Range border formation in the light of dispersal evolution

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Dissertation zur Erlangung des
naturwissenschaftlichen Doktorgrades
der Julius-Maximilians-Universität Würzburg

vorgelegt von

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geboren in
Meiningen

Würzburg 2012

Eingereicht am : ....

Mitglieder der Promotionskommission :

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Tag des Promotionskolloquiums : ....

Doktorurkunde ausgehändigt am : ....

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Am 22. Dezember 2008 verlieh mir die Universität Würzburg den akademischen Grad des "Diplom–Biologen Univ.". Weder erwarb ich weitere akademische Grade, noch versuchte ich den Erwerb dieser.

Würzburg, den 07. Februar 2012

Alexander Kubisch

Für meine Frau.

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CHAPTER 1

Why are species' distributions constrained?

"It certainly is the general rule that the area inhabited by a single species or by a group of species is continuous and the exceptions, which are not rare [...] *be accounted for by former migrations under different circumstances, or through occasional means of transport, or by the species having become extinct in the intermediate tracts."*

Darwin, 1859

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Improving our understanding of the geographical distribution of species is still central to ecological and evolutionary research. Questions related to this issue have been asked since the very beginning of ecological science and are increasing in their importance in the face of globally changing environments. Here I will focus on one of the most relevant topics in biogeography: the formation of distributional limits in space and time. Dispersal plays a key role for these range formation processes. Without individuals emigrating from their natal and immigrating into new habitat, no species could have spread in space. However, although dispersal is known to be highly plastic and evolvable, only few studies have until now focused on the influences of dispersal evolution on range formation. In the following I try to fill this gap by investigating influences of evolving dispersal rates on range formation, expansion and shifts under global climate change.

First I will give a brief overview on the history of biogeography and range border ecology, explain the basics of dispersal evolution necessary in this context and review in more detail several concepts of range border formation. I will close the introduction by giving an outline of the chapters of this thesis.

1.1 A brief review of the roots of range border ecology

Since the 18th century there has been debate about possible mechanisms explaining the spatial distribution of species. Mainly two ideas were discussed: the vicariance and the dispersalist paradigm (Posadas *et al.*, 2006). The vicariance paradigm explained species distributions on the basis of changes in the earth's surface over geological time scales, especially the emergence of ocean barriers (Wiley, 1988). Joseph Dalton Hooker (1817 – 1911), an English botanist and friend of Charles Darwin, was a prominent advocate of this perspective. He was convinced that the only theory matching most observations could be that all species were once very widespread, with their distribution being broken up by climatic and geological changes. In contrast Darwin and Wallace promoted the dispersalist paradigm (Darwin, 1859). They concluded that species' geographical distributions are consequences of dispersal processes. Their approach shifted the biogeographical perspective towards a stronger focus on ecological processes rather than confining all distributions to broad-scale geographical changes. Hence, this approach was often presented in concert with the idea of "changeable" — evolving — species.

Although this debate is not completely resolved and revived in the 1970s, the opposing positions have been replaced by a more differential view. It is generally accepted now that depending on the focal species, geological but also dispersal processes, as well as extinctions, can be predominant factors in shaping species' ranges (Zink *et al.*, 2000).

By supplementing the ecological perspective with evolutionary aspects, Robert MacArthur (1972) laid the corner stone for recent range formation research. In his book *Geographical Ecology* he concluded that it is the interplay between ecological and evolutionary processes that plays the central role for the formation of stable range borders (reviewed and compared to recent research by Holt, 2003). Following and extending the dispersalist idea he thereby shifted the focus of range margin research from an extrinsic perspective, mostly dealing with abiotic aspects like dispersal barriers, to an intrinsic view. MacArthur saw dispersal as the key mechanism for range border formation, a perspective that has been widely accepted since (see e.g. Holt & Keitt, 2005; Gaston, 2009; Oborny *et al.*, 2009). However, there are still large gaps in understanding the interplay of dispersal evolution, other species-specific traits (like Allee effects or habitat specialization), landscape structure and biotic interactions in the formation of (stable) range borders.

1.2 The evolution of dispersal in space and time

Following Ronce (2007) dispersal can be best described as "any movement of individuals or propagules with potential consequences for gene flow across space". To properly understand range border formation and draw conclusions on possible range expansions, contractions, or shifts it is inevitable to investigate the different selective pressures on dispersal under certain environmental settings. It is, however, necessary to keep in mind that these pressures most often occur in concert with each other.

Selection for increased dispersal can be connected to several components of fitness. A direct fitness increase due to dispersal in variable environments can be achieved by a phenomenon called 'bet-hedging' (Philippi & Seger, 1989). This means that by spreading offspring over a landscape, in which conditions for survival are highly stochastic, temporal variance in fitness is decreased and consequently long term fitness increased. The direct fitness of dispersing individuals can also increase due to the ability to colonize new, sparsely populated habitat patches. The strong influence of subsequent colonization success on dispersal evolution can best be seen in range expansions and the associated 'spatial selection' (Phillips *et al.*, 2008), which will be discussed in more detail in section 1.2.4. Temporal variation in population densities, as a consequence of e.g.

environmental stochasticity, also selects for increased dispersal (Cadet *et al.*, 2003; Poethke *et al.*, 2007). In such environments the chances of getting from a densely to a less populated patch are high, as statistically more individuals move from larger to smaller populations than vice versa.

