapes (Figure 3.3B) where hosts are likely to migrate into habitats more similar to their native one.

Effect of habitat–fertility trade-off: In general, dispersal probabilities of hosts evolve to larger levels, when the habitat–fertility trade-off is weaker (compare lines within panels in Figure 3.3). This is fundamentally expected that – as the cost for evolving into a habitat generalist is low – spatially heterogeneity becomes less relevant for the fertility of migrating hosts. Thus, if the incentive for dispersal is large as in the case of strong antagonism, concurrent evolution results in highly dispersive habitat generalists. However, this only happens if such incentives indeed exist. In the commensalisms scenario (and with antagonism if a is very small), evolving dispersal remains much lower than in homogeneous landscapes even if the habitat–fertility trade-off is very weak and individuals become rather habitat specialist (Figure 3.5).

In the case of antagonism, the effect of search efficiency on the evolution of habitat niche width (g) critically depends on the magnitude of the trade-off (which must always be considered in proportion to the prevailing heterogeneity of the landscape; Figure 3.5). If enlarging niche width is too costly (T_s) in terms of fertility, selection always favours very specialized types (close to g_{min}=0.1) irrespective of a, and host dispersal evolves to considerably lower values than in homogeneous landscapes (Figure 3.3A and 3.3B). If the trade-off is very weak (T_w), generalist types prevail, and dispersal evolves to nearly similar values than in homogeneous landscapes except if a is very small. Yet with an intermediate value for the habitat–fertility trade-off, we observe a gradual evolutionary increase in both, habitat niche width and dispersal as a becomes larger. Also note that at very low search efficiency (a=0.005), habitat niche width in the antagonism scenario evolves to similar levels than in the commensalism scenario.

Adding an external extinction risk (ε=0.01) does not fundamentally alter the results presented above. However, such extinction risks introduce an added selective force favouring elevated dispersal and we observe a general increase in evolving dispersal probabilities as well as in habitat niche width (see Figure 3.A1 and 3.A2 in *Appendix I*).

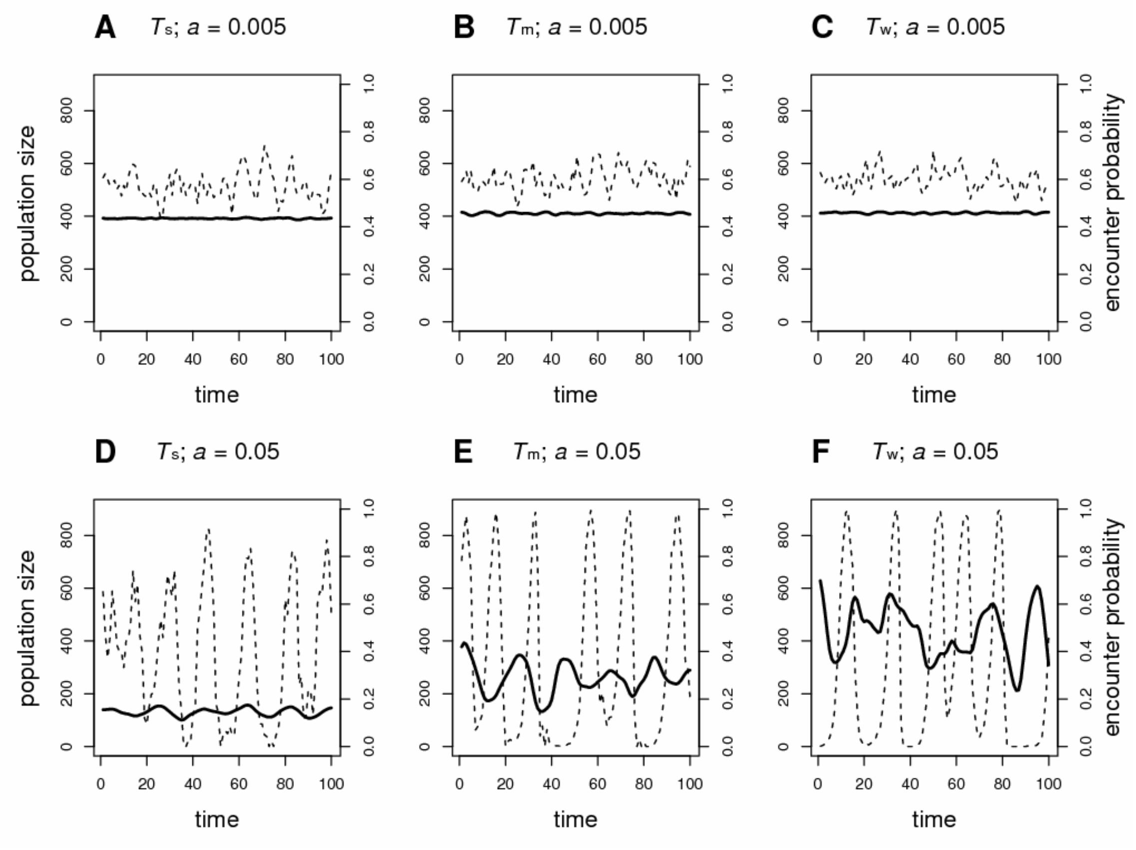

Figure 3.4: Examples for global host population dynamics (solid lines) and the expected encounter probability (dashed lines) from scenarios with different trade-offs (*T*) and search efficiency (*a*; external extinction risk ε=0): (A) strong trade-off (T_s) for *a*=0.005; (B) moderate trade-off (T_m) for *a*=0.005; (C) weak trade-off (T_w) for *a*=0.005; (D) T_s for *a*=0.05; (E) T_m for *a*=0.05; (F) T_w for *a*=0.05.

Effect of landscape structure: The utilization of a spatially-explicit model allows investigating how landscape structure influences results. The evolution of dispersal and habitat niche width respond in opposite directions when comparing results for scenarios on random with those on clustered landscapes: Whereas dispersal probabilities evolve generally towards higher values in the latter (compare Figure 3.3A and 3.3B), the opposite trend holds with respect to niche width (Figure 3.5A and 3.5B). This can be explained by the different spatial arrangement of habitats in the two landscapes. Compared to random landscapes dispersing individuals are generally more likely to immigrate into habitat similar to their natal site in clustered landscapes. The same argument also explains the reduced selection on niche width – as dispersing individuals are likely to arrive in similar habitat they pay little (and gain much) by being a habitat specialist.

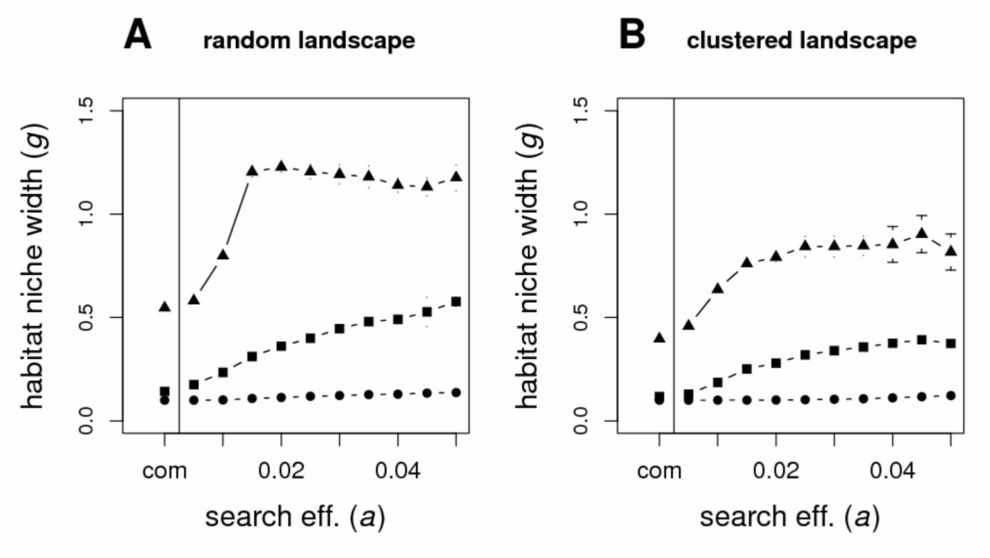

Figure 3.5: Comparison of evolving mean habitat niche width in random (A) and clustered (B) landscapes plotted over search efficiency (*a*)**.** Different symbols represent results for different habitat tolerance–fertility trade-offs (*T*; see *eq.* 3.1): strong trade-off (circles: T_s; *c*=0.25), moderate trade-off (squares: T_m; *c*=1), and weak trade-off (triangles: T_w; *c*=4). The points at "com" represent the results from the commensalism scenario at *a*=0.05.

3.4. Discussion

Our simulations demonstrate the potential for an interesting interdependence of species interactions, landscape heterogeneity, and the evolution of dispersal and habitat niche width. In a previous study (Chaianunporn and Hovestadt 2012*a*), we have already shown that antagonistic interaction may lead to the evolution of much elevated dispersal in hosts and guests (compared to mutualistic or commensalic interactions) except if the effect of parasitoids on their hosts were very mild.

With the addition of habitat heterogeneity and habitat niche width of hosts in this study, this result fundamentally still holds. However, habitat heterogeneity adds another dimension to the problem as it creates – from the perspective of the host species – spatial heterogeneity in the landscape in addition to the spatio–temporal heterogeneity possibly generated by antagonistic interactions. This adds a 'cost of dispersal' – here more accurately a 'settlement cost' (see general review on dispersal costs in Bonte et al. 2011) – for hosts due to the risk of moving from the typically preferred natal habitat to habitat patches of lower quality, a factor known to suppress the evolution of dispersal (Comins et al. 1980; Hastings 1983; Travis 2001; Poethke et al. 2003, 2011). Consequently, we report here the evolution of very low dispersal probabilities in hosts despite the fact that we did not associate dispersal with any direct cost (Figure 3.3). Moreover, in a previous study (Chaianunporn and Hovestadt 2012*a*), evolving dispersal probabilities of guests were always lower than that of hosts, while we get inverse results here. Obviously, introduction of habitat heterogeneity alters the ‘balance’ in terms of spatial landscape heterogeneity in favour of guests: In homogeneous landscape, hosts can colonize any empty habitats in the landscape whereas guests can only colonize patches where hosts established a population – this imposes a settlement cost on guests that their hosts do not have to pay. In a heterogeneous landscape, hosts have, however, the above-mentioned risk of immigrating into poor habitats (mismatching habitats). We know from other studies (Gandon and Rousset 1999; Poethke et al. 2007; Chaianunporn and Hovestadt 2012*a*) that if populations are very stable, and the population size (K) is large (as is the case here), very low dispersal evolves even in homogeneous landscapes as soon as dispersal incurs a small cost. This imposes strong selection on local fitness (fertility) favouring always the more efficient habitat specialists over generalists. This in turn enhances any settlement cost of dispersing, especially in random landscapes.

It is noteworthy, however, that despite the fact that the habitat heterogeneity is as such irrelevant for guests, and we nonetheless witness a strong decline in dispersal of guests in heterogeneous compared to homogeneous landscapes (Figure 3.3). We have shown, however, that the rare extreme habitats tend to maintain smaller host populations in heterogeneous landscape making it more difficult for guests to find hosts in such patches. This introduces indirectly spatial heterogeneity also from the perspective of guest thus also promoting the evolution of lower dispersal. Indeed this effect could in turn increase the benefit for hosts to utilize sub-optimal habitat if that reduces the risk of being parasitized (Chaianunporn and Hovestadt 2011).

Clearly, the more interesting findings of this article concern the simultaneous effect of antagonism and landscape heterogeneity on the concurrent evolution of dispersal and habitat niche width of hosts. At least with larger parasitoid’s search efficiency – reducing handling time or increasing parasitoid’s fertility would have similar consequences – antagonism may lead to strong oscillation of host and parasitoid population in space and time (Figure 3.4). Such temporal variation generally promotes dispersal (Comins et al. 1980; Karlson and Taylor 1995; Travis 2001; Poethke et al. 2003; Gros et al. 2008; Chaianunporn and Hovestadt 2012*a*). However, as dispersal incurs the risk of exposure to different habitat in a heterogeneous landscape, antagonism also favours the evolution of more habitat generalist species. It generally pays less to specialize on rare habitats that are also exposed to strong mass effects (Mouquet and Loreau 2002, 2003), *i.e.* immigration of poorly adapted individuals. This implies more frequent local extinction and lower average host population size in such patches. More generally, habitat heterogeneity and parasitoids are both selective forces reducing host fertility, but with contradictory effects on dispersal evolution. Whereas parasitism mostly promotes dispersal of hosts, habitat heterogeneity relegates it. When one of these selective forces is strong, it will override the effect of the other as we observe in Figure 3.4. In the case of habitat heterogeneity, this is primarily defined by the magnitude of the habitat–fertility trade-off in hosts (see Ravigné et al. 2009; Nurmi and Parvinen 2011); note however that this measure should always be scaled to the range of existing habitat types. When the trade-off is strong, the fitness loss associated with evolving habitat niche width is large, and hosts will evolve into habitat specialist even if they become dispersive under the pressure of antagonists (Figure 3.3A and 3.3B compare to Figure 3.5A and 3.5B). In contrast, if the trade-off is very weak, highly generalist strategies always evolve (the reasonable maximum niche width is defined by the spectrum of habitat available) as soon as dispersal carries even small benefits and is thus selected for. This is the case under strong antagonism or under an externally imposed population extinction risk. Note, however, that in the commensalism scenario, the host species may evolve also into a rather generalist species, if the trade-off is very weak, but nonetheless, does not disperse much. Finally, when the trade-off is moderate, increasing parasitic load (controlled here by search efficiency a) leads to a concurrent selection for increased dispersal and habitat niche width.

Certainly, the interaction between selection forces on dispersal is not limited to that between antagonism and habitat heterogeneity. For certain parameter spaces like small patch capacity, other forces like kin competition could play role an important role in determining the evolution of dispersal and habitat niche width. However, in this study, we chose model parameters that minimize the selective effect of such other forces.

It is important to note that it is difficult to specify a clear cause and effect of relationship with respect to our results. As a species becomes a habitat generalist, the above-mentioned settlement costs for dispersing individuals are reduced, and selection of more dispersive individuals becomes likely. Yet in turn, if conditions require dispersal, this also imposes selective pressure on evolving habitat niche width. Here, this relationship is clearly modulated by the strength of the habitat–fertility trade-off. Our results thus add to the list of theoretical studies that explore how selection on two interdependent traits can lead to interesting feedback effects (Kisdi 2002; Heinz et al. 2009; Nurmi and Parvinen 2011).

Our assumption that a habitat specialist can “evolve” to be a habitat generalist through the evolution of niche width might be unsuitable in some cases, for example when the resource or habitat are discrete. Our scenario better reflects the effect of continuous resources or habitat attributes, such as temperature, pH or sodium concentration. Moreover, according to the habitat–fertility trade-off, generalists are penalized by reduced fertility. This trade-off should reflect the cost that emerges due to developing high tolerance over different habitats and also lowers competitive ability of generalists to specialists in their best habitat. We demonstrate the significance of this cost by implementing three trade-off curves that differ in terms of the severity of the trade-off (in relation to the existing spectrum of habitat conditions) - the results show that this cost is important for both, dispersal and niche width evolution.

Our results further show that habitat arrangement can influence evolution of dispersal and habitat niche width in opposite way. In clustered (autocorrelated) landscapes, we observe the concurrent evolution of more dispersive but less tolerant species compared to the evolution in random landscapes. The spatial arrangement in our experiments is comparable to the ‘fine-grained’ (heterogeneous surroundings in which the individual organism may encounter numerous habitats) and ‘coarse-grained’ environment (surroundings where each organism experiences a single environment) of Levins (1968; also Hollander 2008): Whereas individuals in random landscapes experience fine-grained surroundings, individuals in clustered landscapes live in coarse-grained surroundings. Our findings support the classical view of Levins (1968) that in the coarse-grained environments individuals tends to be more specialized than in fine-grained environments. Empirical support for this expectations comes e.g. from the study of Hollander (2008) who reviewed the literature on plasticity in marine invertebrate. He reports that fine-scaled environmental heterogeneity selects for phenotypic plasticity (niche width) in marine invertebrates. Clearly, what constitutes ‘fine-grained’ or ‘coarse-grained’ lies in the eye of the beholder, and depends on the typical movement, respectively, dispersal distance of individuals: We would have generated identical results if we had – instead of randomizing the autocorrelated landscapes – introduced 'global dispersal' in our simulations (a scenario where individuals simply disperse into randomly selected patches). In this case characteristic dispersal distances were large in relation to the spatial structure of the landscape.

Empirical studies suggest that antagonistic interactions could also affect dispersal and habitat respectively resource utilization directly, i.e. that individuals adjust their behaviour in response to predation or parasitism (phenotypic plasticity respectively conditional response). For dispersal trait, supporting examples exist e.g. in the case of pea aphids (*Acyrthosiphon pisum*) and cotton aphids (*Aphis gossypii*) that produce more dispersal morph under predator or parasitoid attack (Weisser et al. 1999; Sloggett and Weisser 2002; Kunert and Weisser 2003; Mondor et al. 2005). For habitat utilization, our results are concordant with the 'enemy-free space' hypothesis that states that natural enemies can drive hosts to utilize suboptimal habitats that are free of enemies (Jeffries and Lawton 1984; Chaianunporn and Hovestadt 2011; Choutt et al. 2011). This has indeed been observed in many species. For example, the bog fritillary butterfly *Boloria eunomia* can be parasitized at the caterpillar stage by the specialist parasitoid wasp *Cotesia eunomiae* (Choutt et al. 2011). *B. eunomia* females thus frequently lay eggs in suboptimal habitats when in optimal habitats parasite abundance is higher than in such suboptimal habitats. There are further empirical examples for situations where animals switch food species in response to presence of natural enemies (e.g. Lill et al. 2002; Diamond and Kingsolver 2010). Our results indicate that in the long run such effects should also affect the concurrent evolutionary dynamics of habitat niche width and dispersal. To our knowledge, however, corresponding empirical studies have not yet been published.

3.5. Conclusion

In this study, we analyze the impact of two selective forces, namely species interactions and spatial heterogeneity, on the simultaneously evolution of dispersal and habitat niche width. In addition, we account for additional factors that influence this concurrent evolution, e.g. the cost of habitat generalization (the habitat–fertility trade-off) or the spatial arrangement of habitats. Although the model as implemented especially corresponds to the situation of a host-parasitoid system, the principal conclusions derived are in principal more general – the principle issue is whether the antagonistic interaction induces strong population cycling or not. Our results may bear implications with respect to general expectations concerning the response of different species respectively tightly interacting species groups to ongoing landscape and climatic change. Clearly, habitat niche width and dispersal are both important attributes that determine how organisms can respond to and survive under anthropologically imposed (rapid) change (Parmesan 2006; Hof et al. 2011). Our results, in fact, suggest that species involved in intense antagonistic interactions may indeed be more likely to carry attributes that will allow them to cope with such changes.

3.6. Appendix I: Supplementary figures

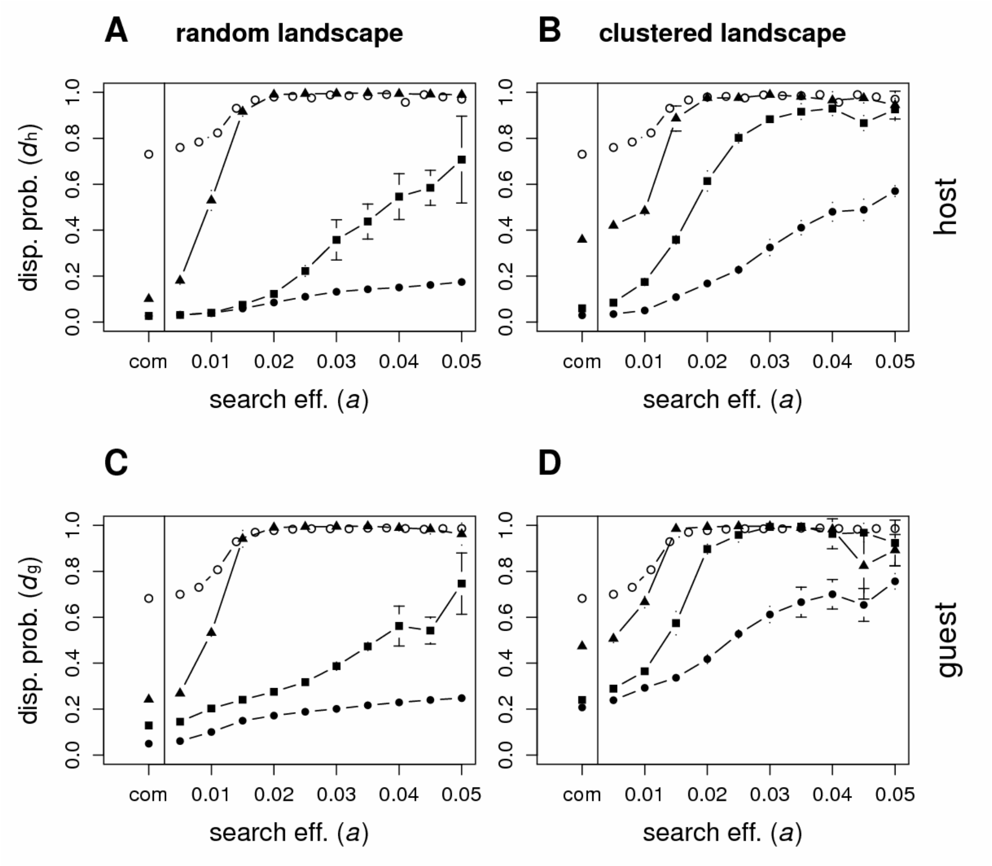

Figure 3.A1: Comparison of evolving dispersal probability of hosts (upper panels) and guests (lower panels) in homogeneous (open circle line) and heterogeneous habitat (closed symbol lines) from the scenarios with external extinction risk ε=0.01. Different symbols represent results for different habitat–fertility trade-offs (T; see *eq.* 3.1): strong trade-off (circles: T_s; c=0.25), moderate trade-off (squares: T_m; c=1), and weak trade-off (triangles: T_w; c=4). The points at “com” represent the results from the commensalism scenario at a=0.05: (A) Dispersal probability of hosts (d_h) in random landscape; (B) in clustered landscape; (C) Dispersal probability of guests (d_g) in random landscape; (D) in clustered landscape.

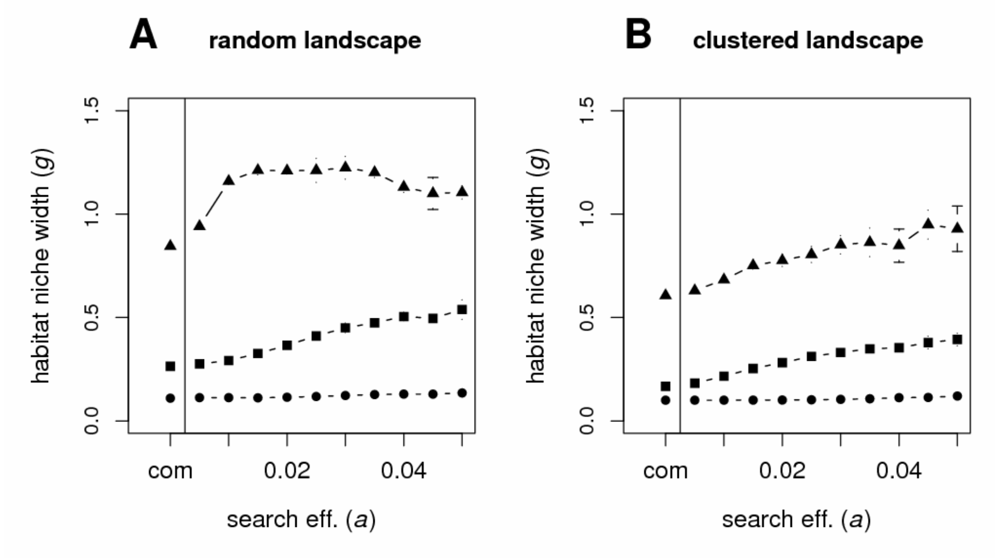

Figure 3.A2: Comparison of evolving habitat niche width (first row) in random (A) and clustered (B) landscapes plotted over search efficiency (*a*) from the scenarios with external extinction risk ε=0.01. Different symbols represent results for different habitat–fertility trade-offs (T; see *eq*. 3.1): strong trade-off (circles: T_s; c=0.25), moderate trade-off (squares: T_m; c=1), and weak trade-off (triangles: T_w; c=4). The points at “com” represent the results for the commensalism scenario at a=0.05.

Chapter 4

Evolutionary responses to the climate change in parasitic systems

With Thomas Hovestadt

4.1. Introduction

It is predicted that by the next century global temperature will raise 0.6–4.0°C (IPCC 2007). Current climate changes have already affected behaviour, diversity, and distribution of many species (Hoegh-Guldberg 1999; Hughes 2000; Peñuelas and Filella 2001; Walther et al. 2002, 2005; Parmesan and Yohe 2003; Root et al. 2003; Badeck et al. 2004; Parmesan 2006; Thomas 2010; Corlett 2012) – increasing temperature leads, for example, to earlier first flight in butterflies (Roy and Sparks 2000; Forister and Shapiro 2003). Moreover, climate change results in range shift, expansion, or contraction in many insect (Parmesan et al. 1999; Battisti et al. 2005; Hickling et al. 2006; Menéndez 2007) and small mammal species (Moritz et al. 2008). Such changes can lead to changing community composition and diversity (Daufresne et al. 2004; Menéndez et al. 2006; Moritz et al. 2008; Urban et al. 2012). Indeed, it is speculated that for species closely interacting with other species, climate change might lead to spatial and/or temporal mismatches between partner species (Visser and Both 2005; Parmesan 2006; Schweiger et al. 2008; Berg et al. 2010; Kiers et al. 2010; Pelini et al. 2010).

Many models that predict species response to future climate use the association between current climate and occurrences of species to define the set of conditions under which a species is likely to maintain viable populations (Pearson and Dawson 2003; Thomas et al. 2004; Araújo and Townsend Peterson 2012). They assume that species would disperse to track the climate change and move along with their optimal habitat (Hill et al. 1999; Parmesan et al. 1999; Thomas et al. 2001; Parmesan and Yohe 2003; Hickling et al. 2006; Moritz et al. 2008). These models often predict that many species will go extinct due to climate change because species may fail to track suitable habitat, with a range consequently contracting (Pounds et al. 1999, 2006; Franco et al. 2006; Thomas et al. 2006). This might happen if species cannot move freely to new habitats due to ecological or evolutionary constraints such as interspecific competition or monopolization effects (Urban et al. 2012), or if fragmented habitats hinders species to follow climate change (Travis 2003), or simply if the speed of the climate change surpasses the movement abilities of organisms (Loarie et al. 2009). The two perspectives, ‘tracking’ or range contraction, would be the only ‘options’ if species are assumed to be unchangeable entities lacking genetic variability to adjust to new conditions. However, in principle, other ecological and evolutionary responses are also conceivable (Davis et al. 2005; Parmesan 2006; Urban et al. 2012). Species may also persist climate change *in situ* or adapt to new climate by evolving new temperature preference (Levitan 2003; Balanyá et al. 2006), by increasing niche width or tolerance (Skelly et al. 2007; Oliver and Palumbi 2011), or adjusting their phenology (Peñuelas and Filella 2001; Badeck et al. 2004; Visser and Both 2005; Franks et al. 2007). For example, during its range expansion, the European butterfly *Aricia agestis* rapidly expanded its niche width from using only the host plant genus *Helianthemum* to using *Geranium* and *Erodium* species (Thomas et al. 2001). There is even evidence that dispersal ability and propensity are increasing in some species at advancing range fronts e.g. cane toads (*Bufo marinus*) at the invasion (range) front have longer legs than toads in long-established populations with which toads can move and arrive new areas faster (Phillips et al. 2006). Moose (*Alces alces*) have even shown different responses in different areas, i.e. they have persisted, undergone habitat shift by changing elevation and topography, or migrated to other areas depending on the pattern of climate change and the capacity of populations (Dawson et al. 2011). This suggests that an (multiple) evolutionary response to climate change may be possible and even affect evolution of different traits (life-history attributes) simultaneously.

Responses of individual species to climate change cannot be seen in isolation – biotic interactions play very important roles in species’ responses to the climate change (Hampe 2004; Brooker et al. 2007; Berg et al. 2010; Gilman et al. 2010; Walther 2010; Dawson et al. 2011; Urban et al. 2012). Phenology shift in one species might affect the whole ecological network, since not every individual in the network can equally respond to climate change, and species range shift might change the species composition in a community (reviewed in Walther 2010). Theoretical and empirical studies show that parasitism can be an important factor affecting dispersal and specialization in hosts (Weisser et al. 1999; Lill et al. 2002; Sloggett and Weisser 2002; Kunert and Weisser 2003; Mondor et al. 2005; Green 2009; Diamond and Kingsolver 2010; Poethke et al. 2010; Choutt et al. 2011; Chaianunporn and Hovestadt 2012*a*, 2012*b*), two traits that are important in the response to changing climate. Unfortunately, only few studies focusing on the concurrent response of interacting species to climate change (Berg et al. 2010; Urban et al. 2012).

In this study, we utilize a spatial explicit individual-based model and assume that a species could principally respond in three different and non-exclusive ways, i.e. (1) by modifying its dispersal ability, (2) by adjusting its optimal habitat (temperature preference), or (3) by expanding its niche width (temperature tolerance). We further consider the role of species interaction (commensalism and parasitism), landscape heterogeneity (in temperature) in this process and how the trade-off associated with niche widening (temperature tolerance) affects the evolutionary response. In contrast to commensalism, parasitism generates population fluctuation which promotes dispersal and habitat niche width (Chaianunporn and Hovestadt 2012a, 2012*b*). Many theoretical studies highlight the role of spatial heterogeneity for dispersal evolution as a cost of dispersal and settlement (Comins et al. 1980; Hastings 1983; Kirkpatrick and Barton 1997; Travis 2001; Poethke et al. 2003, 2011; Chaianunporn and Hovestadt 2012*b*). The cost for generalization is an obvious constraint on the evolution of niche width that indirectly also affects dispersal evolution (Chaianunporn and Hovestadt 2012*b*).

4.2. Model and simulation

Simulation landscape and climate change: We utilize a spatially explicit, individual-based two-species model previously presented by Chaianunporn and Hovestadt (2012*b*). We create spatially explicit lattice landscapes of dimension 32 x 32 grid cells (patches). Each cell *m* is characterized by a continuous number indicating a habitat attribute that represents the environmental mean temperature (H_m). Even though we assume that the habitat attribute is temperature here (or an attribute directly correlated with it), it could also be interpreted as another abiotic factor with continuous variation, such as saline concentration or pH. Mean temperature in each patch fluctuates annually by adding or subtracting a random number from a Gaussian distribution with mean=0 and standard deviation s_t=0.4 in all scenarios – in *c*. 99% of years actual temperature $H_{m,t}$ thus falls within a range of ±1° around H_m. This variation is applied independently to each patch as we see this simulation as local scale landscape. This variability reflects natural annual variability in climate and promotes selection of a certain 'temperature tolerance' (or habitat niche width; see '*Host species*') as a mean to cope with unpredictable variability. The grid of the landscapes is wrapped into a torus in both dimensions (a typical step taken is such simulations) to avoid edge effects. As described in detail in section '*Simulation scenarios*', we generate landscapes with two different spatial characteristics (homogeneous and heterogeneous landscape).

For climate change scenarios, we first carry out simulations over 2000 generations in order to generate populations that are well adapted to the initial conditions in each scenario. After this period, we save populations with the traits of all host and guest individuals in each patch. Populations are then exposed to different 'climate change scenarios' (C): (1) no change in mean temperature (as control) C=0, (2) an increase of C=2.0°C, and (3) an increase of C=4.0°C over 100 years (generations). These should cover the prediction range of global circulation models (IPCC 2007). According to scenario (2) and (3), mean habitat temperature of every patch (t_m) increases annually by 2/100 respectively 4/100 degrees between years 101 and 200. Thereafter increase of temperature stops and mean temperature stays at its new value. During the whole climate change, the annual variability in habitat temperature is still applied. We continue simulations for further 800 generations in order to investigate the evolutionary response after climate change has ceased and the system settles into a new equilibrium.

Species community: Throughout we simulate population dynamics and evolution in a community of two interacting species. We assume two types of interaction in separate simulations: commensalism and parasitism. From now on, we use the term 'guest' as a collective term for a species that always benefits from the interaction and completely depends on the presence of the 'host' species for survival and reproduction. The reproduction of an infected host individual is reduced to zero when the interaction is 'parasitism', whereas fitness of hosts is unaffected if the interaction is 'commensalism'. Hosts can survive and reproduce in the absence of guests.

Each habitat patch can principally support a community of both species. We assume that hosts and guests have a synchronized annual life cycle with discrete generations. Hosts and guests are both haploid organisms reproducing asexually. The order of the life cycle of both species is as follows: (1) after births of hosts and guests, both species perform either natal dispersal to a new target patch or stay in their natal patch; (2) species interaction occurs after dispersal; (3) hosts and guests reproduce with fertilities determined according to the interaction; (4) after reproduction, all adult host and parasite individuals die, and newborn individuals perform dispersal (1).

Host species: In our model, host reproduction generally depends on habitat temperature and competition. Each host individual *j* is characterized by the heritable and evolvable traits h_j and g_j where h_j defines the individual's 'temperature preference' ('optimal habitat') where it performs best and g_j its 'temperature tolerance' (or 'habitat niche width'). The fertility of host individual *j* in habitat *m* at year *t* ($\lambda_{m,j,t}$) is estimated according to a Gaussian distribution as:

$$(4.1) \qquad \lambda_{m,j,t} = T\lambda_0 e^{-(\frac{(H_{m,t}-h_j)^2}{2g_j^{\,2}})}$$

$$\text{with } T = e^{-(\frac{g_j^{\,2}}{2c^2})},$$

where λ_0 is the maximum fertility in optimal temperature (habitat). The fertility of any host individual is thus controlled by the match between the actual temperature of the patch ($H_{m,t}$) and the host's temperature preference (h_j), and the host's temperature tolerance (g_j). By the term *T*, we introduce a trade-off between niche widening (higher temperature tolerance) and fertility imposing a 'sanction' on individuals that evolve wider temperature range – otherwise selection would obviously favour complete temperature generalists. The principle existence of such trade-offs is a fundamentally accepted (but not often tested; e.g. Caley and Munday 2003; Koricheva et al. 2004; Palaima 2007) idea in evolutionary ecology (e.g. McPeek 1996), well captured in the phrase "jack of all trades is master of none". Accordingly, more generalized individuals cannot produce as many offspring in optimal habitat as specialized ones. The trade-off is controlled by parameter *c* ('trade-off parameter'): The smaller the value of *c* is, the higher the cost for higher temperature tolerance. With parameter *c*, we can thus control temperature tolerance evolution by modifying the 'cost' for being a generalist.

The expected number of offspring surviving to reproduction for each host individual is affected by local competition between host individuals and is estimated according to the Beverton-Holt model (Beverton and Holt 1981):

$$(4.2) \quad O_{m,j,t} = I\lambda_{m,j,t}s$$

$$\text{with} \quad s = \frac{1}{1+(\frac{\lambda_0 - 1}{K})N_{H,m,t}},$$

where K defines patch capacity for hosts and $N_{\mathrm{H,m,t}}$ is the number of hosts in patch m at time t. Under commensalism, guests do not affect host reproduction (I=1). In parasitism scenario (I=0), infected hosts (I=0 – only for infected hosts, I=1 for non-infected) do not reproduce (see below), but we assume that they are only killed at the end of their development. They thus still compete with other individuals for e.g. food resources, as is the case in many host species infected by parasites. For this reason, $N_{\mathrm{H,m,t}}$ is not discounted by the number of infected hosts.

In our stochastic simulations, a non-parasitized host individual j in patch m thus produces a Poisson distributed number of surviving offspring with mean $O_{\mathrm{m,j,t}}$. Note that according to this model, realized equilibrium density would depend on how well individuals are adapted to the habitat temperature, and their temperature tolerance – generalists cannot reach the same densities as specialists even in their optimal habitat.

Host–guest interaction: We assume that the probability $p_{\mathrm{m,t}}$ that a host encounters (and interacts with) at least one guest individual within any habitat patch m at year t follows the Nicholson-Bailey equation (Nicholson and Bailey 1935) with Holling's type II functional response (Holling 1959*a* and 1959*b*), i.e.

$$(4.3) \quad p_{m,t} = 1 - e^{-\frac{aN_{G,m,t}}{1+aN_{H,m,t}}},$$

where $N_{\mathrm{G,m,t}}$ and $N_{\mathrm{H,m,t}}$ are the number of guests respectively hosts within patch m at time t, and a the per capita search efficiency of guests. We (implicitly) assume that guests' handling time is one, which implies that a guest individual interacts at most with a single host in its lifetime. Note that the exponential term of *eq.* 4.3 provides the probability of a host to **not** interact with parasites.

As neither the individual attributes of hosts nor guests affect encounter probability except the search efficiency of guests, we use *eq.* 4.3 to first estimate the total number of encounters in the population and then randomly select the corresponding number of guests and hosts, respectively, from the total population as being involved in an encounter. Guests that encounter hosts always reproduce successfully with number of offspring drawn from a Poisson distribution with mean ψ. Note that the guest population is thus implicitly density-regulated by the availability of hosts. Change in fertility of a host interacting with guests depends on the interaction type as mentioned above.

Dispersal: All adult hosts and guests die after reproduction. Newborn hosts and guests decide to disperse or stay in their natal patch. For each individual, this decision is determined by an inherited and evolvable dispersal probability (d_h and d_g for hosts and guests respectively) that determines the individual's probability to disperse; d_h and d_g always take values between 0 and 1. We will use the term 'dispersal probability' to describe the trait from now on. Each individual draws a random number from the interval [0 … 1]. If this number lower than dispersal probability, the individual disperses, otherwise it stays in its natal patch. If an individual decides to disperse, it moves randomly to one of the eight neighbouring patches (Moore neighbourhood; Gray 2003) irrespective of the habitat type of the target cells. After dispersal, the life-cycle continues as explained above.

Evolution: We assume three evolving traits of hosts and one of guests, namely host's temperature preference (h), host's temperature tolerance (g), and the dispersal probability of hosts and guests (d_h and d_g). These traits are typically inherited from the parent, but occasionally mutate with rate μ_h and μ_g for hosts and guests respectively (both fixed at 0.01); such high mutation rate should maintain genetic diversity in case of small population size during climate change. We choose this value because in preliminary simulation runs, populations of host and guest sometimes collapsed under climate change due to lack of genetic variation (see *Discussion*). Mutations of traits occur independently. The mutation process of three traits is similar, *i.e.* a random value from the uniform interval [-0.05, 0.05] is added to the trait value. Whereas temperature preference is allowed to evolve any value between [-∞, ∞], we limit allowable values for dispersal probability to the interval [0, 1] and for temperature tolerance to the interval [0.05, ∞] (very low temperature tolerance is not allowed for technical reasons);

temperature tolerance always evolved towards larger values than the minimum, however, as in annually variable habitat, a minimum temperature tolerance is mandatory for long-term survival.

Simulation scenarios: In this study, we focus on the evolutionary responses of hosts under gradually increasing mean habitat temperature (climate change). We assume that the host species may respond to this change by evolution of all three traits, i.e. temperature preference (h), temperature tolerance (g) and dispersal probability (d). Guests' fitness is independent of habitat and guests can only adjust dispersal probability. Based on our previous studies (Chaianunporn and Hovestadt 2012*a*, 2012*b*), we hypothesize that hosts evolutionary responses to climate change will be modulated by the kind of interaction, landscape attributes, and the trade-off associated with niche widening.

In our scenarios, we compare the influence of two types of interaction, i.e. commensalism and parasitism as described above. We fix the search efficiency of guests (a) in both scenarios at 0.04. We also carried out parasitism scenarios with a lower search efficiency (a=0.01). However, results resemble those for commensalism, as parasites with low search efficiency do not induce as strong population dynamics as parasites with high search efficiency (for more details see Chaianunporn and Hovestadt 2012*a* and 2012*b*); we thus do not provide corresponding results here. Secondly, we compare the effects of two different values for the tolerance–fertility trade-off that defines the disadvantage associated with generalization (high cost for generalization: T_H, c=1, and low cost: T_L, c=4; see *eq.* 4.1). Thirdly, we compare effects of different landscapes. The first is a 'homogeneous landscape', in which the (initial) mean temperature of all habitats is similar, i.e. H_m=0, but habitat temperature fluctuates according to rules described before. The other type of landscapes is a non-correlated, random 'heterogeneous landscape'. We generate this landscape in the same way as the random landscape described in Chaianunporn and Hovestadt (2012*b*). Initially habitat mean temperatures H_m are thus drawn from a fractional Brownian motion process (Chipperfield et al. 2011) with mean zero and standard deviation s_s=2s_t (the range of habitat temperatures is approximately [-2, 2]). Note that a mean temperature H_m assigned to grid cell m remains unchanged throughout a simulation run except for the systematic increase imposed during climate change.

Table 4.1: Summary of model parameter definitions and ranges of values used

Symbol	*Description*	*Values*
t_m	habitat temperature of patch m	mean = 0°C
s_t	temporal (random) variability in habitat temperature	s_t =0.4
K	patch capacity for hosts	K=1000
λ_0	intrinsic host growth rate	λ_0=5
a	per capita search efficiency of a guest	a=0.04
ψ	mean number of offspring for guests	ψ =2
μ_h and μ_g	mutation rate of hosts and guests	μ_h *and* μ_g=0.01
h	temperature preference (optimal habitat) of hosts	evolving
g	temperature tolerance of hosts	evolving
d_h	dispersal probability of hosts	evolving
d_g	dispersal probability of guests	evolving
Simulation scenario parameters		
C	climate change over 100 years (generations)	C=0°C; 2.0°C; 4.0°C
s_s	spatial variability in temperature	s_s=0 for homogeneous landscape s_s=0.8 for heterogeneous landscape where $t_m \in [-2, 2]$
c	conversion cost for generalization (tolerance–fertility trade-off); see *eq.* 4.1	c=1; high cost T_H c=4; low cost T_L
I	interaction type; see *eq.* 4.2	I=0; parasitism I=1; commensalism

Initialization and analyses: Patches are initialized with K host individuals and a small number of guests (10 individuals) in order to avoid the collapse of host population at the beginning of the simulation in parasitism scenarios. We assign K = 1000 for all scenarios. With such a high K value effects of demographic stochasticity are reduced (see Chaianunporn and Hovestadt 2012*a*). Dispersal probabilities of hosts and guests are initialized by drawing random values from the uniform interval [0, 1] for each individual. Temperature preference of hosts are initialized with random values from the uniform interval [-2.5, 2.5] and temperature tolerance is initialized with random values from uniform interval [0.05, 2.05]. A summary of all model and simulation parameters and their standard values can be found in Table 4.1.

For each parameter combination, we carry out ten simulation replicates with different landscape arrangement (for scenario with homogeneous landscape, the landscape is always similar among replicates). For graphical presentation, we calculate averages of means and standard deviations estimated for each of the ten replicates and for each of the three evolving host traits (dispersal, temperature preference, temperature tolerance) at time 100 (before climate change) and 200 (at the end of climate change). Due to the large population size, standard deviations of trait values are for a set of randomly selected individuals (one individual from each local population, i.e. 32x32=1024). We mainly present the results from the scenarios with an increase of 4.0°C because in the 2.0°C scenarios, hosts show principally similar but obviously weaker responses. We show the moving average with a window=20 of host population size for the visualization reason because in parasitism scenarios (*Appendix I*), the host population fluctuates intensively. To present the response in three traits, we plot mean and standard deviation of three traits in arrow plots. On these plots, we rescale the mean for temperature preference by dividing by the temperature increase (4°C) – resulting values thus fall into the range between 0 and 1.

4.3. Results

Generally, our simulations show that climate change could lead to a concurrent evolutionary response in all three traits of hosts. In Figure 4.1, we show just one set of exemplary trajectories for the simulation of the commensalism scenario in heterogeneous landscape with low cost of generalization (for other sets of trajectories see *Appendix I*). Increase in habitat mean temperature leads to reduction of total population size by about 1/3 over the 100 years (generations) of climate change. In parallel, we witness an increase in dispersal probability, more temperature tolerance, and –obviously – in temperature preference; note that the increase in temperature tolerance seems to precede that in dispersal and temperature preference. After climate change ceases, population size, dispersal probability and temperature tolerance slowly return to the pre-change values while the temperature preference ultimately adjusts completely to the new (post-change) conditions. It should be noted, however, that temperature tolerance takes about 400 generations to return to the pre-change values, while dispersal returns within *c*. 180 to this level. This might be, however, different among scenarios (see *Appendix I*).

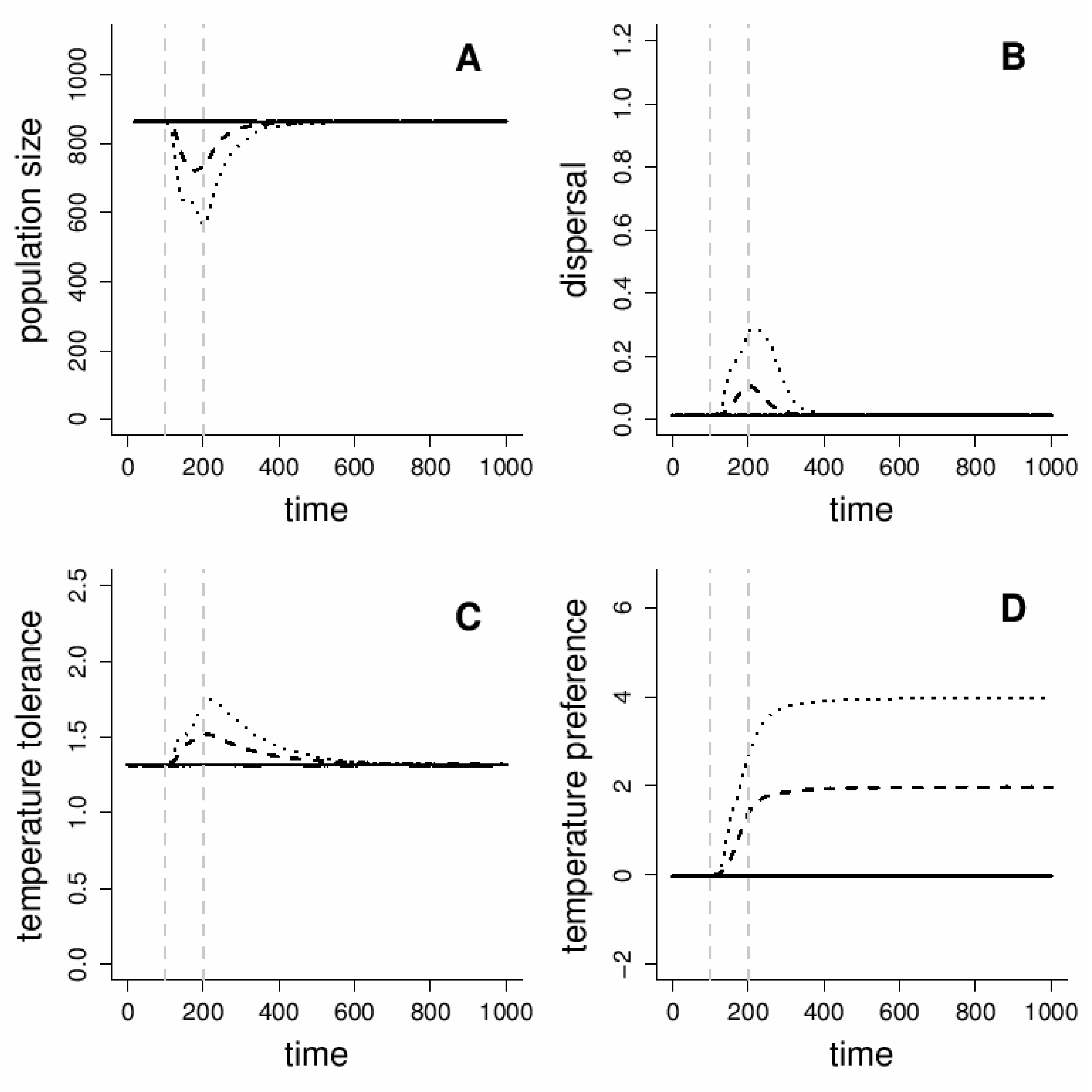

Figure 4.1: An example of host’s responses to climate change over time. Results originate from the commensalism scenario (I=1) with heterogeneous landscape and low cost of generalization (c=4). The lines in each subfigure represent the results from three different climate scenarios: no change (solid line), C=2.0°C (dashed line) and C=4.0°C scenario (dotted line). Two vertical dashed grey lines shows the time step at the beginning of climate change (101st) and the end (200th) of climate change: (A) Host’s population size (Note that the population size showing here is the moving average with a window=20); (B) host’s mean dispersal probability; (C) host’s mean temperature tolerance; (D) host’s mean temperature preference.

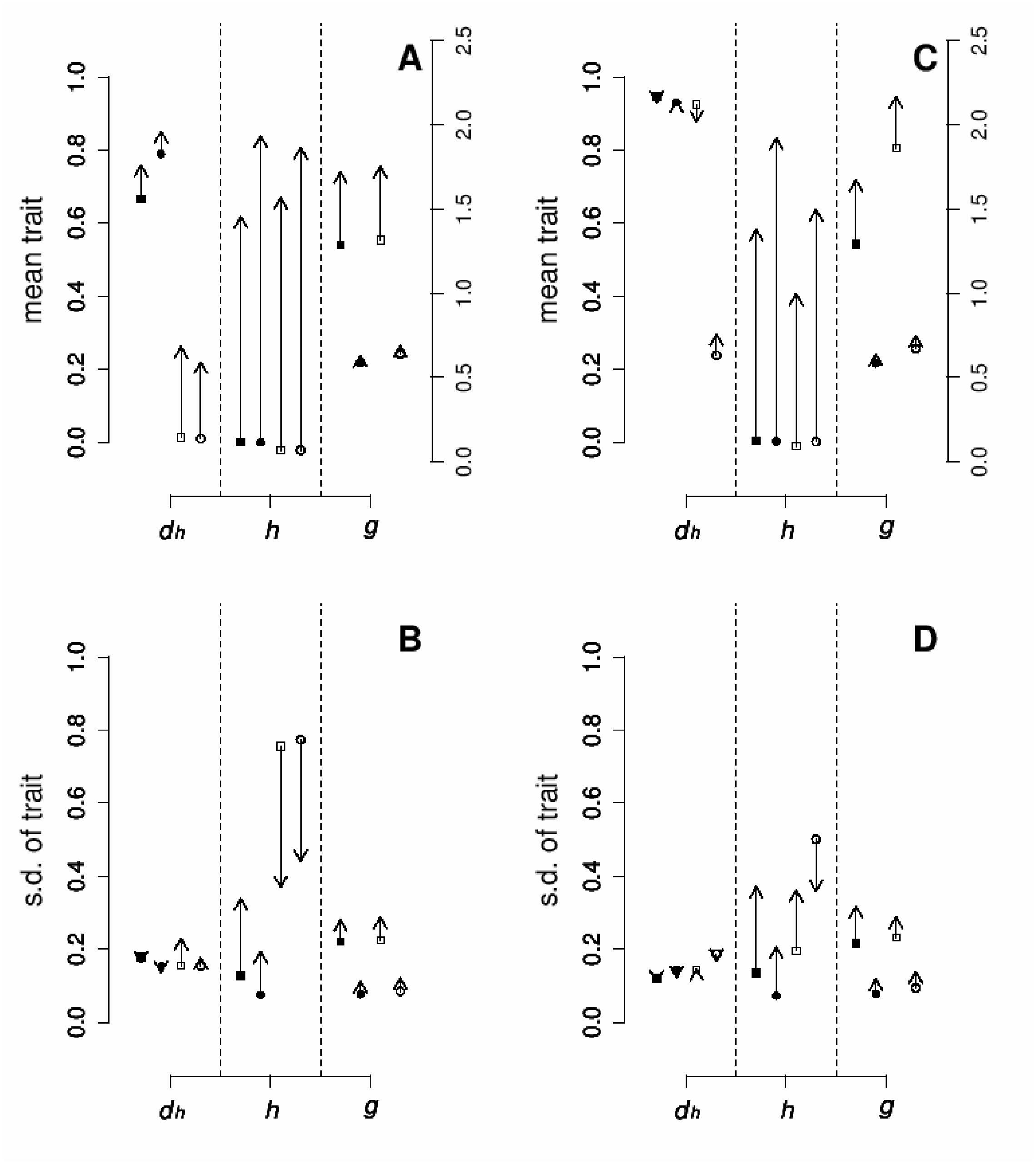

Figure 4.2: Effects of species interaction, landscape heterogeneity and cost for generalization on the host's evolutionary responses. Symbols represent mean or standard deviation (s.d.) of traits before climate change (generation 100), arrow heads indicate means or s.d. at the end of climate change (generation 200; C=4°C). Closed symbols show results for homogeneous landscapes, open symbols for heterogeneous landscapes. Shape of symbols represents results for different cost (c) of generalization (squares for low cost – c=4, and circles for high cost – c=1). Results for evolving host dispersal probability, temperature preference, and temperature tolerance are indicated by d_h, h, and g on the x-axis. The scale for temperature tolerance is different from the two other traits and is shown on the axis on the right side. (A) Mean trait values for commensalism scenarios (I=1); (B) Standard deviations of traits for commensalism scenarios; (C) Mean trait values for parasitism scenarios (I=0); (D) Standard deviations of trait for parasitism scenarios (for more detail see *Model and simulation*).

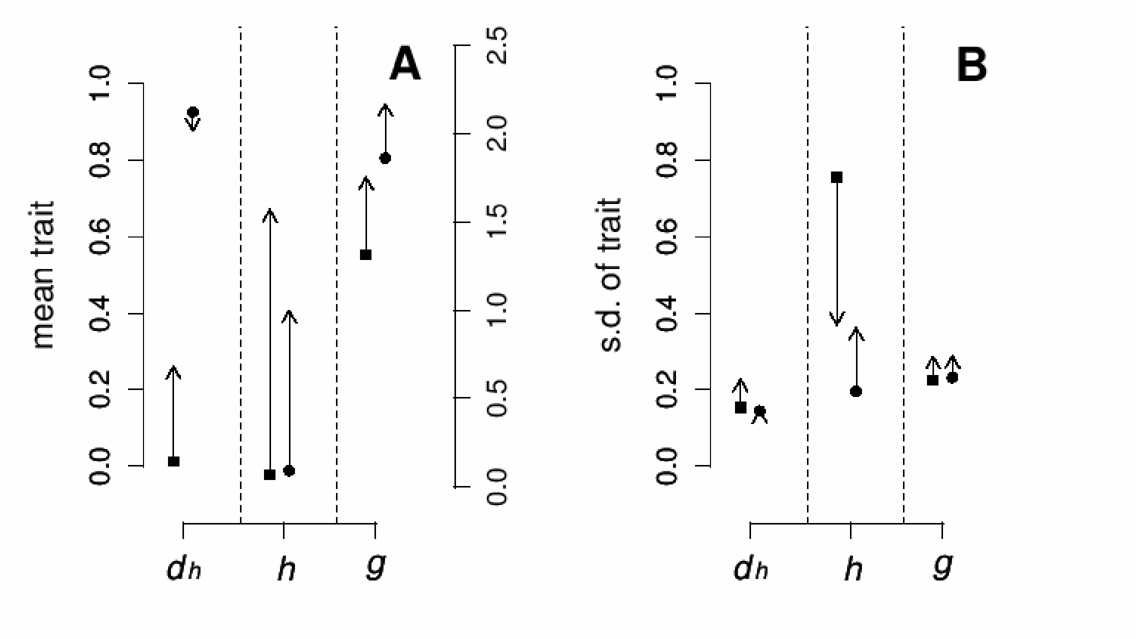

Figure 4.3: Evolutionary responses of hosts in commensalism (I=1) and parasitism (I=0) scenarios in heterogeneous landscapes and with low costs for generalization (c=4). Closed symbols represent mean or standard deviation of traits before climate change (generation 100) and arrow heads indicate mean traits at the end of climate change (generation 200). Square symbols show results for commensalism and circles results for parasitism scenarios. (A) Mean trait values; (B) Standard deviations of trait values (for more details see *Figure4. 2*).

Responses in dispersal: Before climate change, evolving dispersal probability of hosts is determined by all three factors (Figure 4.2A and 4.2B). Spatial heterogeneity generally leads to limited dispersal under commensalism, as heterogeneous landscapes add an implicit settlement cost for dispersing individuals in comparison to homogeneous landscape (Bonte et al. 2011; Chaianunporn and Hovestadt 2012*b*). In contrast, parasitism promotes the evolution of very high dispersal probability (>0.8) due to the strong population dynamics induced (Chaianunporn and Hovestadt 2012*a*). This effect of parasitism on host dispersal is reduced, however, when generalization is costly (c=1; T_H), i.e. $d_h \approx 0.2$. Further, the effect is limited to heterogeneous landscape, since moving in homogeneous landscape does not impose the abovementioned settlement costs and thus does select for a higher temperature tolerance. Climate change induces a substantial increase in dispersal probability in the commensalism scenario, especially in heterogeneous landscapes, while under parasitism, only slight changes in dispersal can be observed. The population wide variability in the dispersal trait is little affected by climate change in all scenarios (Figure 4.2B and 4.2D).

Responses in temperature preference: Before onset of climate change mean temperature preference expectedly and perfectly matches the prevailing mean habitat temperature in all scenarios ($\bar{h} \approx 0$). Climate change obviously mandates an adjustment of this trait to new conditions. In none of the scenarios can evolution fully track climatic conditions during the period of change, but under commensalism, habitat preference traces climate change better (faster) than under parasitism in heterogeneous landscapes (Figure 4.2A and 4.2C); the discrepancy is especially large in scenarios with a low trade-off cost for generalization (c=4). The response is always more rapid if the trade-off costs for generalization is high (c=1). Beside the change in the trait mean, we observe a considerable effect of climate change on variance in temperature preference (Figure 4.2B and 4.2D). In homogeneous landscapes, trait variance considerably increases, especially, if trade-off costs for generalization are low. In heterogeneous landscapes, however, we see a substantial decline in trait variance (from much higher starting values) during climate change under commensalism. This effect is considerably lower under parasitism if generalization is ‘expensive’ (c=1). If the trade-off cost of generalization is low (c=4), the variance in temperature preference even increases under parasitism.

Responses in temperature tolerance: The cost for generalization is the most important factor determining temperature tolerance evolution (Figure 4.2A and 4.2C). As expected, the higher the cost is, the less the temperature tolerance initially evolves. Climate change only induces noticeable generalization if trade-off costs are low (c=4) in any scenario, and generally induces a slight increase of variance in this trait. The initial temperature tolerance (before climate change) and response in this trait are similar in all scenarios except in the parasitism scenario in heterogeneous landscape at low trade-off costs where a higher temperature tolerance is selected for.

Effects of interspecific interaction: In summary, we recognize that in homogeneous landscapes the hosts’ evolutionary response to climate change is very similar under commensalism and parasitism. We find that differences in response between the two types of interaction are most obvious in heterogeneous landscape and under low cost of generalization; we provide a head-to-head comparison in Figure 4.3. Before climate change, parasitism selects for higher dispersal probability and temperature tolerance than commensalism. However, parasitism is also associated with the establishment of much lower variance in temperature preference. Under climate change, dispersal probability massively increases in the commensalism scenario (from a very low level), whereas dispersal hardly changes (from very high value) in the parasitism scenario. Host temperature preference responds much slower to climate change under parasitism than under commensalism so that after 100 generations, at the end of climate change, and ‘adaptation gap’ (discrepancy between mean preferred temperature an mean ambient habitat temperature) of c. 2.4 °C has formed in this scenario (the gap is only c. 1.3 °C in the commensalism scenario). Interestingly, climate change induces an opposing effect on trait variance of temperature preference in the two scenarios – in commensalism it substantially falls from a high value while trait variance increases under parasitism (Figure 4.4). Finally, temperature tolerance expands under both types of interaction, but niche width is and remains higher under parasitism.

4.4. Discussion

Evolutionary responses of hosts under climate change: In our simulations we allow for the evolution of three traits that may play an important role in response to climate change, namely dispersal probability, temperature tolerance (or niche width), and temperature preference (optimal habitat); note that for simplicity we assume that temperature preference or optimality (h) is related to temperature per se but it could also represent adaptation to other attributes that correlate with habitat temperature, e.g. vegetation height or habitat dryness (Allen et al. 2010; Elmendorf et al. 2012).

Changes in dispersal induced by climate change have also been focused on, predicted and reported (Hill et al. 1999; Parmesan et al. 1999; Thomas et al. 2001; Parmesan and Yohe 2003; Hickling et al. 2006; Moritz et al. 2008). However, to our knowledge, an adjustment in temperature preference and niche widening (changing in temperature tolerance) as a potential response has drawn less attention in the context of climate change, even though they are potential ‘strategies’ to deal with climate change – especially if the latter also results in an increase in climatic variability as is suggested by current climate models (Skelly et al. 2007; Dawson et al. 2011). Here, we test effects of different parameters/attributes potentially affecting the evolutionary response in any of the three traits, i.e. spatial habitat heterogeneity that typically limits dispersal evolution (Comins et al. 1980; Hastings 1983; Travis 2001; Poethke et al. 2003, 2011; Chaianunporn and Hovestadt 2012*b*), the habitat–fertility trade-off cost associated with temperature tolerance, and the impact of parasitism that can limit diversity of temperature preference trait (see more details below).

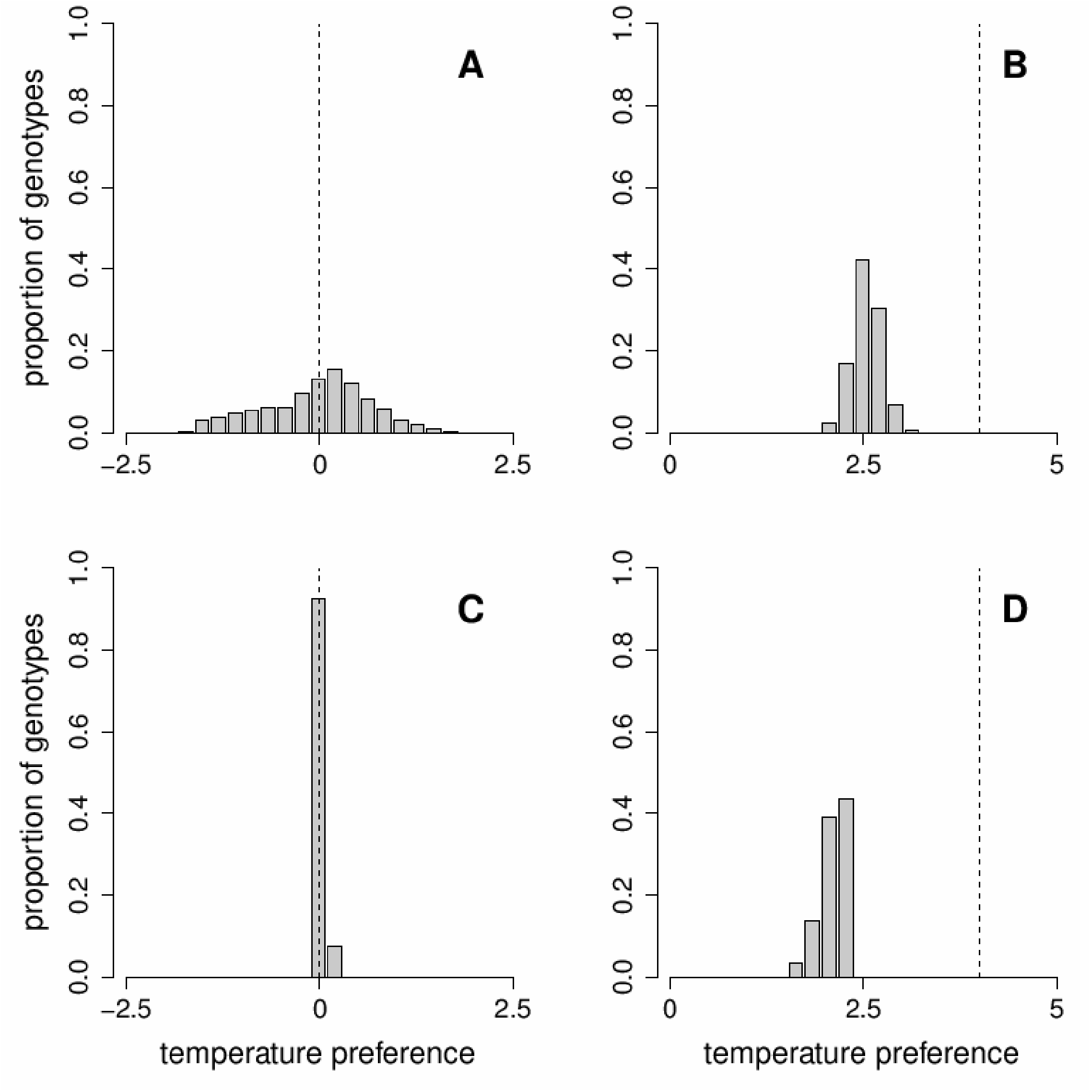

Figure 4.4: Histograms of hosts' temperature preference distribution before (generation 100) and after climate change (generation 200; *C*=4°C) for commensalism and parasitism scenario (low cost for generalization, *c*=4, and heterogeneous landscape). The y-axis presents the proportion of traits falling into specified categories. The dash line indicates mean habitat temperature at corresponding time step (0°C for before and 4°C after climate change). (A) commensalism before; (B) commensalism after climate change; (C) parasitism before; (D) parasitism after climate change.

In homogeneous landscapes, we find little difference – before and under climatic change – in host trait evolution between the parasitism and commensalism scenarios. The modification of the trade-off cost indicates, however, that increase of temperature preference could, to a certain degree, be a compensatory response to limiting temperature tolerance: We recognize that the adjustment in temperature preference h is faster (*c*. 80% vs. 60% by the end of climate change phase) when the evolution of temperature tolerance (g) is prevented by a too strong the tolerance–fertility trade-off; such a relationship has already been predicted by Whitlock (1996).

In heterogeneous landscape, spatial heterogeneity has little effect on the evolution of temperature tolerance beyond that mandated by temporal variability in temperature (see below). If the trade-off cost for generalization is lower, however, higher tolerance evolves in heterogeneous landscapes in association with high dispersal probability if hosts are exposed to parasites. The adjustment in temperature preference to climate change is, in turn, especially low in this scenario (*c*. 40%). Under no conditions, however, selection can completely adjust temperature preference to prevailing conditions during the phase of on-going change (mainly because of small mutation step on this trait in each mutation event, i.e. ≤ 0.05 per mutation event) resulting in an ‘evolutionary lag’ or mal-adaptation to ambient conditions. A complete adjustment only occurs considerable time after climate change has ceased.

In this study, we assume no direct costs to dispersal but only a ‘settlement cost’ (see Bonte et al. 2011) associated with moving to non-optimal habitats (only in heterogeneous landscape). For this reason, the evolution of high dispersal probability is selected for in homogeneous a landscape to avoid kin-competition (Hamilton and May 1977; Comins et al. 1980; Gandon and Rousset 1999; Bach et al. 2006; Poethke et al. 2007). Introduction of an explicit dispersal cost would clearly change this, possibly with an associated effect on the diversity of locally adapted ‘habitat specialists’.

In comparison to commensalism, parasitism has thus two effects on the system. Parasitism promotes the evolution of dispersal due to the strong spatio-temporal dynamics in host populations induced (for more details see Chaianunporn and Hovestadt 2012*a*). As a consequence, parasitism also limits the emergence of diversity in temperature preference (in heterogeneous landscapes) as hosts which are continuously on the move have to follow a ‘generalist’ strategy with a high tolerance and a preference for the average temperature: Figure 4.4C demonstrates the distribution of hosts' temperature preference under parasitism before the climate change that is very narrow in comparison to the corresponding distribution in the commensalism scenario (Figure 4.4A). For the responses to climate change, this lack of genetic diversity in temperature preference slows down the response to climate change in this trait, but may (partially) be compensated by increasing tolerance. It must be noted that the lacking diversity of temperature preference does prevent the colonization of the more extreme temperature already before climate change sets in contributing – in addition to the direct effects of parasitism – to a reduction in effective host population size. Lower population size, however, reduces the rate at which new (and favourable) mutations may appear in the population. After climate change, the shape of the distribution of habitat preferences in the parasitism scenario is actually more similar to the commensalism scenario (due to small population size of parasites as well), but lags further behind the ambient temperature than in commensalism scenario (Figure 4.4B and 4.4D), i.e. maladaptation becomes larger.

Even though three types of evolutionary response are always allowed, we do not necessarily see a response in all three attributes in every scenario. For example, temperature tolerance does only increase under climate change if the trade-off associated with such an increase is not too severe. Dispersal propensity shows a strong (especially proportionally strong) response only where it is initially very low. In the changing environment, dispersal becomes a necessity for tracking changing climate and move to more suitable microclimatic pockets (Hof et al. 2011) as philopatric individuals would become increasingly maladapted. That dispersal is sufficient to allow 'habitat (temperature) tracking' is actually an implicit assumption of 'climate envelope models' (Thomas et al. 2004; Thuiller et al. 2005, 2011; Lawler et al. 2009). We want to also point out, however, that there may exist even further ecological and evolutionary responses to climate change, e.g. shifts in phenology (Visser and Both 2005; Parmesan 2006) or change of interaction partners (Kiers et al. 2010). Estimating the (additional) role of such responses and how they might interact with the responses considered here may require even further investigation.

Influence of other parameters: First, we want to point out that the range of temperature values provided in our scenarios should not be taken too literally. The important point is that the evolution of temperature tolerance and the evolutionary response to climate change should critically depend on how the magnitude of temporal variability scales to the cost of generalization. This depends mainly on three key parameters of our model, namely the unpredictable year-to-year temporal variability in climatic conditions (s_t), the spatial heterogeneity (s_m), and the trade-off cost (here fertility reduction but it could also affect other fitness components) associated with generalization (c). It may indeed be a challenging task to quantify these parameters for a real system and matters may further be complicated if costs (fertility reduction at optimum habitat) associated with generalization are non-linear or would even show a threshold behaviour.

The role of spatial and temporal heterogeneity may at a first glance seem similar, but the important difference are that individuals cannot avoid temporal variability according to our model assumption; in reality, this might, however, be possible by e.g. active choice of suitable microclimatic conditions (Hof et al. 2011). The only evolutionary response to this ‘problem’ is thus the evolution of a sufficient temperature tolerance with the latter determined by the underlying trade-off. Spatial heterogeneity, in contrast, may be mostly irrelevant for the evolution of temperature tolerance as long as individuals do not need to disperse much. Under scenarios promoting low dispersal, we thus see the evolution of a wide spectrum of locally adapted temperature preference (Figure 4.4A) whereas temperature tolerance is not different from that evolving in homogeneous landscapes despite the fact that spatial heterogeneity (s_m) is twice as large as temporal heterogeneity (s_t).

In this study, we assume seemingly unrealistically high mutation rates (μ_h *and* μ_p=0.01) that may be rare in nature (Lynch 2010). Technically such high mutation rates allow a quick evolutionary response leading to higher survival chances of populations exposed to climate change. The fact that we see strong changes in habitat preference even in homogeneous landscapes clearly indicates that mutations were indeed the ultimate source of new genotypes that were not originally present when climate change sat in. It is difficult, though, to directly compare ‘mutation events’ in our model and those in nature, because the mutation process behind complex behavioural traits such as dispersal, temperature preference, or temperature tolerance is not well understood and certainly more complicated than in our model of haploid organisms. Some studies highlight, however, that changes in e.g. thermal tolerance or thermal preference can indeed occur rapidly within few generations (Good 1993; Skelly and Freidenburg 2000;

Balanyá et al. 2006; Skelly et al. 2007). This makes our assumption of rapid evolutionary response of species to the climate change more credible.

Further note that in our simulations, we consider a closed regional dimension only, i.e. we do not assume a large-scale gradient in temperature conditions. Real systems are typically not closed, however, and a likely resource – especially if species are dispersive – of genetic innovation may thus be immigrants from other regions, where conditions are e.g. already warmer (Kubisch and Poethke 2011); such immigrants would basically take the same role as a new favourable mutant.

To avoid dealing with even further issues we focus here only on the responses of host species to climate change but totally ignore its effect on guest species. We want to briefly mention that in our system guests are fundamentally more sensitive since they cannot survive and reproduce without hosts. Additional simulations (results not shown) indicate that under more extreme conditions (e.g. faster climatic change, higher trade-off costs) guests might go extinct whereas hosts survive. This warrants further investigation, especially as guest species are often targets of conservation efforts, such as *Maculinea* butterflies that are closely associated with host ants (Settele and Kuehn 2009; Thomas et al. 2009).

Relevance of the results: Many studies predict the potential impacts of climate change on species distribution and biodiversity by using “bioclimate envelope models” (Thomas et al. 2004; Thuiller et al. 2005, 2011; Lawler et al. 2009). This approach has been criticized because it ignores many factors that could potentially affect the prediction like biotic interactions, potential evolutionary response, or inter-individual variation in dispersal abilities (Pearson and Dawson 2003; Hampe 2004). Supporting findings evidence that evolutionary responses to climate change can occur even in brief periods (Good 1993; Skelly and Freidenburg 2000; Balanyá et al. 2006; Skelly et al. 2007). We show here that the (mitigating) evolutionary responses might even be ‘multidimensional’ including several traits and that selection on different attributes can be interactive and compensatory. Moreover, our results emphasize that the effect on interspecific interactions (in our case parasitic interaction, but see Kubisch et al. *in press* for interspecific competition) may possibly play a very important role for correctly predicting the responses to climate change.

Our simulation results also indicate that – as long as dispersal is rare (such as in case of commensalism) – landscape heterogeneity may promote regional coexistence of genetic diversity in temperature preference providing an ‘ad hoc’ source of genetic diversity if environmental conditions change. Under such conditions managing for habitat heterogeneity – specifically creating warm habitat – might be an option to mitigate effects of future climatic change by selecting for ‘warm adapted’ genotypes already now (Levitan 2003; Balanyá et al. 2006). However, if conditions (e.g. parasitic interactions) rather promote the evolution of dispersive habitat generalists uniformly adapted to the most abundant (average) habitat conditions, such a management strategy may be ill-advised as it would possibly just reduce the amount of average habitat available and thus host population size.

The simulations presented here constitute, only a ‘conceptual approach’ to explore what kind of ‘multi-dimensional’ evolutionary responses to climate change might be possible and how the nature of responses may depend on external conditions. Our simplistic approach should only be taken as an outline towards developing (evolutionary) models that relate to real world systems. Clearly a more detailed evaluation of the critical assumptions and model parameters would be necessary, before such application-orientated models and predictions could be generated. The challenge may especially be demanding to quantify the potential to ‘generate’ evolutionary innovations (e.g. by immigration, mutation, recombination) and the possible role of trade-offs associated with selection on niche-widening or other changes in life-history attributes associated with climate change.

4.5. Appendix I: Supplementary figures

Figure 4.A1–4.A7: Host's responses to climate change over time in different scenarios. The lines in each subfigure represent the results from three different climate scenarios: no change (solid line), C=2.0°C (dashed line) and C=4.0°C scenario (dotted line). Two vertical dashed grey lines shows the time step at the beginning of climate change (101st) and the end (200th) of climate change: (A) Host's population size (Note that the population size showing here is the moving average with a window=20); (B) host's mean dispersal probability; (C) host's mean temperature tolerance; (D) host's mean temperature preference. The scenarios are presented by following: commensalism (I=1) or parasitism scenario (I=0) with homogeneous (s_s=0) or heterogeneous landscape (s_s=0.8) and low (c=4) or high cost for generalization (c=1): (4.A1) I=1, s_s=0, c=4; (4.A2) I=1, s_s=0, c=1; (4.A3) I=1, s_s=0.8, c=1; (4.A4) I=0, s_s=0, c=4; (4.A5) I=0, s_s=0, c=1; (4.A6) I=0, s_s=0.8, c=4; (4.A7) I=0, s_s=0.8, c=1.

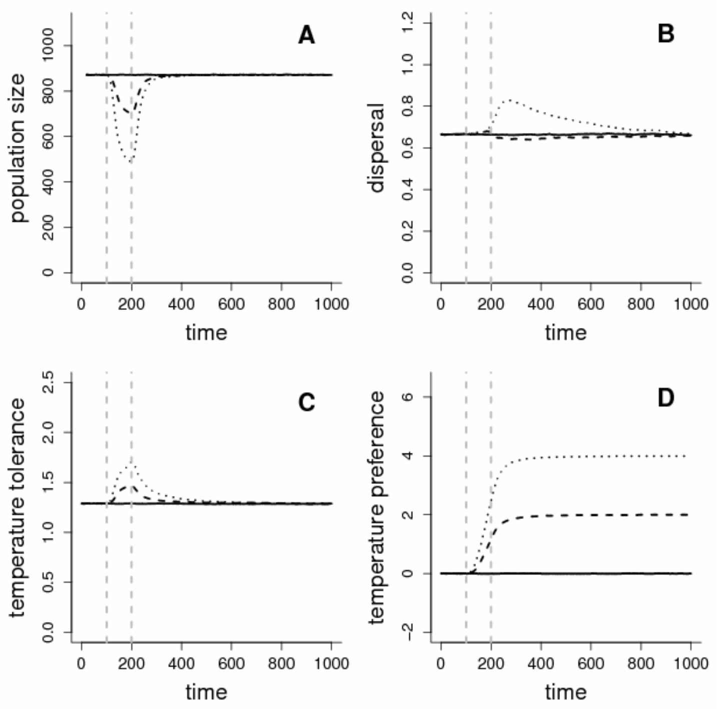

Figure 4.A1: Commensalism scenario (I=1) with homogeneous landscape (s_s=0) and low cost for generalization (c=4).

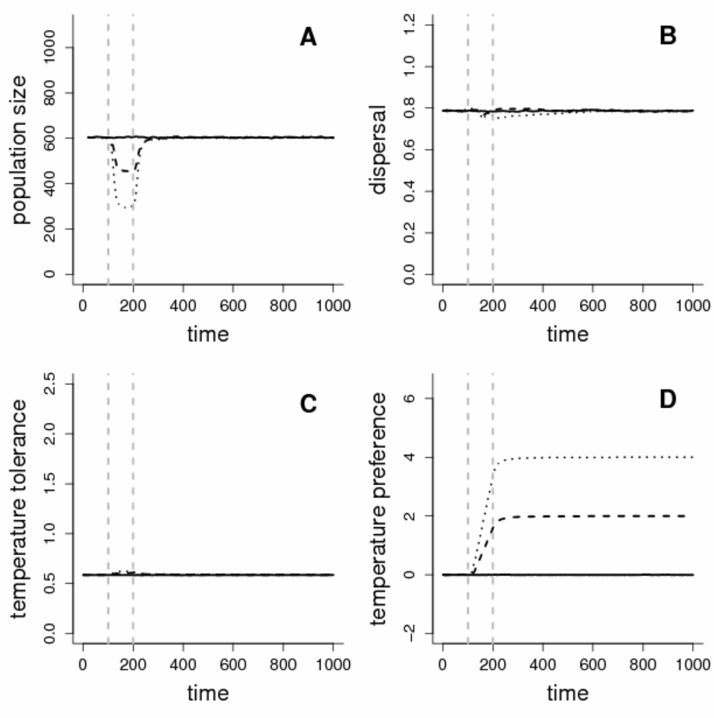

Figure 4.A2: Commensalism scenario (*I*=1) with homogeneous landscape (s_s=0) and high cost for generalization (*c*=1).

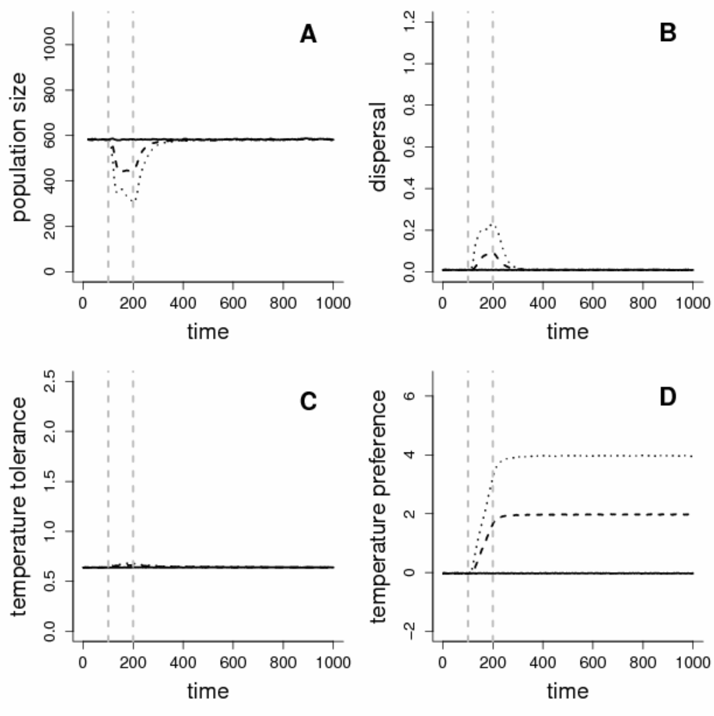

Figure 4.A3: Commensalism scenario (*I*=1) with heterogeneous landscape (s_s=0.8) and high cost for generalization (*c*=1).

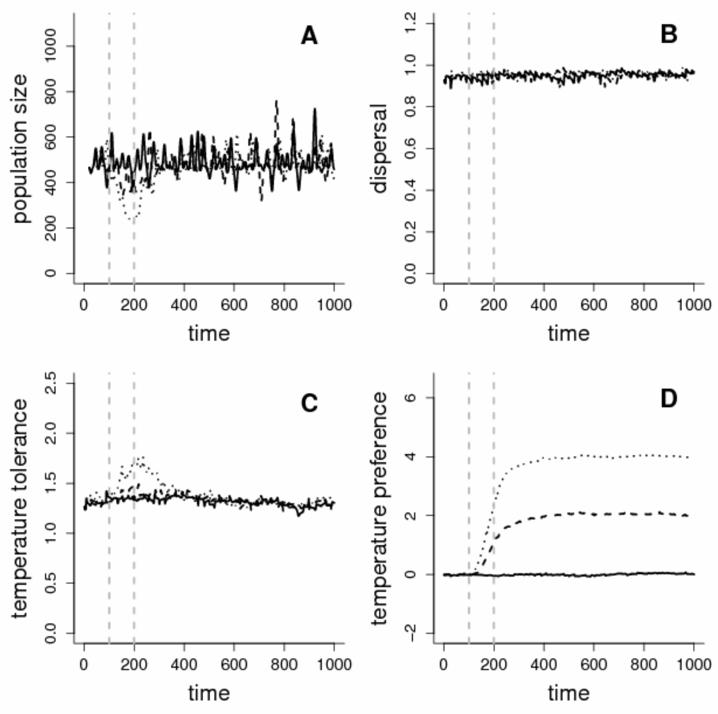

Figure 4.A4: Parasitism scenario (*I*=0) with homogeneous landscape (s_s=0) and low cost for generalization (*c*=4).

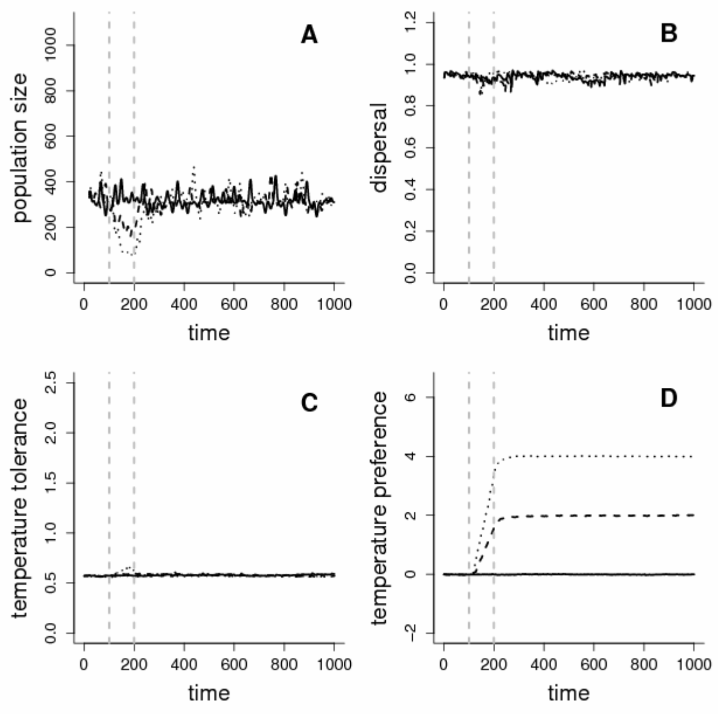

Figure 4.A5: Parasitism scenario (*I*=0) with homogeneous landscape (s_s=0) and high cost for generalization (*c*=1).

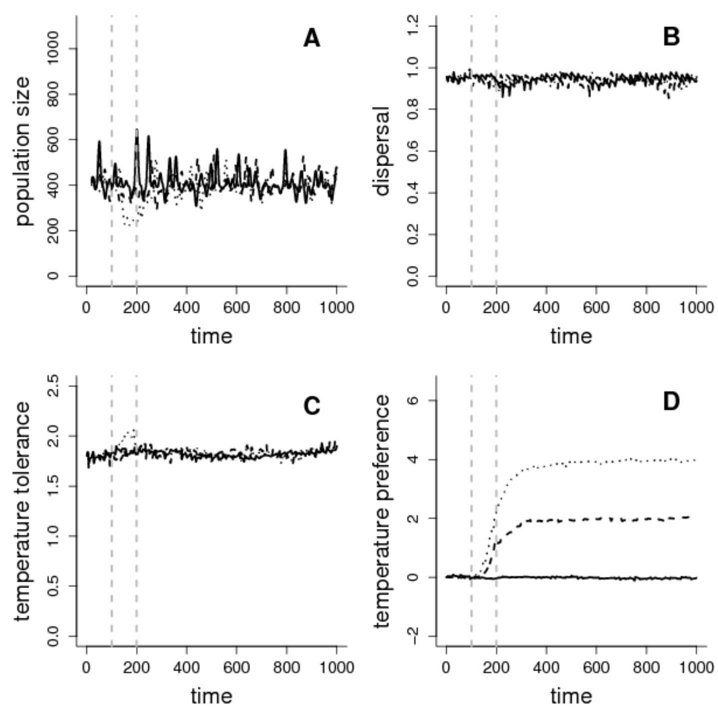

Figure 4.A6: Parasitism scenario (I=0) with heterogeneous landscape (s_s=0.8) and low cost for generalization (c=4).

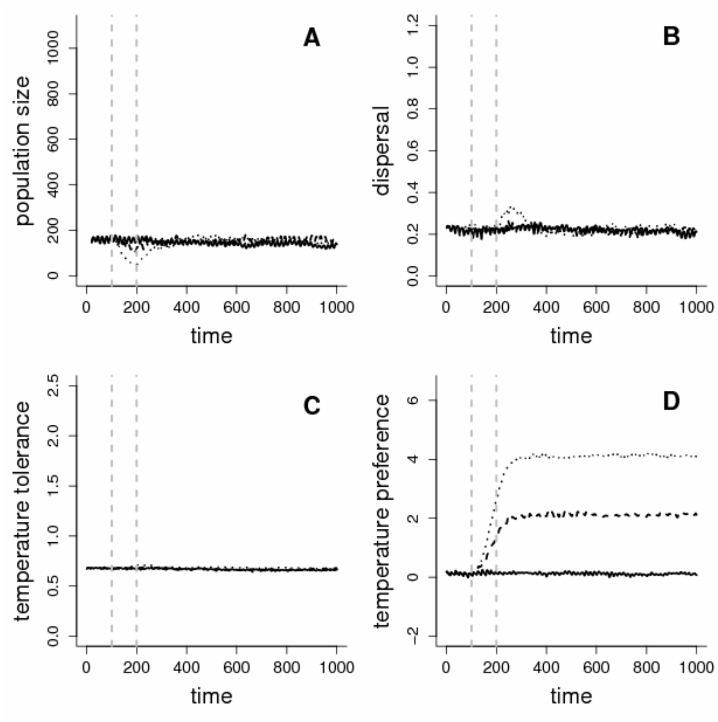

Figure 4.A7: Parasitism scenario (I=0) with heterogeneous landscape (s_s=0.8) and high cost for generalization (c=1).

Chapter 5

Consensus and dispersal evolution – a potential feedback effect[1]

With Thomas Hovestadt

5.1. Introduction

In some systems, certain ‘marker traits’ play an important role for the adoption of new members into (social) groups respectively the reproductive success of (immigrating) group members. Possible examples include bird song where singing the ‘right’ dialect may promote male reproductive success (Tomback and Baker 1984; Slabbekoorn and Smith 2002), while strangers singing ‘unfamiliar’ dialects suffer from reduced mating success. Other examples include chemical profiles in social insects (Zinck et al. 2009; Meunier et al. 2011; Sturgis and Gordon 2012) that affect interaction between group and non-group members and the adoption of new queens into colonies. Interestingly, there may be nothing specific about a certain dialect or a certain chemical profile – the fitness relevance primarily emerges because local groups reach a ‘consensus’ on how a proper group member should sing, smell, or look like and thus impose costs on rare phenotypes (positive frequency dependent fitness).

Different groups may show different levels of tolerance towards deviant individuals. In ants, for example, member of some social groups attack strangers with violence (Hölldobler and Wilson 1990). However, in other ant species, colonies accept unrelated (immigrating) individuals with different phenotypes into their groups (review in Heinze and Keller 2000). For example, unrelated, non-nestmate queens can be adopted into a colonies of *Formica truncorum* (Sundström 1997), *Acromyrmex subterraneus molestans* (Souza et al. 2005), and *Formica exsecta* (Holzer et al. 2008). Young queens can take over established colonies in *Leptothorax nylanderi* (Foitzik and

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[1] This chapter has been submitted as: Chaianunporn, T. and Hovestadt, T. Consensus and dispersal evolution – a potential feedback effect. *Behav. Ecol.*

Heinze 1998), and *Platythyrea punctata* (Kellner et al. 2010). Two or more colonies may fuse into one in *Leptothorax nylanderi* (Foitzik and Heinze 1998), *Linepithema humile* (Vásquez and Silverman 2008; Vásquez et al. 2009), *Platythyrea punctata* (Kellner et al. 2010) and *Dorylus molestus* (Kronauer et al. 2010).

This is a puzzle because according to the inclusive fitness theory (Hamilton 1964), adoption of unrelated individuals into a cooperative group should decrease relatedness within the group and thus undermine cooperation. The ability to distinguish group members from non-group members is thus vital to the social life (Hölldobler and Wilson 1990). Moreover, the acceptance of non-related individuals that bears different traits could itself modify the signal that individuals in the group use for group recognition. For example according to the odour diversity hypothesis (Hölldobler and Wilson 1977; Vander Meer and Morel 1998), the presence of new queens (or workers in case of colony fusion) in an ant colony can lead to modification of chemical cues that characterize the colony odour profile because multiple queens should produce a broader spectrum of chemical substance. This might have a consequence for the workers' ability of to discriminate foreign individuals from group members. A change in the nest-mate recognition signal by adoption of new individuals into colonies has indeed been observed in some ant species, e.g. during the colony fusion of the African army ant *Dorylus molestus* (Kronauer et al. 2010) or after adoption of new queens in *Ectatomma tuberculatum* (Zinck et al. 2009).

As an alternative to direct kin-selection, the recognition traits involved might be interpreted as phenotypes that are controlled by 'green beard' genes (Hamilton 1964; Dawkins 1976). Holders of the trait could thus recognize other bearers of the same trait and target cooperative behaviour toward them. It has however been argued that – because of the complicated threefold assumption underlying the idea (bearing the trait, recognizing it, cooperating with it) – such genes were unlikely to emerge (Hamilton 1964; Dawkins 1976; Maynard Smith 1976; Grafen 1998). Further, for the classic green beard genes, the genetic model predicts that green beard genes would soon go to fixation (Wade and Beeman 1994; Gardner and West 2010), unless it has deleterious effects on the fecundity of the trait holder (e.g. in the red fire ant, *Solenopsis invicta*; Keller and Ross 1998). It is thus questionable, why traits, such as chemical profiles or certain song dialects, do not go fixation, and how variants of such trait may (regionally) coexist. Further, traits involved in recognizing group members may not even have a genetic basis like in the case of song dialects that are presumably culturally transmitted from fathers to sons (Slabbekoorn and Smith 2002). Finally, the situations described in the previous paragraphs are not necessarily about targeting cooperative (altruistic) behaviour but rather about ‘sanctions’ imposed on non-bearers, e.g. by not accepting ‘foreigners’ as mating partners.

In this work, we draw attention to a simple mechanism that may possibly contribute to the maintenance of group recognition system (group consensus) with such a marker trait due to a positive feedback effect. We use the term ‘group’ loosely here – we neither imply any social structure or cooperative behaviour of group members nor assume that the decision to ‘adopt’ new members is truly a group decision. It may just as well be exhibited individually, e.g. when choosing their mating partner. We propose a simple model for the maintenance (for emergence see *Discussion*) of the diversity in recognition traits. Although this model describes similar phenomena explained by the ‘green beard model’ (Hamilton 1964; Dawkins 1976), it holds some different assumptions: (i) A cooperative or altruistic behaviour directed towards other bearers of marker traits is not required, (ii) the only advantage is group access (respectively positive interaction), and (iii) the trait is not necessarily genetically determined. Thus, the relatedness is not explicitly considered in the model.

We focus on two factors, which should play an important role in this phenomenon, i.e. the group tolerance toward deviant individuals and the dispersal of individuals between groups. The latter has a critical effect on the ‘mixing’ of individuals with different traits (and of different kin) and dispersal is consequently one of the most important aspects that determine the mode of colony founding and reproduction in social insects (Hölldobler and Wilson 1990; Keller 1993; Pedersen and Boomsma 1999; Seppä et al. 2004; Sundström et al. 2005; Berghoff et al. 2008; Helmkampf et al. 2008). Similarly, dispersal is one of factors that determine the divergence of the dialects between bird populations (Wright and Dorin 2001; Colbeck et al. 2010).

5.2. Model and simulation

Basic population model: We use a simple analytical model to investigate the feedback effect of dispersal and group tolerance on the mixing of phenotypes within groups and the coexistence of phenotypes at the metapopulation level. In individual-based simulations, we further clarify how evolution of dispersal proceeds under such adoption systems and how spatial structure possibly feeds back the stable coexistence of different marker traits.

We assume a perennial and haploid species that form stable groups, but do not cooperate. After reproduction, a fraction of adult individuals dies and is replaced by adoption of newborn individuals selected according to the mechanism explained below. Every newborn individual must be adopted by a group in order to survive and reproduce. A newborn may either try to join its natal group of adults, or migrate to a non-natal group (as such free of costs) and attempt adoption there. Once an individual is adopted into a group, it stays in this group for the rest of its life. All adult group members have the same reproductive output.

Trait recognition and adoption: We assume that each individual possesses a 'marker' trait (g_i) that plays a role in the acceptance of newborn individuals by a group. This trait may represent certain chemicals (scent) or a specific song dialect of the organism, but it is not necessarily inherited genetically, but may also be learned from parents or other group members. Here we only allow two discrete phenotypes namely g_x and g_y. Each group has a 'group profile' ($\bar{g}$) that is formed by mixing the markers of group members, and it is equal an arithmetic mean of marker value that is calculated from the marker traits of all adult group member. Each group (or its members) has a fixed tolerance trait k.

This group tolerance and the difference between the group profile and the individual's specific trait determine the adoption probability of newborn individuals (either immigrating or born within group) in an un-normalized Gaussian function as following:

$$a = e^{-\frac{(g_i - \bar{g})^2}{k^2}} \tag{5.1}$$

where g_i is the trait of the individual. Whenever an individual carries exactly the same trait as the group profile ($g_i - \bar{g} = 0$), it has the greatest adoption probability (see below). The decline in the adoption is determined by the group tolerance (k). If a group has a high tolerance (high *k*), it may frequently adopt individuals with phenotypes that deviate even substantially from the group profile.

A newborn individual has only one attempt in the adoption process; if not accepted it will be killed. Both native and non-native offspring are selected according to the same adoption rule. Note that if a group adopts many individuals with a different phenotype, the group profile $\bar{g}$ may itself change over time.

For simplicity, we first evaluate the dynamics in a simple system with two groups (group *i* and group *j*). The proportion of phenotype g_x in group *i* develops from time step *t* ($x_{i,t}$) to *t*+1 ($x_{i,t+1}$) as follows:

$$x_{i,t+1} = \frac{x'_i}{x'_i + y'_i} \quad \text{with} \tag{5.2}$$

$$x'_i = m a_{xi} x_{j,t} + (1-m) a_{xi} x_{i,t} + x_{i,t}(1-\mu) \text{, and} \tag{5.3}$$

$$y'_i = m a_{yi} y_{j,t} + (1-m) a_{yi} y_{i,t} + y_{i,t}(1-\mu) \text{,} \tag{5.4}$$

where *m* is the proportion of newborn individuals that migrate to the non-native group (dispersal probability – same for g_x and g_y and both groups), and the term 1-*m* is the corresponding proportion of individuals that stay in their natal group. The terms $x_{i,t}(1-\mu)$ and $y_{i,t}(1-\mu)$ reflect the adult survivors of phenotype g_x and g_y in group *i* where μ is an annual mortality of adult individuals; adult survival is not affected by an individual's trait. The terms a_{xi} and a_{yi} determine the adoption probabilities for individual with phenotype g_x respectively g_y and are calculated according to *eq.* 5.1 as:

$$a_{xi} = e^{\frac{-(1-x_{i,t})^2}{k^2}} \quad \text{and} \tag{5.5}$$

$$a_{yi} = e^{\frac{-x_{i,t}^{\,2}}{k^2}} \text{.} \tag{5.6}$$

Without loss of generality, we assume that g_x=1 and g_y=0. The group mean trait $\overline{g}$ in group *i* at time *t* is thus equal to $x_{i,t}$. Note that the proportion of individuals with trait g_y (y_i) is always $1-x_i$.

According to *eq.* 5.2, the change in the proportion of phenotype *x* in group *i* is given by:

$$\frac{\Delta x_i}{\Delta t} = \frac{x'_i}{x'_i + y'_i} - x_i \,, \tag{5.7}$$

and correspondingly for *x* in group *j*. At equilibrium ($\frac{\Delta x.}{\Delta t} = 0$), the zero change isoclines for phenotype g_x in group *i* respectively *j* are given by the following equations (see *Appendix I* for full derivation):

$$x_i = \frac{(1-m)(a_{xj} - a_{yj})(1-x_j)x_j - m a_{yj} x_j}{-m a_{yj} x_j - m a_{xj}(1-x_j)} \text{, and} \tag{5.8}$$

$$x_j = \frac{(1-m)(a_{xi} - a_{yi})(1-x_i)x_i - m a_{yi} x_i}{-m a_{yi} x_i - m a_{xi}(1-x_i)} \,. \tag{5.9}$$

Equilibrium points emerge where the two isoclines intersect. From *eq.* 5.5, 5.6, 5.8 and 5.9, we can identify three factors that play a role in the determination of equilibrium points, namely the proportion of phenotype g_x in each group (this defines $\overline{g}$ of the groups), group tolerance *k* (*k* and $\overline{g}$ both determine *a* values) and dispersal between groups (*m*). Note that annual mortality *μ* as well as birth rate do not affect location of isoclines even though mortality plays a role for the rate of change out of equilibrium. For presentation, we further generate ‘vector fields’ with arrows indicating the direction and magnitude of change (phenotypic trajectories) for different combinations of x_i and x_j (calculations based on iterations of *eq.* 2). We analyse the behaviour of the system for different values of group tolerances ($k \in [0.2,\ 1.6]$) and dispersal probability ($m \in [0.01,\ 0.25]$).

We carry out individual-based simulations to gather further insight about additional factors likely to also influence the system (for detailed description of simulations see *Appendix II*). Importantly, the simulations allow us to implement dispersal probability as an evolvable trait. Compared to the analytical model provided above these simulations account for kin-selection by default (Poethke et al. 2007). Using the simulations, we (i) validate the conclusion drawn from the analytical model, (ii) control how establishment of type coexistence interacts with the evolution of dispersal, and (iii) compare simulation results for two groups with those with ten groups.

In scenarios with dispersal evolution, we carry out simulations with the different initial proportion of phenotype g_x (x) in each group. The proportion x in each group and the evolving dispersal probability after 1000 generations is presented in the results. In the scenario with 10 groups, we either assume a linear ‘stepping stone arrangement’ of groups with dispersal between adjacent groups only (nearest-neighbour dispersal); the last group is, however, a neighbour of the first group. Alternatively, we assume ‘global dispersal’ where dispersing individuals immigrate into a randomly selected group. The latter simulations are all initialized with x=0.5 in all groups. We carry out 1000 simulations for each scenario, and the distribution of the regional mean phenotype at time step 1000 is reported.

5.3. Results

Analytical model: The two-group model suggests that regional coexistence of individuals with two different phenotypes of the marker trait is possible for a range of values for group tolerance (k) and dispersal probability (m). In Figure 5.1, we vary the group tolerance whereas dispersal probability is fixed at 0.1. Depending on parameter values up to 9 equilibrium points (intersections of isoclines) may emerge. Which of the stable equilibrium points would ultimately be reached depends on the starting conditions ($x_{i,0}$, $x_{j,0}$) as visualized by arrows in the vector fields added in Figure 5.1. In all cases, two trivial stable equilibriums emerge at x_i=x_j=0, respectively at x_i=x_j=1, i.e. with regionally monomorphic populations of either phenotype g_x or g_y. At low tolerance values, two additional stable equilibrium points emerge with (nearly; see below) complete dominance of each phenotype in one of the local populations (x_i~1, x_j~0) or (x_i~0, x_j~1; Figure 5.1A). These equilibrium points thus reflect regional coexistence of the two phenotypes of the marker trait. In order to reach coexistence, the initial proportion of *x* must be high in one group and low in the other. As group tolerance *k* becomes larger, the stable equilibrium points move increasingly inwards from (1, 0) and (0, 1) which allow a local coexistence between two phenotypes (Figure 5.1B – 5.1D) until they finally vanish (Figure 5.1E – 5.1F).

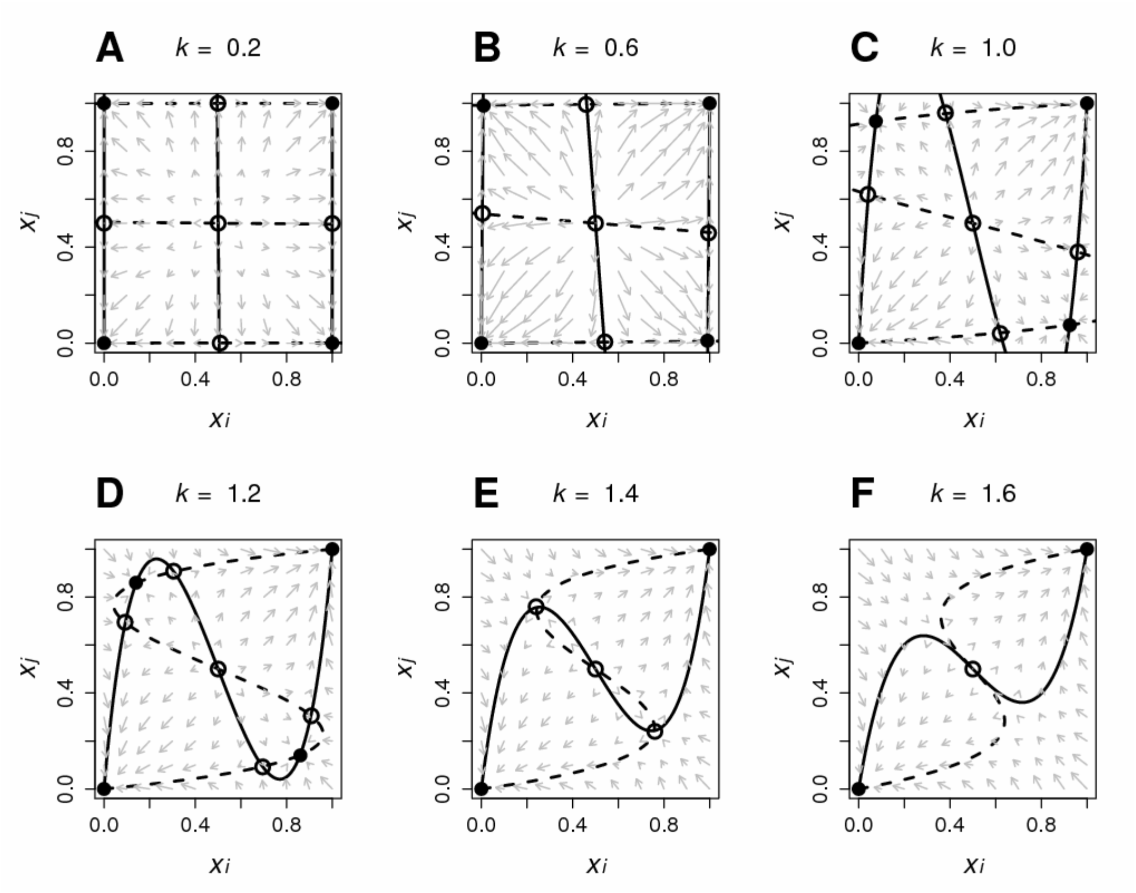

Figure 5.1: Isoclines, equilibrium points and phenotypic trajectories of the two group model at different levels of group tolerance (*k*) and a fixed dispersal probability (*m*=0.1). The solid lines represent the zero isoclines of group *i* and the dashed lines represent that of group *j* plotted over the proportion of phenotype g_x in group *i* and *j* (x_i and x_j respectively). Closed black points indicate stable and open points represent unstable equilibrium points. The direction and magnitude of change from different starting proportion for x_i and x_j towards equilibrium are presented by the arrows. Note that equilibrium points are stable if the phenotypic trajectories in its surrounding are pointing towards them, and unstable if the trajectories are directed away: (A) *k*=0.2; (B) *k*=0.6; (C) *k*=1.0; (D) *k*=1.2; (E) *k*=1.4; (F) *k*=1.6.

The effect of dispersal probability *m* on coexistence is fundamentally similar to that of *k* (Figure 5.2) – with low dispersal, we see the emergence of four stable equilibrium points (regional or local coexistence; Figure 5.2A – 5.2C), of which the two coexistence points vanish as dispersal probability become larger (Figure 5.2D – 5.2F).

This congruence of effects of group tolerance and dispersal is not surprising as both parameters affect the ‘mixing’ of individuals between populations. If dispersal probability is high, many individuals arrive at the non-natal patch (to participate in the ‘adoption lottery’), if group tolerance is high immigrants have good chances of being adopted even if they carry the rarer of the phenotypes in that group.

Note that with regional coexistence also a local coexistence of both phenotypes (at very different abundances though) is assured due to the continuous immigration of the disadvantaged type from the other patch where the locally rare phenotype experiences a corresponding fitness benefit. Locally the rare type may become more common the larger group tolerance and/or the larger dispersal between groups.

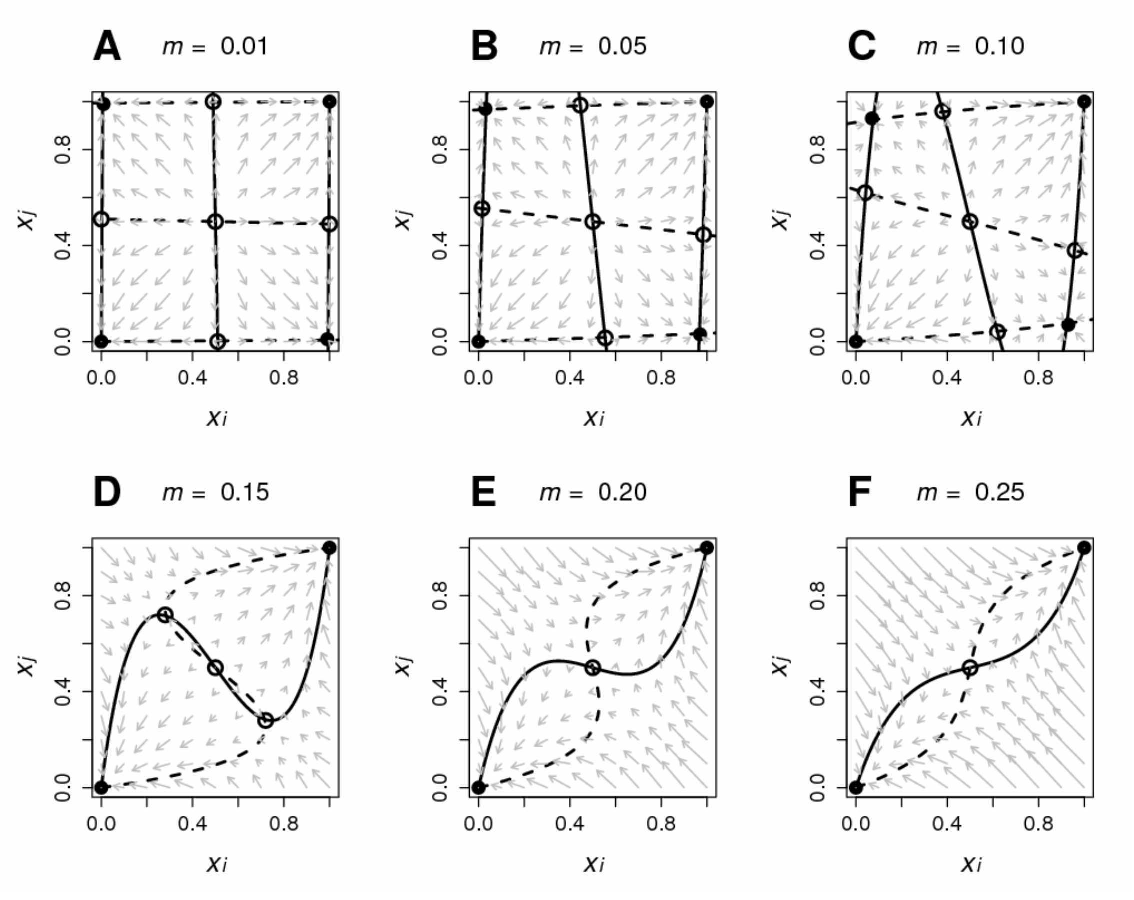

Figure 5.2: Isoclines, equilibrium points and phenotypic trajectories of the two group model at fixed group tolerance (*k*=1) and different dispersal probability (*m*). See Figure 5.1 for further descriptions: (A) *m*=0.01; (B) *m*=0.05; (C) *m*=0.10; (D) *m*=0.15; (E) *m*=0.20; (F) *m*=0.25.

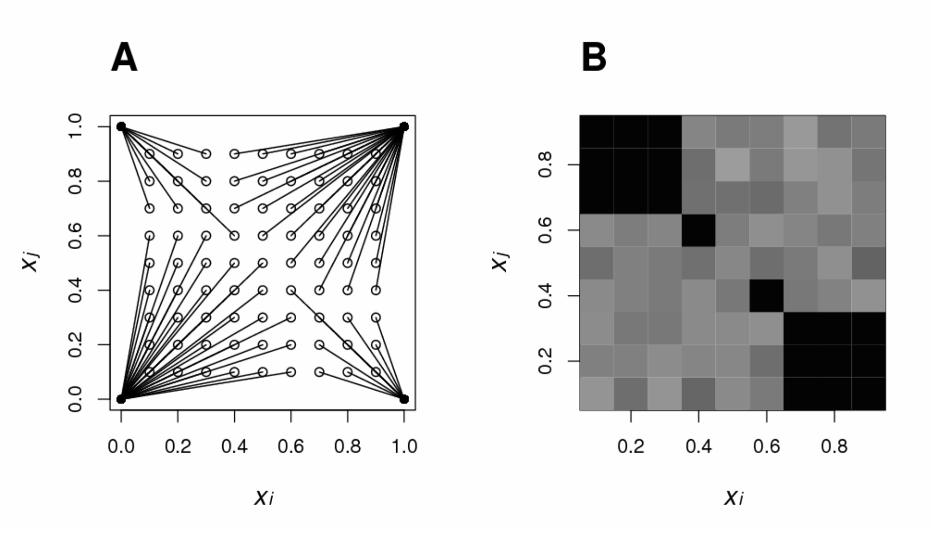

Figure 5.3: The direction of change of the proportion of phenotype g_x and evolving dispersal probability from the simulations with dispersal evolution. (A) The direction of change of the proportion of phenotype g_x in group i and j (x_i and x_j respectively). The open points represent the proportion of x_i and x_j at the beginning of the simulations and the black points indicate these proportions at the end of the simulations (1000 time steps). The lines show the direction of change. (B) The evolving dispersal probability at the end of the simulations plotted over the initial proportion of g_x in each group (x_i and x_j for group i and j, respectively). The grey colours code the dispersal probability: the darker the colour, the lower the dispersal probability (k=0.6).

Simulations: Our simulations fundamentally confirm the results of the analytical model (Figure 5.3A corresponding to Figure 5.2A – for details see below). However, with evolution of dispersal allowed, the simulations indicate that local coexistence becomes less likely (more specifically, the rarer phenotype becomes locally even rarer), but regional coexistence becomes more stable, because lower dispersal probabilities are selected for as soon as spatial heterogeneity in group structure emerges. In consequence (if not reaching the regionally monomorphic state), the system evolves from a state e.g. resembling Figure 5.2C to one similar to Figure 5.2A. In Figure 5.3B we show the evolving dispersal probabilities depending on starting conditions: whenever the system approaches coexistence low dispersal evolves while whenever it settles into regional fixation of a single marker high dispersal probabilities establish.

The coexistence of phenotypes of the marker trait is promoted by enlarging the dimension of the system from two to ten patches (Figure 5.4) provided that dispersal is nearest-neighbour. For example, with k=1.6 and m=0.1, regional fixation is the only possible outcome in two-group system (Figure 5.1F and 5.4A). However, in the ten-group system with nearest neighbour dispersal, regional fixation occurs only in c. 12%

of simulations (Figure 5.4B). In this system, discrete clusters of different phenotypes may quickly form even from rather homogeneous starting conditions (*x*=0.5 for all groups). With global dispersal, however, results are very similar to the corresponding results for the two-group system and are thus not shown.

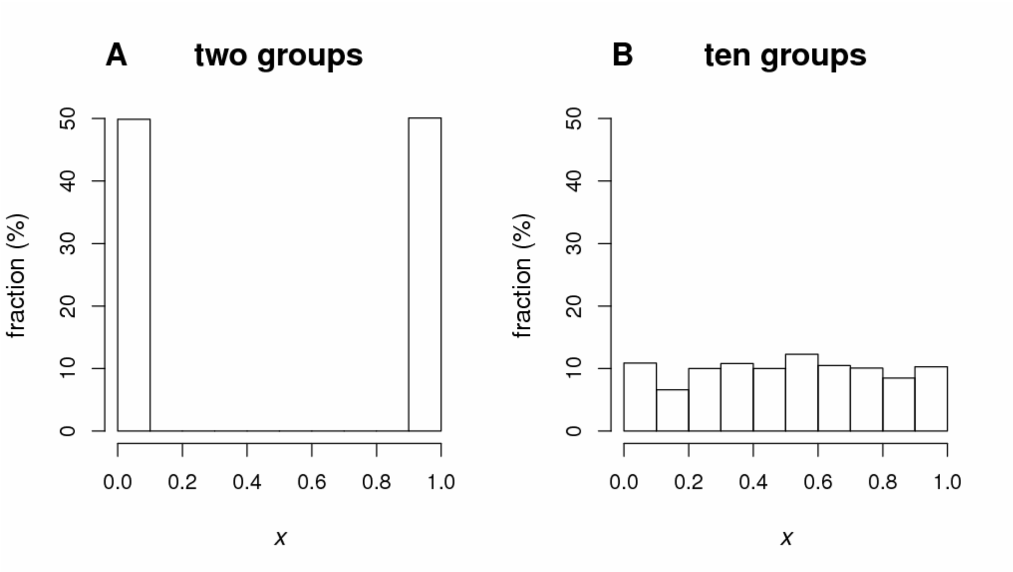

Figure 5.4: Comparison of the regional proportion of g_x (x) between the scenarios with two groups and ten groups (only results for nearest neighbour dispersal is shown here – see *Results* for detail). The bar plot shows the distribution of the regional x proportion at time step 1000: (A) Scenarios with two groups; (B) Scenarios with ten groups – nearest neighbour dispersal (k=1.6, m=0.1). Local populations were initialized with x_i=0.5, i.e. at the unstable equilibrium point. Note that with these parameters the analytical model predicts regional dominance (cf. Figure 5.1F) of either type as happens in the two-group simulations (A).

5.4. Discussion

In this study, we investigate the role of dispersal and group tolerance for the maintenance of recognition systems with a marker trait (stable coexistence) – the model as presented does not provide an explanation on why such recognition systems, group consensus and different tolerance levels emerge in the first place (but see remarks below). It is also important to recognize that the marker trait under investigation has as such no effect on fitness but affects the frequency-dependent likelihood of acceptance in a group characterized by a group consensus. The original green beards and its variant foresee interaction between individuals that are modified by presence or absence of the green beard; such behaviour can be altruistic or harmful (reviewed in Gardner and West 2010). In our model, altruism is not an issue and harming occurs (only) inasmuch that strangers are denied access to the group or are, for example, not accepted as mating partner. Other than the classic green beard model (Hamilton 1964; Dawkins 1976; Wade and Beeman 1994; Gardner and West 2010), our model thus does not necessarily lead to regional fixation. We also want to point out that – even though we talk about groups – the mechanisms presented here do not require a concerted decision by members of a tightly interacting (social) group. It would just as well work out if members ‘socialized’ in a certain group or local population individually discriminate against bearers of ‘strange’ markers as is the case in female birds that refuse to mate with males singing foreign dialects (Tomback and Baker 1984; Slabbekoorn and Smith 2002). Moreover, it is assumed that the trait is not necessarily genetically determined, but it can be a learned trait. However, in the course of the time, the process can promote kin structure and increases within group relatedness.

Our analytical model shows that stable coexistence of different recognition traits becomes possible under low dispersal and low group tolerance (Figure 5.1 and 5.2). In contrast, high dispersal probability and/or high group tolerance lead to regional fixation of one phenotype. This can be explained as follows: At very low group tolerance ($k \leq 0.2$), even small deviation of phenotype proportion results in a large disadvantage (lower adoption probability) for the rarer phenotype, and this leads to a local fixation of one phenotype due to strong positive frequency-dependence. With large group tolerance, on the other hand, the difference in adoption probability between abundant and rare phenotypes is small. It is thus more likely that a phenotype abundant in one group infiltrates another group where this phenotype is initially the less frequent type, ultimately leading to regional fixation of the regionally more abundant phenotype.

This spectrum of possible outcomes in our results may be reflected in e.g. the variety of aggressive responses observed in ants. Under very low group tolerance, group members attack all strangers as observed in many ant species (Hölldobler and Wilson 1990) leading to group-wise (or local) fixation of one recognition phenotype. When group members are more tolerate, coexistence of different phenotypes in one group is possible as is the case in species where colonies adopt immigrants with different phenotypes (Sundström 1997; Heinze and Keller 2000; Souza et al. 2005; Holzer et al. 2008). An even larger tolerance, can lead, in contrast, to the loss of diversity in marker traits, with group members showing no aggression against individuals originating even from locations far apart like in the supercolonies of the Argentine ant *Linepithema* *humile* (Giraud et al. 2002; van Wilgenburg et al. 2010). Our results show that this phenomenon can be considered together in one continuous spectrum of group tolerance.

Dispersal clearly modulates the effect of group tolerance, as it is the other fundamental mechanism affecting the exchange of individuals between groups. At low dispersal, groups recruit almost only own offspring that are likely to carry the majority phenotype, which in turn carries a fitness benefit. Consequently, the proportion of the locally abundant phenotype continuously increases through positive feedback. Note, however, that higher dispersal promotes coexistence within groups because it leads to the influx of the corresponding rarer phenotype into each group. However, when individuals massively migrate between patches, the fitness expectation of phenotypes mostly depends on regional abundance rendering the system instable and leading to regional fixation.

Our simulations indicate however, that regional coexistence becomes a much more likely outcome if the system is simply enlarged (more groups), allowing for the establishment of more complex spatial structure. In this case, regional convergence on one type may become very unlikely: Clusters of like recognition traits may form due to limited dispersal. These clusters would become highly resistant to invasion even if the type is regionally quite rare (cf. Berec 2002; Chave et al. 2002; Chaianunporn and Hovestadt 2012*a*). We confirm that the coexistence arises due to spatial structure and not simply due to the number of groups: In contrast to the simulations with nearest neighbour dispersal, the simulations with global dispersal result in regional fixation like the two-group system.

In addition, our simulation experiments indicate that the establishment of regional coexistence, on the one hand, and the maintenance of high dispersal, on the other, would be an unlikely combination. When the dispersal evolution is allowed, individuals with a low tendency to disperse are selected for due to the strong spatial variance in fitness expectation emerging as soon as different trait groups establish. Spatial heterogeneity is long known to select against dispersal (Hastings 1983; Poethke et al. 2011). This selective route will ultimately also terminate local coexistence of different types, simply because few immigrants of different type will even attempt to be adopted.

This may be the moment to point out that our assumptions concerning dispersal were indeed quite conservative in our simulations, rather favouring regional fixation. In real world situations, dispersal is typically associated with a variety of costs (Bonte et al. 2011) so that much less dispersal typical occurs than what we assume at initializing our simulation runs (see e.g. Poethke et al 2003). Landscapes that impose other costs of dispersal between groups, e.g. due to fragmentation, would thus promote the coexistence of different marker phenotypes as dispersal would typically assume small values. In contrast, in our simulations, dispersal is completely free of costs if a recognition trait comes to regional fixation, and due to the action of kin-competition very high dispersal probabilities evolve (Hamilton and May 1977; Comins et al. 1980; Poethke et al. 2007).

In summary, our results indicate that the stable coexistence of multiple marker types would be quite likely once established and even be stabilized by the evolutionary feedback on dispersal between groups. Further, once established the system should be quite immune against invasion by non-discriminatory (tolerant) types as any ‘intolerant’ groups could maintain reproductive rights (or other fitness benefits) for group members, while they could themselves easily take over non-discriminatory groups. This latter point is important, as it would allow for the maintenance of discriminatory behaviour even if the latter were associated with some cost; however, this issue requires further investigation.

What we leave open, however, is the question how such a system would get started, i.e. how recognition traits and discriminatory behaviour do emerge in the first place. A benefit for selecting group members or simply interaction partners (e.g. as mates) based on (trustworthy) markers may indeed (originally) emerge for other reasons. Certain traits may serve other purposes too e.g. protecting against intrusion of parasites (e.g. Brandt et al. 2005; Martin et al. 2011) or be helpful in cooperative behaviour. Marker traits may also signal acquaintance with (or adaptation to) local conditions. Selecting mating partners based on such traits may thus assure avoidance of migration load (Garcia-Ramos and Kirkpatrick 1997; Bolnick and Nosil 2007). Our results suggest, however, that ‘discriminatory behaviour’ may continue to exists even if such (original) benefits cease to exist and that the regional coexistence of marker traits may be stabilized by an evolutionary feedback effect reducing dispersal between trait groups.

5.5. Appendix I: The calculation of zero isoclines in the system

From the *eq.* 5.7, the zero isocline of the group *i* lies where $\frac{\Delta x_i}{\Delta t} = 0$, or

(5.A1) $$0 = \frac{x_i'}{x_i' + y_i'} - x_i \, .$$

By simple rearrangement and noting that y_i=1-x_i, we can rewrite the equation as following:

(5.A2) $$x_i \cdot y_i' = y_i \cdot x_i' \, .$$

We replace x_i' and y_i' by *eq.* 5.6 and 5.7,

(5.A3) $$\begin{aligned} & x_i (m a_{yi} y_j + (1-m) a_{yi} y_i + y_i - \mu y_i) \\ & = y_i (m a_{xi} x_j + (1-m) a_{xi} x_i + x_i - \mu x_i) \, , \end{aligned}$$

where a_{xi} and a_{yi} are defined as in the *eq.* 5.5 and 5.6. We rearrange terms as follows:

(5.A4) $$\begin{aligned} & m a_{yi} x_i y_j - m a_{xi} x_j y_i = \\ & y_i ((1-m) a_{xi} x_i + x_i - \mu x_i) - x_i ((1-m) a_{yi} y_i + y_i - \mu y_i) \end{aligned}$$

or

(5.A5) $$m a_{yi} x_i y_j - m a_{xi} x_j y_i = (1-m)(a_{xi} - a_{yi}) x_i y_i \, .$$

Since y=1 - x, then the isocline in group *i* is given by

(5.A6) $$x_j = \frac{(1-m)(a_{xi} - a_{yi}) x_i (1 - x_i) - m a_{yi} x_i}{- m a_{yi} x_i - m a_{xi} (1 - x_i)} \, .$$

In the same way, the zero isocline of the group *j* is given by:

(5.A7) $$x_i = \frac{(1-m)(a_{xj} - a_{yj})x_j(1-x_j) - ma_{yj}x_j}{-ma_{yj}x_j - ma_{xj}(1-x_j)} \; .$$

5.6. Appendix II: Individual-based simulations

In the individual-based simulations, we assume that an individual carries two traits, namely a marker trait with two phenotypes (g_i) and a dispersal trait (m; see below). The tolerance trait (k), however, is a fixed character of the species, and it is similar for all individuals, respectively groups. For simplicity, we further assume that the species is a haploid and perennial organism, reproducing asexually. The life cycle of an individual is visualized in Figure 5.A1. The description of the simulation cycle is as following:

(I.) *Initialization*: At first, we initialize every simulation with K individuals in each group where K is the equilibrium group size. In order to avoid effects of demographic stochasticity, we assume large groups (K=5000). At the beginning, each group contains $Kx_{i,0}$ individuals with marker trait g_x and $K(1-x_{i,0})$ with trait g_y where $x_{i,0}$ is the initial proportion of trait g_x for group i. The dispersal trait coding for dispersal probability is drawn from a uniform distribution between 0 and 1.

(II.) *Estimation of 'group profile'*: At the beginning of each time step, a group profile ($\bar{g}$) is calculated based on the markers of all adults in that group. The group profile simply corresponds to the fraction of individuals carrying marker g_x because we assume g_x=1 and g_y=0.

(III.) *Reproduction*: All adult individuals produce a Poisson distributed number of surviving offspring with mean fecundity $\lambda_{i,t}$ for group i at time t. $\lambda_{i,t}$ is density-dependent and similar for all individuals in a group and calculated according to the Ricker equation (Ricker 1954):

$$\lambda_{i,t} = \mu e^{\left(\frac{h(1-N_{i,t})}{K}\right)} \qquad (5.A8)$$

where μ is the annual mortality of adult individuals, μe^h is the maximum growth rate (λ_0), and $N_{i,t}$ is the number of adult individuals in group i at time t. With the inclusion of the annual adult mortality in *eq.* 5.A8, we make sure that on average the number of newly produced offspring corresponds to the number of dying adults in each year. We assume μ=0.3 and $e^h\approx7.39$ for all simulations. Any offspring inherits the marker and the dispersal trait from its parent. However, in simulations that dispersal evolution is allowed, occasionally, the dispersal trait of a newborn may mutate with probability 0.001 to a random value drawn from a uniform distribution with range 0 to 1.

(IV.) *Adult mortality*: After reproduction, adult individuals die with probability μ. Note that by computing the group profile before death we assume that dead individuals still influence the group profile. This might be appropriate if death occurs shortly before the adoption phase, if markers of the individuals persist for some time (as odours generated by the working daughters of a now deceased ant queen), or of marker preference of offspring is 'imprinted' early in life.

(V.) *Dispersal*: Newborn individuals disperse or stay in their natal patch. For each individual, this decision is determined by the inherited dispersal trait (*m*) that assigns the individual's probability to migrate to another group. The dispersal process of newborns is as described in *Model and simulation*.

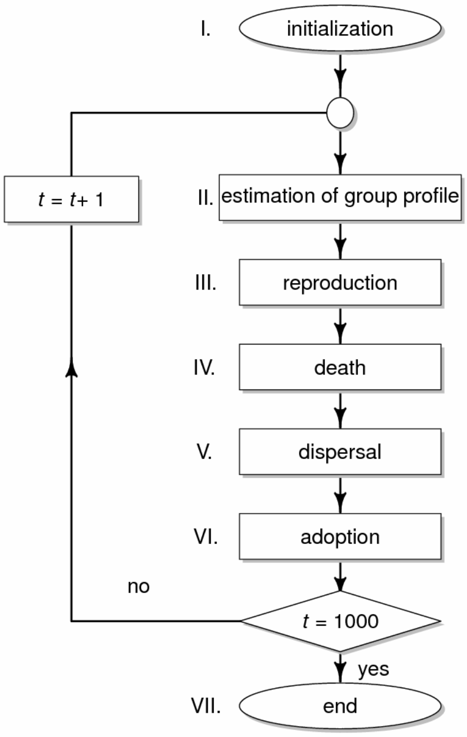

Figure 5.A1: The life cycle of the simulated organism.

(VI.) *Adoption*: A newborn individual, independent of whether it disperses or not, is adopted by a group with the adoption probability a estimated according to *eq.* 5.5 respectively 5.6. If the newborn is rejected by a group, it is killed. After the adoption process, the newly adopted individuals turn into adults, t is increased to $t+1$, and the simulation cycle is repeated. In our simulations we iterate the cycle over 1000 time steps.

Chapter 6

Dispersal and species interaction under changing environment: Conclusion and perspectives

6.1. Dispersal and species interaction under changing environment

Dispersal and species interaction are two cores elements of the metacommunuity approach (Leibold et al. 2004), but the relationship between them is not well studied. More specifically, many aspects of potential feedback effects of dispersal evolution on species interaction and *vice versa* are not well understood, especially in multispecious communities or under spatial and temporal habitat variability. In this thesis, I provide some first steps in closing this gap at the theory level. I have addressed various aspects relating to possible evolution in communities of interacting species considering trait coevolution across, but also concurrent evolution of traits within species. I consider co-evolution under different conditions, namely different community structure (one host–one guest and two host–two guest species – Chapter 2), different spatial landscape (spatial homogeneity and spatial heterogeneity with different spatial arrangement – Chapter 3), and temporal fluctuation and climate change (Chapter 4). Moreover, I explore the consequence of dispersal and group tolerance interacting together in determination of group formation and in turn, the effect of group formation on dispersal evolution (Chapter 5).

It is long known that avoidance of local (resource) competition, bet-hedging, reduction of kin competition and inbreeding avoidance are fundamental factors promoting the evolution of dispersal (Hamilton and May 1977; Comins et al. 1980; Gandon 1999; Gandon and Michalakis 1999; Ronce et al. 2000a; Bowler and Benton 2005; Poethke et al. 2007; Gros et al. 2008) – the truly relevant argument underlying all these mechanisms is that dispersal may be worthwhile (despite costs associated with it) because dispersing individuals may trade in poor local against more favourable fitness expectations elsewhere on the one hand, and may reduce variability in fitness at the level of the lineage on the other. Until now, however, it has received little attention how interspecific interaction may affect fitness expectations at the landscape level and how these effects would depend on, respectively interact with dispersal.

In chapter 2, I thus begin with investigating dispersal evolution (in hosts and guests) in communities with different types of interspecific interaction in homogeneous landscapes (for the schematic illustration of the systems see Figure 1.3) and find a number of interesting results. As expected, parasitic interaction promotes dispersal, and mutualistic interaction tends to reduce dispersal of host and guest species in comparison to a neutral system (commensalistic interaction). However, this observation might be different in communities with different structure (here I compare one host–one guest (1H1G) and two hosts–two guests systems (2H2G)). I schematically sum up these findings in table 6.1 – note that I show only the effect on the dispersal probability of the host species as the evolved dispersal probability of the guest species were generally lower, but highly correlated with that of host species. This is due to the effect that I assume that a host has an ability to colonize any empty patch, because they can reproduce in the absence of its guest, whereas a guest cannot colonize a patch as long as their host has not established there. This adds an implicit dispersal cost for guests compared to their hosts.

In table 6.1, I oversimplify as many factors affect and determine the optimal dispersal probability of the system. For example, in the 1H1G scenario, parasitism does not always lead to high dispersal probability; the effect of parasites on dispersal probability depends on the intensity of the parasitic interaction and intensity of resulting population dynamics. Parasitism does not lead to noticeable higher dispersal as long as parasitic interaction does not causes strong population fluctuation (here controlled by search efficiency of parasites). This is concordant with the observation in single species system that stochastic demography and spatio-temporal variability, chaotic population dynamics, or asynchronous population cycles among sites could all promote dispersal (Doebeli and Ruxton 1997; Parvinen 1999; Ronce 2007). In my investigation, I ‘controlled’ the transition from stable to oscillating population dynamics by modifying the searching efficiency of parasites. However, other factors in host–parasite interaction could similarly affect this dynamics, namely the effect of parasites on host’s fecundity, mean number of offspring produced by successful parasites, or the handling time of parasites.

Table 6.1: Effects of interspecific interaction on dispersal probability of the host species. The commensalism scenario serves as reference as hosts are not affected by this interaction type.

interaction type	1H1G system	2H2G system
commensalism	o	o
mutualism	o	–
parasitism	++	+

(o: dispersal probability is unaffected; ++: highly increased; +: increased; –: decreased)

Results become more complex if we consider more specious 2H2G communities. In the 2H2G parasitic scenario, increasing species number adds negative frequency-dependence to the system. The negative frequency-dependence results in fitness advantage of rare species and leads to strong population fluctuations in parameter space where the dynamics are stable in the 1H1G scenario. Dispersal probability is nonetheless reduced in comparison to the 1H1G system as the success of parasites and thus the damage done to the hosts is lower due to the risk of 'host-mismatch' emerging in the 2H2G system. Clearly, this effect would become even larger if more host species and their specialized partners were added to the system.

A completely reverse mechanism leads to a similar reduction in dispersal (at much lower level) in the 2H2G mutualistic system. If the system does not collapse into a 1H1G system, we see here the emergence of stable spatial patterns due to (local) positive frequency-dependent selection. As soon as the abundance of species pairs becomes unbalance (deviates from a 1:1 ratio), the more frequent species pair will have a greater advantage from the interaction, and drive out the rarer pair from the local community. This process might lead to regional coexistence of two species pairs, but local fixation of one species pair (dominance of different species pairs in different patches) and low dispersal probability is selected because of high settlement cost of rarer species pair as immigrants of rarer pair can not compete with dominant pair. In this aspect, this system is analogous with the system presented in chapter 5 and two systems show the similar result when evolution is allowed: low dispersal probability is selected and dominance of different types (species) in different local communities emerges.

In chapter 2, I have only considered the effect of species interactions itself on the emergence of landscape heterogeneity – spatial heterogeneity that selects against dispersal and spatio-temporal dynamics that promotes it. However, real landscapes usually show also heterogeneity, i.e. in habitat types and attributes. In chapter 3, I thus explore the ‘evolutionary behaviour’ of 1H1G systems in heterogeneous landscapes. This adds two new aspects to the studied system. First, an emerging asymmetry in the costs of dispersal for hosts and guests as only host’s fitness depends on habitat type; hosts suffer from a ‘settlement cost’ if the disperse from favourable to unfavourable habitat (see Bonte et al. 2011) that does *per se* not apply to guests. This, however, raises a second new and interesting issue, the concurrent evolution of dispersal and host’s habitat niche width. I also allow for the evolution of habitat preference (temperature preference in chapter 4) but postpone more detailed evaluation of this issue to chapter 4. Under commensalism, where dispersal is low and a specialist strategy is preferred, hosts adapt to local habitat conditions (habitat preference matches to local habitat attribute). In contrast, in case of parasitism, which promotes dispersal, local adaptation is rare and selection favours highly dispersive generalist (with a preference for average habitat) phenotypes. In other words, parasite attack reduces degree of local adaptation in the system. For this reason, in parasitic system, hosts do not adapt to extreme habitats that thus possibly work as sink populations. Habitat arrangement might also play an important role on the degree of local adaptation. This issue is thus worth further investigation, for example by comparison local adaptation in fractal or gradual landscapes versus that in landscapes with distinctly separated habitats.

Unsurprisingly, spatial heterogeneity also leads to the reduction of dispersal probabilities of hosts in comparison to homogeneous landscape as already observed in single species models (Comins et al. 1980; Hastings 1983; Travis 2001; Poethke et al. 2003, 2011). Further, dispersal probability of hosts in heterogeneous landscape is lower than that of guests due to asymmetry of dispersal cost, whereas in homogeneous landscape where the dispersal cost (mortality) of hosts and guests is equal, the dispersal probability of guests is generally lower than that of hosts. However, spatial heterogeneity has also an indirect effect on guest’s dispersal because of the emergent heterogeneity in patch occupancy by hosts. This ‘secondary’ heterogeneity also reduces dispersal probability in guests. The effect (for hosts and guests) also depends on the habitat–fertility trade-off that determines cost of niche widening and habitat arrangement (see more details below).

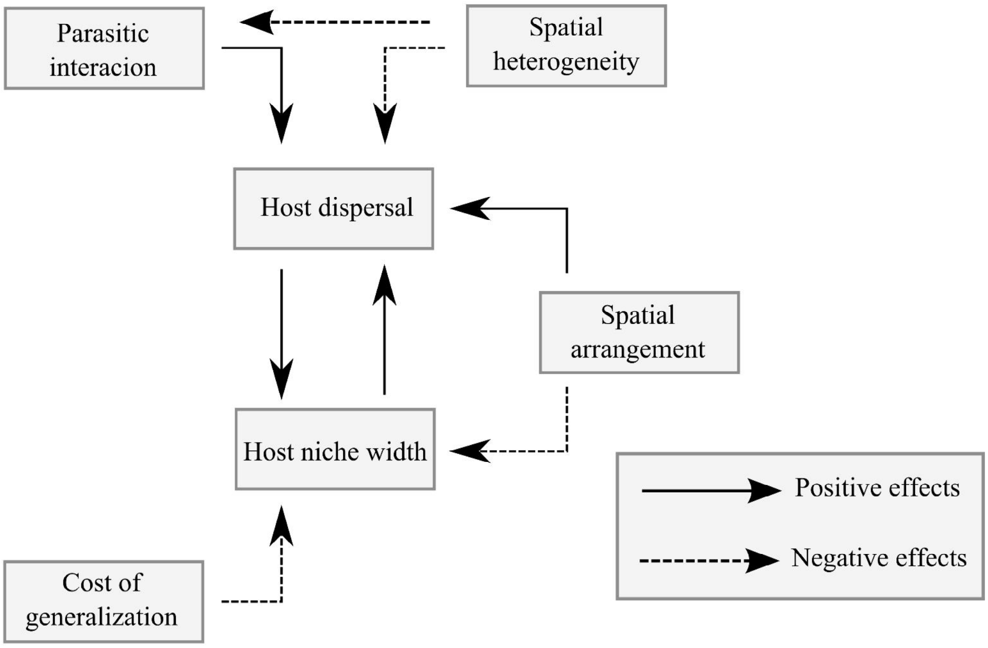

Figure 6.1: Schematic presentation of the interdependence of species interactions, landscape heterogeneity, and the evolution of dispersal and habitat niche width. Note that the effect of spatial arrangement demonstrated here refers to the change from random to autocorrelated landscapes.

The more interesting aspect emerging in my simulations in chapter 3 is the interdependence between the evolution of dispersal and habitat niche width. When dispersal probability of hosts is elevated (e.g. as a consequence of parasitic interaction), habitat niche width is also increased. The effect depends on the habitat–fertility trade-off that determines the costs for becoming a habitat generalist (wider niche width). At high cost of generalization, the expansion of niche width is limited. This also limits the evolution of dispersal probability, as the landscape is ‘perceived’ as more heterogeneous from the perspective of narrow-niched individual and also results in restricted dispersal in guests. This observation agrees with the prediction that habitat specialists should disperse less readily than habitat generalists (Brown and Pavlovic 1992; Day 2000; Parvinen and Egas 2004). The relationship between dispersal and habitat niche width becomes clearer when the evolution of these two traits in different habitat arrangements, i.e. random and clustered (autocorrelated) landscapes, are compared. In clustered landscapes, more dispersive, but also more specialized hosts (narrower niche width) evolve in comparison to random landscapes: In clustered landscapes, neighbouring patch tends to have similar attribute to the natal patch. In the other words, in the near surrounding the clustered landscapes are more homogeneous than in random landscapes. For this reason, an individual in clustered landscape can be more dispersive, as it is likely to immigrate into habitat similar to its natal patch – this in turn mitigates the (costly) need to also become a generalist when evolving high dispersal. I summarize the interdependent effects of species interactions, landscape heterogeneity, and the evolution of dispersal and habitat niche width studied in this chapter in Figure 6.1.

In the previous scenarios, I have assumed that fundamental landscape properties remain constant in time. However, current predictions concerning global climatic change (as possibly other anthropogenic changes imposed) undermine the validity of this assumption. After introducing spatial heterogeneity in chapter 3, in chapter 4, I thus add temporal variability (more specifically a temporal trend) into the system, to analyse the possible response of interacting systems to climate change. I focus on three possible evolutionary responses to such change, namely dispersal evolution, expansion of niche width (or temperature tolerance), and changing in temperature preference (local adaptation). Firstly, increasing dispersal may help individuals to move along with changing climate or move to a suitable microclimate pocket (Scherrer and Körner 2010; Hof et al. 2011). Scherrer and Körner (2010) performed infrared thermometry of alpine landscape and found that the microhabitat temperature differences are larger than the temperature change predicted by IPCC (2007). It is thus expected that the temperature mosaics could be refuges for organisms in a warming climate. Secondly, individuals that would expand their niche could tolerate wider range of temperature and can use more habitats. Finally, evolution in temperature preference provides the (obvious) route to adapt to the new temperature conditions.

In my simulations, I demonstrate that host species could indeed evolutionary respond to climate change by changing all these three traits. Clearly, the ‘ideal’ way to adaptation would be an adjustment in temperature preference because dispersal evolution and expansion of temperature tolerance (niche width) are both associated with costs. Dispersal might move a well-adapted individual away from its most suitable temperature (much less of a risk if individuals can actively choose habitat) and clearly is often associated with direct investment costs and specific risks (not even included in the simulations). Increase in niche width penalizes an individual because of the habitat–fertility trade-off causing a generalist having lower fitness than a specialist in optimum habitat.

Table 6.2: Effects of parasitism, spatial heterogeneity and high cost of generalization on dispersal, niche width and local adaptation (temperature preference) before and after climate change. I use the scenario with commensalism, homogeneous landscape and low cost of generalization as a reference case. The local adaptation is referred to combination of mean and standard deviation of temperature preference in chapter 4.

	evolutionary trait	**parasitism**	**spatial heterogeneity**	**high cost of generalization**	**climate change**
before climate change	dispersal	+	–	–	+
	niche width	+	o	–	+
	local adaptation[1]	–		o[2]/–[3]	–
after climate change	dispersal	–[4]	+	–	
	niche width	o	o	–	
	local adaptation	+	+	+	

(o: a trait is unaffected; +: increased; –: decreased; [1]the local adaptation is only relevant in heterogeneous landscape. The effect of spatial heterogeneity is thus not shown; [2]for commensalism; [3]for parasitism; [4]note that in this case, the dispersal probability before climate change is already high)

However, my simulation results indicate that quantitatively, the evolutionary response to climate change may depend on circumstances and when one of these responses is constrained, evolution may lead to adjustment in different ways. For example, due to gene flow and unpredictability of local environmental conditions associated with frequent dispersal, parasitism promotes the evolution of dispersal thus preventing the evolution of hosts adapted to local conditions, especially to conditions in extreme and rare habitats. This leads to a possible lack of genetic diversity in temperature preference as more generalized hosts adjusted to average conditions prevail. However, this lack of genetic diversity is compensated by more a stronger evolutionary response in temperature tolerance. Another example is that high trade-off costs for generalization may mostly block the response in temperature tolerance thus causing a stronger response in temperature preference. I summarize the effect of each factor on each evolutionary trait and its response in table 6.2.

At first glance, the system investigated in chapter 5 seems quite distinct from the systems investigated in the previous chapters. It is actually, however, based on the same model structure as the model in chapter 4 (see figure 1.4 for the direct comparison); the principle difference is that individuals have not to cope with habitat heterogeneity, but with group heterogeneity that affects the chances of immigrating individuals in the adoption process. In addition, I initially consider the consequences of different fixed dispersal and group tolerance traits for group formation, but do not consider the evolution of these two traits (dispersal evolution is introduced, though, in an added set of simulations). Nonetheless, the selective processes at work resemble those in the 2H2G mutualistic scenario in chapter 2 – the success in an immigrants' prospective depends similarly on the frequency of its own genotype (in the mutualism scenario of its own species) in the group (community) it attempts to enter.

Interestingly, dispersal and tolerance are important for determining group formation, trait coexistence, and adoption of different traits into a group because generally, dispersal and group tolerance have comparable effects, i.e. high dispersal or high tolerance should both lead to a homogenization of marker traits as they both affect the rate of 'effective dispersal' between groups. At moderate dispersal probability and/or group tolerance, I find the coexistence of different phenotypes of the marker trait in one group (local coexistence), which emphasizes the possibility of acceptance of individuals with different marker phenotypes that observed in nature, such as adoption of non-nestmate queens in ants (Sundström 1997; Foitzik and Heinze 1998; Souza et al. 2005; Holzer et al. 2008; Kellner et al. 2010). Spatial structure of marker trait distribution can modify the results in the way that the regional coexistence of different marker phenotypes is possible in the parameter space where only regional fixation emerges in scenarios without spatial structure. Indeed, the very conditions that favour local dominance of a single type may also promote regional coexistence of different types (once such diversity has established) as the factors guarding local populations against infiltration of alien types also prevent spreading the locally dominant type into groups of different composition. And again, this argumentation may equally apply to mutualistic communities with many different co-adapted mutualistic pairs that compete with each other. While positive frequency-dependent selection should promote local dominance of a single pair it may also promote regional coexistence.

In this model, I, however, use the simplest assumption about a linear cost and benefit structure of adoption process (there is no explicit cost in adoption, and benefit of adoption is linear increase of the total group fecundity and resources are equally shared among individuals) in order to understand the basic of the system. It can, however, be adapted by using other cost and benefit structures to explore different systems. For example, in systems with reproductive skew where resources are limited and reproduction is unequally shared among individuals (reviewed in Nonacs and Hager

2011), or in systems with social parasites, which imitate the group profile to penetrate into a group (such as chemical mimicry of its host *Temnothorax*'s chemical profile in the slavemaking ant *Protomognathus americanus* – Brandt et al. 2005) and cause fitness loss in the group (Lenoir et al. 2001).

6.2. Conclusion and perspectives

In this thesis, I focus on roles of interspecific interaction on evolution of different traits in different ecological contexts (pairwise and multispecies system, spatial and temporal heterogeneity – chapter 2–4) and consequences of dispersal and tolerance for the formation of 'trait groups' (chapter 5). The results from chapter 2 to chapter 4 highlight the role of interspecific interaction on the ecological and evolutionary dynamic systems. Interspecific interaction like parasitism and mutualism can determine the optimal dispersal probability of each partner. Parasitism (or possible other forms of antagonistic interactions) may clearly modify the evolution of traits and their responses to spatial and temporal heterogeneity, and especially to climate change compared to those seen in single species systems. Moreover, I especially want to point out that the evolutionary outcome of dispersal evolution in multispecies communities may differ from that predicted for pairwise species system because added attributes of frequency-dependent selection may complicate the dynamics of the evolutionary response – and this holds for parasitic as well as mutualistic interactions. Indeed, this issue clearly warrants further investigation as the interaction between landscape heterogeneity and species interactions may strongly influence the emergence of community diversity patterns (Chaianunporn and Hovestadt 2011). Nonetheless, with respect to dispersal evolution, species interactions do not necessarily introduce fundamentally new mechanism beyond those already considered underlying the evolution of dispersal in single species systems: Ultimately species interactions just contribute to the emergent spatial and temporal variability in fitness expectations known to affect the evolution of dispersal (Comins et al. 1980; Hastings 1983; Holt and McPeek 1996; Kirkpatrick and Barton 1997; Travis 2001; Poethke et al. 2003, 2011). What separates species interactions (and my models) from abiotic factors generating such heterogeneity (studied in previous papers; e.g. Holt and McPeek 1996) is that their influence on spatial or temporal pattern formation involves complex ecological and evolutionary feedback effects. I summarize these relationships between interspecific interaction, spatial heterogeneity, and temporal stochasticity on dispersal evolution in figure 6.2.

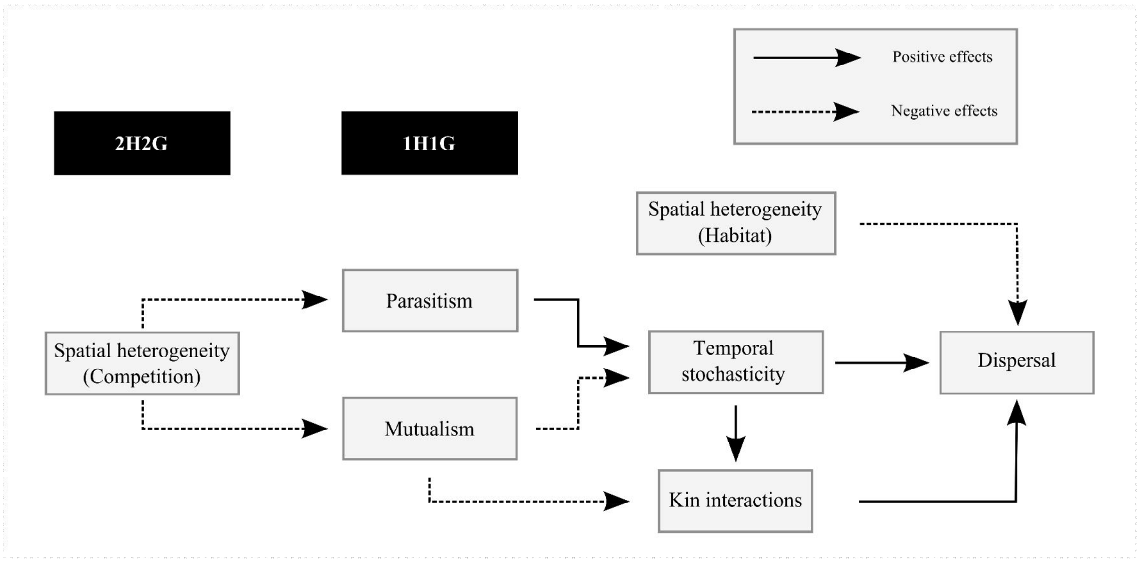

Figure 6.2: Schematic presentation of factors investigated in this thesis and their observed effects on dispersal evolution. Note that here I show two spatial heterogeneity. The first spatial heterogeneity (habitat) emerges due to explicit spatial landscape assumed (investigated in chapter 3), whereas the second aspect of spatial heterogeneity (competition) emerges due to presence of two competitive host species (investigated in chapter 2)

In order to understand the evolving metacommunity dynamics, we should thus improve our understanding of this complexity. Especially, dispersal should not be considered as an independent trait of a single species, but as a coevolving trait of which evolution can be affected by species interactions, but that also influences the evolution of other traits. The aspect of "community-dependent dispersal" (French and Travis 2001) should be revisited and draw larger attention in both theoretical and empirical work.

In this thesis, I show just some examples on how complexity in a species system can influence dispersal evolution. My preliminary observation raises questions on how dispersal evolves in even more complex species systems with different types of interaction or even in food webs. In turn, how does dispersal evolution influences community structure and diversity? How many species can coexist in such a system? Would it lead to any differences between local and regional diversity? In this perspective, I already show an effect of dispersal evolution on the local and regional diversity in chapter 2 that in the 2H2G mutualistic scenario, when the dispersal evolution is allowed, a species pair might be dominant in one local patch, but different patches might be populated by different species pairs. This results in distinct between local and regional diversity. However, we still do not know how far this mechanism would carry in even more specious communities.

I always assume in the multispecies system that host species are competitive equivalent and each guest species specialize on a single host species. Competitive equivalence follows the unified neutral theory of biodiversity of Hubbell (2001) who assume similar fitness for all species in equilibrium, and it is suitable to my system in chapter 2. However, in nature, species might not always have equal competitive abilities and inferior types (with respect to fertility) compensate their fitness disadvantage by lower parasite risk. Moreover, such interactions might be more complex: guests might not always specialize on a single host species – especially throughout its entire range and a host species might interact with more than one guest species. These two aspects are worthwhile for further investigations.

For the later aspect, there is an example in the host shift observed in many *Maculinea* species. Single populations of *Maculinea* are normally completely adapted to a single host species, but different populations in different locations might specialize on different host species (Als et al. 2004; Jansen et al. 2011): In total, *M. alcon* and *M. rebeli* use seven *Myrmica* species as major hosts within Europe. Such complex species interactions can be predicted from results of this study because parasitic interaction leads to evolution of high dispersal in both host and guest species and results in high turnover in species and types. Nonetheless, in this system, more specific modelling approaches should provide more understanding of proximate and ultimate causes of host shifts, which should be important for conservation and management of such species groups.

Although according to the competitive exclusion principle (Hardin 1960), complete competitors cannot coexist and coexistence of *n* species on less than *n* resources should not be evolutionarily and ecological stable, many theoretical studies demonstrate that coexistence of multiple specialist species or generalist–specialist species utilizing one or two resources (here host species) is possible in certain trade-off structure and parameter space (Wilson & Yoshimura 1994; Kisdi 2002; Egas et al. 2004; Abrams 2006*a*, 2006*b*). This aspect can be adapted for host–guest interaction systems: a single host species may thus interact with more than one antagonistic species (at same trophic level) at one location. However, to my knowledge, comparable studies for host–parasite systems do not existed. The characteristic of a host–parasite system differs clearly from a resource–exploiter system, since both partners of a host–parasite system are able to evolve and move. Therefore, it is interesting to investigate this aspect for host-parasite systems in more detail, especially, how coexistence would be changed in ecological and evolutionary dynamic systems? In addition, how the dispersal evolution does influence the stability of this system?

In this thesis, I only investigate the responses of pairwise systems to spatial heterogeneity and climate change – and potential temporal stochasticity induced by the species interactions themselves. It would be interesting to expand this approach to multispecies systems because it can be expected that community diversity affect both spatial and temporal heterogeneity thus leading to a geographic mosaic of species interactions, with a corresponding geographic mosaic of coevolution (a selection mosaic among populations, favouring different evolutionary trajectories to interactions in different populations; Thompson 1999*a*, 1999*b*, 2005). This should include evolution of dispersal, habitat niche width (temperature tolerance) and habitat (or temperature) preference on which I focus in this thesis. Further, any (theoretical) study considering the evolutionary response to climate change can produce meaningful results only if we account for interactions with competing species (of the same guild) – otherwise we a left with typically two unrealistic predictions only: Global range expansion or global extinction (Kubisch et al. *in press*).

Although my thesis is theory orientated, predictions and conclusions should ideally be examined empirically too. However, since I deal with simultaneous effects in two or more species and spatial population structure at different scales, it may not be easy to provide supporting (or contradicting) empirical evidences. Some recent works, however, show possible routes for experimentally testing predictions in complex system. The first system is a mesocosm study with the two-spotted spider mite *Tetranychus urticae* which investigates selection and heritability on dispersal distance (Bitume et al. 2011). Results point out the role of density and maternal effects on dispersal. Such an experimental system could be developed into multispecies system for studying the effect of interspecific interaction on dispersal evolution as many natural enemies of the mite exist and are already used in experiment, such as the phytoseiid mite *Iphiseius degenerans* (Fantinou et al. 2012), the ant *Tapinoma melanocephalum* (Osborne et al. 1995), the mealy bug predator *Cryptolaemus montrouzieri*

(Coccinelidae), the spider mite predator *Neoseiulus californicus* (Phytoseiidae) and the aphid parasitoid *Aphidius colemani* (Braconidae; Urbaneja et al. 2008).

Another example empirical system is a microcosm of microorganisms, such as *Pseudomonas fluorescens* and its viral parasite, phage Φ2, or *Pseudomonas aeruginosa*–bacteriophage PP7 as host–parasite pair. This system is already utilized for study of many aspects of ecology and (co-)evolution of host–parasite system mediated e.g. effects of spatial heterogeneity on stability of host–parasite coexistence (Brockhurst et al. 2006), impact of migration rate on coevolution of resistance and infectivity (Brockhurst et al. 2007; Vogwill et al. 2008); interaction of dispersal and natural enemy on spatial synchrony and stability (Vogwill et al. 2009). This microcosm system is suitable for studying evolutionary process because the organisms have very short generation time. Moreover, their dispersal can be directly manipulated (Vogwill et al. 2008).

Others have already established model systems to study the responses of organisms under future climate condition such as the predatory mite *Phytoseiulus persimilis*, a predator of the two-spotted spider mite, under increasing temperature (Skirvin and Fenlon 2003), or the aphid *Uroleucon nigrotuberculatum* and the pea aphid *Acyrthosiphon pisum* under elevated CO_2 and/or O_3 concentrations (Mondor et al. 2004, 2010). The aphid *U. nigrotuberculatum* also shows an interesting characteristic because similar to observation in several aphid species (Weisser et al. 1999; Sloggett and Weisser 2002; Kunert and Weisser 2003; Mondor et al. 2005), the production of winged offspring (dispersal morph) of this species can be induced in present of antagonistic partner (Mondor et al. 2004). This could thus be an interesting study system to prove some of my theoretical findings about ecological and evolutionary responses to the climate change.

In this thesis, I investigate the interdependence between dispersal, species interactions and spatial and temporal heterogeneity – all of which are fundamental elements of the metacommunity approach. Nonetheless, I suggest that many theoretical and empirical aspects are still left to explore. Improving understanding of the many different processes affecting evolution in metacommunities would provide us with more accurate tools for assessing the magnitude of anthropological threats to biodiversity, how systems may respond to such threats, and support us in choosing suitable conservation and management strategies for each biological communities.

Summary

A metacommunity approach will be a useful framework to assess and predict changes in biodiversity in spatially structured landscapes and changing environments. However, the relationship between two core elements of metacommunity dynamics, dispersal and species interaction are not well understood. Most theoretical studies on dispersal evolution assume that target species are in isolation and do not interact with other species although the species interactions and community structure should have strong interdependence with dispersal. On the one hand, a species interaction can change the cost and benefit structure of dispersing in relation to non-dispersing individuals. On the other hand, with dispersal, an individual can follow respectively avoid species partners. Moreover, it is also important to explore the interdependence between dispersal and species interaction with spatial and temporal heterogeneity of environment because it would allow us to gain more understanding about responses of community to disturbances such as habitat destruction or global climate change, and this aspect is up to now not well-studied.

In this thesis, I focus on the interactive and evolutionary feedback effects between dispersal and various types of interspecific interactions in different environmental settings. More specifically, I contrast dispersal evolution in scenarios with different types of interactions (chapter 2), explore the concurrent evolution of dispersal and habitat niche width (specialization) in spatial heterogeneous landscape (chapter 3) and consider (potential) multidimensional evolutionary responses under climate change (chapter 4). Moreover, I investigate consequences of different dispersal probability and group tolerance on group formation respectively group composition and the coexistence of ‘marker types’ (chapter 5). For all studies, I utilize individual-based models of single or multiple species within spatially explicit (grid-based) landscapes. In chapter 5, I also use an analytical model in addition to an individual-based model to predict phenomenon in group recognition and group formation.

In chapter 2, I explore the evolution of dispersal in communities with commensalic, mutualistic or parasitic interaction in pairwise (one host and one guest species) and multispecies system (two host species and two specialized guest species). Throughout I use the term ‘guest’ as a collective term for species that always benefit from the interaction and completely depend on the presence of their ‘host’ species for survival and reproduction. In contrast to guests, hosts can principally survive and reproduce in the absence of guests (even in mutualistic systems). The fitness of host species, however, depends on the type of interaction with guests: The reproduction of an infected host individual is reduced to zero when the interaction is ‘parasitism’, whereas fitness of hosts is unaffected or increased if the interaction is ‘commensalism’ or ‘mutualism’, respectively. I assume that each habitat patch (grid cell) may contain one (pairwise system) or two (multispecies system) pairwise populations of hosts and guests – in the later case, host species compete over resources, but guests are completely specialized on one host species. The local population dynamics in each patch follows a stochastic version of the Nicholson-Bailey.

Simulation results show that generally, the dispersal evolution in guests generally correlates with that of hosts. In comparison to a neutral system (commensalism), parasitism promotes dispersal of hosts and parasites, while mutualism tends to reduce dispersal in both partners. In parasitism scenario, search efficiency of guests plays an important role in determining the evolving dispersal probability because it defines the intensity (even the emergence) of population fluctuations and the frequency of local population extinction – such temporal variability is well known to promote dispersal evolution. Dispersal mortality and external extinction risks (e.g. due to abiotic effects) can interact and influence the effect of interspecific interactions on dispersal evolution.

In more specious metacommunities composed of two host and two guest species, aspects of frequency-dependent selection are introduced that ultimately lead to evolution of lower dispersal probabilities under mutualism as well as parasitism than in one host and one guest species communities – this happens for completely different reasons, however. Under mutualism, positive frequency dependent selection reduces fitness expectations of host and guest individuals immigrating into local communities dominated by the alternative species (pair). This possibly stable (but global collapse into a simpler two species community is possible) spatial heterogeneity imposes selection against dispersal in all species. In the parasitism scenario, negative-frequency dependent selection lowers search success of parasites, resulting in a reduced effect on host's fitness in turn weakening the selective pressure favouring dispersal.

In chapter 3, I expand the previously described model by implementing landscape heterogeneity of a continuous habitat attribute that affects only the fertility of hosts. This allows investigation of concurrent evolution of dispersal and host's habitat preference and niche width, which determine fitness (fecundity) of hosts in optimal and non-optimal habitats. To avoid the evolution of universal generalist, I take the (trivial) assumption that habitat specialists (narrow niche width) have higher fitness in optimal habitat, but can use a narrower spectrum of habitats compared to habitat generalists, i.e. I assume a trade-off between habitat generalization and fecundity, which I call the 'habitat–fertility trade-off'.

Based on this model, I compare effects of three different factors on the concurrent evolution of dispersal and habitat niche width, i.e. the type of species interaction (commensalism and parasitism), the severity (cost) of the habitat–fertility trade-off, and the influence of landscape structure (habitat autocorrelation). Depending on the trade-off, parasitic interactions may promote, in comparison to commensalism, evolution of wider habitat niche and higher dispersal probability in hosts. Lower dispersal probabilities of both hosts and guests evolve in heterogeneous compared to homogeneous landscapes but other than in homogeneous landscapes, guests typically evolve higher dispersal probabilities than their hosts in heterogeneous landscapes; only hosts face the additional 'settlement cost' due to risk of immigrating into sub-optimal habitat as I assume that guest's fitness is independent from habitats. High searching efficiency of parasites (promoting strong population dynamics) and a low cost of habitat–fertility trade-off lead to selection of hosts with high dispersal probability, adapted to average habitats and with wide habitat niche (dispersive habitat generalist). If conditions favour evolution of low dispersal types (e.g. commensalism), we also see evolution of locally adapted but 'narrow-niched' individuals (non-dispersive habitat specialist). Landscape structure affects the evolution of dispersal and habitat niche width in opposite ways: In clustered (autocorrelated) landscapes, where nearby habitats tend to be similar, dispersal probabilities evolve to higher, but habitat niche width to lower levels than in random landscapes.

In chapter 4, I expand the model from chapter 3 by adding random temporal fluctuation of habitat attribute representing the annual temperature fluctuations occurring in nearly any natural system. In addition, I introduce climate change scenarios by gradually increasing environmental temperature over a certain time interval. Since species can respond to the climate change in many ecological and evolutionary ways, I focus on how host may respond to such temperature increase by tracking evolutionary change in dispersal, temperature tolerance (niche width) and temperature preference (optimal habitat). Again, I contrast outcomes for different scenarios and combinations thereof i.e. commensalism vs. parasitism, homogeneous vs. heterogeneous landscapes and with different habitat–fertility trade-offs (high vs. low cost of generalization). I find that host species potentially show an evolutionary response to climate change in all three traits simultaneously. Those responses sometimes interact or may be compensatory with each other depending on conditions. Parasitism limits the change in temperature preference (that is the adaptive tracking of changing conditions), but promotes a compensatory increase in temperature tolerance and high dispersal. High costs of generalization restrict an increase in temperature tolerance thus fastening the response in temperature preference. Spatial heterogeneity can lead to increase of change in dispersal as it allows individuals to disperse to more suitable habitats. Nonetheless, it does not affect selection on two other traits much. These results emphasize the role of biotic interactions (here just parasitism) and interactions with landscapes in the evolutionary response to climate change because they influence not only the evolution but also the diversity of traits. Moreover, I generally stress the utility of a ‘multi-dimensional’ approach for studying possible effects of climate change in order to more completely assess and predict effects of such change on species.

In chapter 5, I address a seemingly very different issue than in the previous chapters, but the mechanisms underlying it are indeed quite similar to those already addressed in chapter 2. In some systems, certain traits may play an important role for the acceptance of members into a group, respectively their reproductive success. Such ‘marker traits’ might as such be irrelevant to fitness, e.g. as may be true for bird song dialect or chemical surface profiles of social insects. The ‘green beard model’ is often to explain the evolution of such systems. However, the theory predicts that green beard traits should always go to fixation, while in nature diversity in such traits is observed. I thus develop an analytical model along with an individual-based model to explore consequences of dispersal and group tolerance to individuals carrying deviant markers for group formation and the emergence of local and/or regional coexistence of different markers. I assume a simple system consisting of just two groups. Individuals may carry either of two different markers playing a role in group recognition. Adoption of immigrants as well as newborn individuals into a group depends on the similarity between their trait and the group's average trait as well as the group's tolerance towards deviants. Results show that either low group tolerance or low dispersal is required for the stable coexistence of distinct phenotypes at the regional level. Increasing either tolerance or dispersal promotes also local coexistence, but may ultimately result in the regional dominance of a single type. Local coexistence is an unlikely result, however, if evolution of dispersal is allowed: positive frequency-dependence (locally, the dominant phenotype is always favoured) selects against dispersal. This effect should, in turn, however, stabilize the regional coexistence of trait groups. The fundamental mechanisms underlying evolution in this system, in fact, very much resemble those already observed in the two-hosts-two-mutualists scenarios considered in chapter 2: Locally, the bearer of the more abundant marker trait form a 'mutualistic bond' (at the same time often benefiting kin) defending against the infiltration of carriers of the other marker.

In this thesis, I show the possibly important role of interspecific interactions and their interaction with other ecological and life-history attributes including species diversity, landscape heterogeneity, temporal fluctuation, trade-off and the concurrent evolution of dispersal and other traits. Interspecific interactions can modify the spatial and temporal variability of the system. Such an effect is known to have influence on dispersal evolution. However, the effects of species interaction might differ from other factors as interaction partners can move and evolve. For this reason, they can cause complex selection pressure and evolutionary feedback on evolutionary traits. Moreover, Findings emphasize that for the assessment of responses to environmental change and the design of conservation strategies, we should consider the response and the future of species not just in isolation (the metapopulation approach), but by also considering how they interact with other species (the metacommunity approach).

Zusammenfassung

Ein „Multi-Arten“ Ansatz („metacommunity approach“; im Weiteren als Meta-Gemeinschaften bezeichnet) ist eine immer noch neue und wichtige Methode zur Einschätzung und Vorhersage von Änderungen der Biodiversität in räumlich strukturierten Habitaten. Dabei werden denkbare Reaktionen von Arten nicht isoliert betrachtet, sondern auch im Kontext von Interaktionen mit anderen Arten. Bisher wurde dabei die Beziehung zwischen zwei essentiellen Mechanismen, die in Meta-Gemeinschaften eine große Rolle spielen – Ausbreitung („dispersal“) und interspezifische Interaktion – wenig untersucht. Die meisten theoretischen Untersuchungen zur Ausbreitung erfolgen mit der Annahme, dass Arten in keinen Interaktionen mit anderen Arten stehen – in natürlichen Systemen interagieren die meisten Arten jedoch mit anderen. Interspezifische Interaktionen können außerdem die Kosten-Nutzen-Bilanz von Ausbreitenden im Vergleich zu Nicht-Ausbreitenden ändern. Andererseits kann ein Individuum durch Ausbreitung Interaktionspartnern folgen beziehungsweise sie vermeiden. Es ist deshalb zu erwarten, dass die interspezifischen Interaktionen und Ausbreitung stark interagieren. Weiter ist es wichtig, die gegenseitige Abhängigkeit der interspezifischen Interaktionen und Ausbreitung unter unterschiedlicher räumlicher und zeitlicher Heterogenität der Umwelt zu untersuchen, damit wir die Antwort einer Lebensgemeinschaft auf Umweltstörung, z.B. Habitatzerstörung und Klimawandel, besser verstehen können.

Ich fokussiere mich in dieser Doktorarbeit deshalb auf die evolutionäre Rückkopplung zwischen Ausbreitung und verschiedenen Arten interspezifischer Interaktionen unter unterschiedlichen Umweltbedingungen. Zunächst vergleiche ich die Evolution der Ausbreitung in Systemen mit unterschiedlichen Interaktionstypen (Kapitel 2). Als nächstes untersuche ich die gleichzeitige Evolution der Ausbreitung und Habitatsspezialisierung in räumlich heterogenen Landschaften (Kapitel 3) und betrachte die (denkbare) multidimensionale Antwort auf den Klimawandel (Kapitel 4). Darüber hinaus untersuche ich den Einfluss von Ausbreitungswahrscheinlichkeit und Gruppentoleranz auf die Koexistenz von unterschiedlichen ‚Markermerkmalen’, anhand derer sich Gruppenmitglieder identifizieren lassen (Kapitel 5). Ich setzte dafür

hauptsächlich individuenbasierte Modelle von einer oder mehreren Arten mit räumlich expliziten (gitterbasierten) Landschaften ein. In Kapitel 5 entwickle ich zusätzlich auch ein analytisches Modell.

In Kapitel 2 erforsche ich die Evolution von Ausbreitung (Emigrationswahrscheinlichkeit) in Lebensgemeinschaften mit kommensalistischer, mutualistischer, oder parasitischer Interaktion. Außerdem vergleiche ich Zweiarten- (eine Wirtsart und eine Gastart; 1H1G) mit dem Mehrartensystem (zwei Wirtsarten und zwei Gastarten, die jeweils auf eine Wirtsart spezialisiert sind; 2H2G). In dieser Arbeit verwende ich dabei den Term ‚Gast' als einen Sammelbegriff für Arten, die von der Interaktion einen Fitnessvorteil haben und für Überleben und Fortpflanzung völlig abhängig von der Wirtsart sind. Hingegen kann eine Wirtsart sich auch ohne Gäste überleben und fortpflanzen (auch in mutualistischen Systemen). Parasitismus führt im Modell zur Unfruchtbarkeit befallener Wirte, bei Kommensalismus bleibt die Fitness von Wirten unverändert, während die Interaktion mit Mutualisten die Fertilität von Wirten verdoppelt. Ich simuliere dabei gitterbasierte Landschaften, in denen jede lokale Fläche (Gitterzelle) jeweils (potentiell) Populationen von einem Wirt-Gast Paar (1H1G) bzw. zwei Paaren (2H2G) beherbergen kann. In 2H2G Systemen konkurrieren dabei die Wirtsarten um Ressourcen, während die Gastarten jeweils nur auf eine Wirtsart spezialisiert sind. Die lokale Populationsdynamik in jeder lokalen Fläche folgt dem Nicholson-Bailey Modell.

Die Simulationsergebnisse zeigen, dass im Allgemein die evolvierten Ausbreitungswahrscheinlichkeiten der Gäste mit der ihrer Wirtsarten stark korreliert. In 1H1G Systemen erhöht Parasitismus die Ausbreitungswahrscheinlichkeit von Wirten und Gästen im Vergleich zum Kommensalismus (Referenzsystem), während Mutualismus sie verringert. Im Falle von Parasitismus beeinflusst dabei die Sucheffizienz der Parasiten die Ausbreitungsevolution, weil diese die Stärke der Populationsdynamik und die Häufigkeit des lokalen Populationsaussterbens beeinflussen. Der Effekt des Parasitismus kann somit weitgehend auf bekannte ausbreitungserhöhende Effekte zeitlicher Populationsdynamik zurückgeführt werden. Ausbreitungsmortalität und externe Aussterbensrisiken (z.B. wegen abiotischer Faktoren) können auch den Effekt der interspezifischen Interaktionen auf die Ausbreitungswahrscheinlichkeit beeinflussen.

Im Vergleich zu 1H1G Systemen spielt in 2H2G Systemen der Aspekt der frequenzabhängigen Selektion eine große Rolle und führt sowohl unter Parasitismus, als auch Mutualismus, zur Evolution geringerer Ausbreitungswahrscheinlichkeit. Die Mechanismen hinter dieser Verringerung sind für die beiden Systeme aber grundsätzlich verschieden. Unter Mutualismus reduziert die positiv frequenzabhängige Selektion die Fitnesserwartung von Wirts- und Gastsart, die in Lebensgemeinschaften immigrieren, wo ein anderes Artenpaar dominant ist. Die führt zu stabiler räumlicher Heterogenität und zur Selektion gegen Ausbreitung aller Arten. Das System ist allerdings teilweise global instabil und kann zu einem 1H1G System zusammenbrechen. Im Parasitismussystem verringert dagegen die negativ frequenzabhängige Selektion die Erfolgsrate der Parasiten und somit auch den Einfluss von Parasiten auf die Wirtsfitness. Deshalb ist der Selektionsdruck, welcher von Parasiten auf die Ausbreitung ihrer Wirte ausgeht, auch reduziert.

In Kapitel 3 erweitere ich das vorher beschriebene 1H1G Modell, indem ich Landschaftsheterogenität einer kontinuierlichen Habitateigenschaft, wie z.B. Bodenbedingungen, im Modell implementiere. Dabei nehme ich an, dass nur die Fitness (Fertilität) der Wirtsart von dieser Habitatseigenschaft abhängig ist und sich Wirte evolutionär auf bestimmte Bedingungen anpassen können - für die Gastart spielt die Landschaftsheterogenität dagegen keine Rolle. In der Auswertung fokussiere ich mich auf die gleichzeitige Evolution von Ausbreitung, Habitatpräferenz (optimales Habitat) und Nischenbreite der Wirtsart, die zusammen die Fitness in optimalen bzw. nicht-optimalen Habitaten bestimmen. Damit nicht nur extreme Generalisten entstehen, nehme ich an, dass ein Habitatspezialist (enge Nischenbreite) höhere Fertilität im optimalen Habitat hat, aber sich nur in einem engeren Habitatspektrum fortpflanzen kann als ein Habitatgeneralist. Mit anderen Worten, es gibt einen Trade-off zwischen Fertilität und Nischenbreite, den ich ‚Habitat–Fertilität Trade-off’ (HFTO) bezeichne.

Ich vergleiche die Effekte von drei unterschiedlichen Faktoren auf die Evolution der Ausbreitung und Nischenbreite der Wirtsart, nämlich die Art der Interaktion (Kommensalismus vs. Parasitismus), unterschiedlich starker HFTO, sowie der räumlichen Autokorrelation der Habitateigenschaft (Landschaftsstruktur). Im Vergleich zum Kommensalismus kann Parasitismus sowohl die Ausbreitungswahrscheinlichkeit, als auch die Nischenbreite von Wirten erhöhen – dieser Effekt wird aber durch einen hohen HFTO reduziert. Im Vergleich zu homogenen evolviert in heterogenen

Landschaften eine niedrigere Ausbreitungswahrscheinlichkeit bei Wirten wie Parasiten. Darüber hinaus bleibt die Ausbreitung der Wirte geringer als die der Gäste, während dies in homogenen Landschaften umgekehrt ist. Dies erklärt sich dadurch, dass Wirte nun zusätzliche Ausbreitungskosten („Ansiedlungskosten“) erfahren, da sie in ungeeignete Habitate immigrieren könnten. Für Gäste entstehen keine solchen Kosten. Bei hoher Sucheffizienz der Parasiten (hohe Populationsdynamik) und niedrigem HFTO kommt es zur Selektion von Wirten mit hoher Ausbreitungswahrscheinlichkeit, breiter Habitatnische und Präferenz für mittlere (durchschnittliche) Habitatbedingungen. Wenn Bedingungen auf geringe Ausbreitung selektieren (z.B. Kommensalismus), kommt es zur Evolution von lokal angepassten Habitatsspezialisten mit enger Nische. Die Landschaftsstruktur beeinflusst die Evolution der Ausbreitung und Nischenbreite in unterschiedlichen Weisen: in autokorrelierten Landschaften evolviert eine höhere Ausbreitungswahrscheinlichkeit und gleichzeitig engere Nische als in ebenfalls heterogenen, aber unkorrelierten Zufallslandschaften.

Arten könnten auf Klimawandel grundsätzlich in unterschiedlicher ökologischer und evolutionärer Weise reagieren. Zu evolutionären Reaktionen gehören besonders naheliegend die Evolution der Temperaturpräferenz (Anpassung), der Toleranz (Nischenbreite) und in der Ausbreitung (höhere Ausbreitung, um den sich verschiebenden Optimalbedingungen „zu folgen“). In Kapitel 4 modifiziere ich deshalb das Modell des vorherigen Kapitels indem ich zeitliche Schwankungen der Habitateigenschaft hinzufüge. Diese sollen damit Habitattemperatur reflektieren, die von Jahr zu Jahr schwankt. Darüber hinaus führe ich Klimawandel als systematische Erhöhung der Umwelttemperatur über eine bestimmte Zeitspanne ein. Außerdem variiere ich weitere Systemparameter, wie den Interaktionstyp (Kommensalismus oder Parasitismus), die Landschaftsheterogenität (homogen vs. heterogen) und die Stärke eines HFTOs. Es zeigt sich, dass die Wirtsart durch gleichzeitige Evolution aller drei Merkmale auf Klimawandel reagieren kann – die Stärke der evolutionären Reaktion der drei Merkmale hängt aber von den Bedingungen ab und ist teilweise kompensatorisch mit anderen Merkmalen. Parasitismus beschränkt die „adaptive Verfolgung“ der Temperaturerhöhung (Änderung in der Temperaturpräferenz), begünstigt aber die Evolution breiterer Nischen und fördert Ausbreitung. Bei einem starken HFTO ist die Evolution der Temperaturtoleranz limitiert; dafür kommt es zur stärkeren Reaktion in der Temperaturpräferenz (Anpassung). In räumlich heterogenen Landschaften kann es zu einem starken Anstieg der Ausbreitungsneigung kommen, da dadurch die

Möglichkeit besteht, in nun besser geeignete Habitate einzuwandern. Die Landschaftsheterogenität hat aber wenig Einfluss auf die evolutionäre Reaktion in Temperaturpräferenz und -toleranz. Die Ergebnisse weisen auf die mögliche Bedeutung biotischer Interaktionen und der Interaktionen mit der Landschaft für die Reaktion von Organismen auf den Klimawandel hin, weil Interaktionen sowohl die Evolution, als auch die Diversität von Merkmalen beeinflussen können. Außerdem empfehle ich, dass wir verstärkt multidimensionale evolutionäre Reaktionen von Arten betrachten sollten, damit wir genauere Einschätzungen und Vorhersagen zum Einfluss des Klimawandels auf Arten entwickeln können.

In einigen biologischen Systemen gibt es Merkmale, die wichtig für die Aufnahme neuer Individuen in eine Gruppe sind, obwohl die Merkmale sonst nicht fitnessrelevant sein müssen. Beispiele sind Gesangsdialekte in Vögeln oder chemische Profile sozialer Insekten. Die ‚Greenbeard’ Theorie versucht, die Existenz und Evolution solcher Merkmale zu erklären. Die Theorie erwartet aber, dass solche Merkmale normalerweise zur Fixierung kommen, während in der Natur häufig kleinräumige Diversität und Koexistenz solcher Merkmale beobachtet wird. Zur Erklärung dieser Koexistenz und dem Erhalt lokaler bzw. regionaler Diversität dieser „Erkennungsmerkmale“ verwende ich in Kapitel 5 sowohl ein analytisches, als auch ein individuenbasiertes Modell. Das Modell betrachtet zwei lokale Gruppen einer Art, die durch Ausbreitung Individuen austauschen können. Es gibt ein Erkennungsmerkmal, das in zwei Phänotypen auftreten kann. Die Adoption neuer Mitglieder (sowohl Einwanderer, als auch in einer Gruppe neu Geborene) hängt dabei von der Ähnlichkeit zwischen dem Merkmal der neuen Individuen und dem Gruppenmittelwert dieses Merkmals, sowie der Toleranz der Gruppe gegenüber abweichenden Individuen ab. Das Ergebnis zeigt, dass entweder niedrige Gruppentoleranz oder niedrige Ausbreitungsrate benötigt wird, um die stabile Koexistenz unterschiedlicher Phänotypen auf regionaler Ebene zu ermöglichen; lokal dominiert aber ein Merkmal. Mit steigender Gruppentoleranz und/oder Ausbreitung ist auch lokale Koexistenz möglich – je höher aber Toleranz und Ausbreitung, umso wahrscheinlicher kommt es zur globalen Dominanz eines Phänotyps. Lokale Koexistenz ist aber unwahrscheinlich (ein Typ ist lokal allenfalls sehr selten), wenn Evolution der Ausbreitung erlaubt wird, da positiv frequenzabhängige Selektion (lokal wird der häufigere Phänotyp immer bevorzugt) gegen Ausbreitung selektiert. Dieser Effekt stabilisiert aber gleichzeitig die regionale Koexistenz. Die grundlegenden Mechanismen für die Evolution dieses Systems sind dabei denen sehr ähnlich, die ich bereits im 2H2G Mutualismussystem (Kapitel 2) aufgezeigt habe: auf lokaler Ebene sind die Träger des häufigeren Erkennungsphänotyps (oder der häufigeren Art) im Vorteil, da sie eher „adoptiert“ werden bzw. eher mit ihren mutualistischen Partnern interagieren. Beide Mechanismen benachteiligen Immigranten des jeweils selteneren Typus (der selteneren Art), erzeugen damit implizite Besiedlungskosten und selektieren somit gegen Ausbreitung.

In dieser Doktorarbeit demonstriere ich die Bedeutung interspezifischer Interaktionen sowie ihres Zusammenspiels mit anderen Faktoren wie Artenvielfalt, räumlicher Heterogenität, zeitlichen Schwankungen, oder Trade-offs für die gleichzeitige Evolution von Ausbreitung und Nischenmerkmalen. Die Effekte von interspezifischen Interaktionen auf Ausbreitung können hauptsächlich auf ihre Wirkung auf räumliche und zeitliche Variabilität des Systems zurückgeführt werden, mit den bereits grundsätzlich bekannten Folgen davon. Die interspezifischen Interaktionen unterscheiden sich trotzdem von anderen Faktoren, weil die Interaktionspartner sich bewegen und evolvieren können. Deswegen ergeben sie einen komplexen Selektionsdruck und evolutionäre Rückkopplungen auf die Merkmale. Darüber hinaus betonen diese Ergebnisse, dass wir bei zukünftigen Prognosen im Artenschutz oder bei anderen Fragestellungen, Arten nicht isoliert voneinander (wie bei Meta-Populationsuntersuchungen und -modellen) betrachten, sondern interspezifische Interaktionen mit berücksichtigen sollten (Meta-Gemeinschaften). Es hat sich in meiner Arbeit gezeigt, dass gerade in Mehrartensystemen interspezifische Interaktionen evolutionäre Reaktionen auf Umweltdynamik dramatisch beeinflussen könnten.

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2003 – 2004	Bachelor thesis “Population structure of edible frogs *Kaloula mediolineata* in Tak province, Thailand”
2003 – 2004	Participating in the survey on the diversity of amphibian in Thailand and in research titled “Geographic distribution of salamanders genus *Tylototriton* in Thailand”
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Scholarship

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List of publications

Chaianunporn, T. and Hovestadt, T. *submitted*. Consensus and dispersal evolution – a potential feedback effect. *Behav. Ecol.*

Chaianunporn, T. and Hovestadt, T. 2012. Evolution of dispersal in interacting metacommunities. *J. Evol. Biol.* 25: 2511–2525.

Chaianunporn, T. and Hovestadt, T. 2012. Concurrent evolution of random dispersal and habitat niche width in host-parasitoid systems. *Ecol. Model.* 247: 241-250.

Chaianunporn, T. and Hovestadt, T. 2011. The role of mobility for the emergence of diversity in victim–exploiter systems. *J. Evol. Biol.* 24: 2473–2484.

Khonsue, W., Chaianunporn, T. and Pomchote, P. 2010. Skeletochronological assessment of age in the Himalayan Crocodile Newt, *Tylototriton verrucosus* (Anderson, 1871) from Thailand. *Tropical Natural History* 10: 181–188.

List of conference contributions

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Chaianunporn, T. and Hovestadt, T. 2012. Concurrent evolution of dispersal and habitat tolerance in antagonistic systems. *Oral presentation at the 42nd Annual Conference of the GFÖ in Lüneburg, Germany*.

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Authors’ contribution

In the following, the contributions of all authors are listed who participated in the creation of manuscripts that this cumulative thesis is built on.

Chapter 2: Chaianunporn, T. and Hovestadt, T. 2012. Evolution of dispersal in interacting metacommunities. *J. Evol. Biol.* 25: 2511–2525.

The study was designed by T. Chaianunporn and T. Hovestadt. The simulation program was developed by T. Chaianunporn. The simulation experiments were designed by both authors. T. Chaianunporn performed experiments, analyzed the data, and created a first draft of manuscript. Both authors contributed to further revision.

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