If not only direct, but also indirect fitness benefits of dispersal are considered, kin competition emerges as a major determinant of emigration (Hamilton & May, 1977; Poethke *et al.*, 2007). When dispersal is costly and conditions are spatially homogeneous, an individual has no direct benefit regarding its fitness due to emigration. However, when it leaves a patch more resources are available for its remaining kin, increasing its inclusive fitness (Hamilton & May, 1977).

Of course there are also forces that favor selection for reduced dispersal in populations. The probably most influential factors in this respect are costs related to dispersal. Leaving a habitat patch increases the probability of dying during the transition process, e.g. due to predation. Additional costs can be implied by decreased fecundity due to an increase of investment into movement abilities (for a general review of dispersal costs see Bonte *et al.*, in press). These costs select strongly against dispersal and increase with habitat fragmentation, as in more fragmented landscapes the proportion of unfavorable matrix is higher relative to the favorable habitat (Wilcove *et al.*, 1986).

It has also been shown that spatial variation in habitat conditions impedes a selective pressure against dispersal (Hastings, 1983). In comparison to the above described effects of temporal variation in conditions on dispersal, no bet hedging is possible when variation is only of spatial nature. In such a landscape there is a clear fitness difference caused by the strength of resource competition in large compared to small patches. When a disperser migrates from a large to a smaller patch, it ends up in habitat with stronger competition. Hence, long term fitness can only be increased by decreasing dispersal. Because more individuals live in large patches than in small ones, the average dispersal propensity of the whole metapopulation is lowered.

1.2.1 Dispersal evolution in spatially explicit landscapes

The selective pressures described above have strong impacts on the evolution of dispersal and can amplify or oppose each other (Ronce, 2007). This interplay between different selective forces becomes especially important when space is heterogeneous. Regarding the topic of this thesis — the formation of range borders — it has often been observed that sharp distributional limits of species occur along smooth transitions in the landscape (Polechová *et al.*, 2009). Transfer experiments revealed that individuals of some species brought outside their range persisted well in the new areas (Prince & Carter, 1985). These results indicate that intrinsic population processes might prevent the spread of species (in addition to extrinsic, i.e. environmental, factors). To understand these intrinsic processes it is an inevitable first step to investigate the influence of the landscape's spatial configuration on the evolution of dispersal.

Gros *et al.* (2006) investigated the influence of habitat size and the distance of individuals within a population from an absorbing habitat border on the local adaptation of dispersal strategies. They showed that larger dispersal distances evolve in the core of the range compared to the edge. However, it is well known that most environmental characteristics are neither spatially homogeneous nor occurring in sharp transitions. Smooth environmental gradients are often found in nature (Körner, 2007). Dytham (2009) extended Gros' study by incorporating different environmental gradients. Gradients were applied in growth and death rate, distance dependent dispersal costs and patch size. The results of this simulation study showed that the type of gradient leading to the formation of a stable range border strongly determined the evolved pattern of dispersal strategies along the landscape. Gradients increasing temporal and/or spatial variance as well as kin structure, like a patch size gradient, led to higher dispersal distances at the range margin, while a gradient in dispersal costs led to selection against dispersiveness and hence to lower distances at the margin compared to the core.

These two selected studies on dispersal evolution in spatially explicit landscapes emphasize the potentially strong influence of landscape configuration on dispersal evolution, indicating possible severe consequences for range border formation in spatio-temporally variable environments.

1.2.2 Dispersal evolution under global climate change

The consequences of the recorded and projected changes of the global climate for biodiversity and the distribution of species are one of the central topics of recent ecological and evolutionary research (e.g. Opdam & Wascher, 2004; Brooker *et al.*, 2007; Atkins & Travis, 2010). Climate change is usually characterized by two major mechanisms: the change in mean conditions (e.g. temperature or precipitation) and the increase in the variance of conditions (e.g. a higher stochasticity in annual temperatures or an increase in the frequency of extreme climatic events; Jentsch *et al.*, 2007). Much effort has been invested into the investigation of potential consequences for species' ranges (see subsection 1.5).

However, implications of climate change on dispersal evolution are still unclear. Species living in landscapes with strong environmental gradients in temperature, could undergo strong selection for increased emigration rates when climate is changing and temperatures increase. As conditions change over time, previously locally adapted individuals are increasingly maladapted to their natal habitat. They could, however, cope with climate change by increased dispersal, heightening the chance to end up in habitat patches with suitable temperatures. Preliminary simulations have revealed such results for metapopulations living in abiotic gradients where temperature increases globally. However, in these simulations the reproductive system shows a strong influence on emerging dispersal rates and hence the ability of species to cope with increasing temperatures. Sexually reproducing organisms can afford larger rates of gene flow, because maladapted genes are less detrimental in their effect due to recombination. In asexual systems, however, the negative effect of maladapted genes is not buffered by recombination, resulting in lower dispersal rates evolving (Becker *et al.*, in prep.).

An increase in the variance of environmental conditions, i.e. an increase in spatio-temporal variability of abiotic conditions for populations, will lead to higher dispersal (see above; Philippi & Seger, 1989). However, not many studies have directly investigated reactions of species' dispersal to increased extreme events, yet. One example is given by Hochkirch & Damerau (2009). The authors showed a rapid range expansion of the bush cricket *Metrioptera roeselii* after the European heat wave in 2003. The species shows a dispersal dimorphism with a large fraction of flightless individuals and few dispersive macropters. Following the climate anomaly a surprisingly large amount of macropters was detected in the surveyed populations that could colonize new habitats. A sudden range expansion was the consequence. This increased occurrence of macropteric individuals could have been caused by the higher temperatures increasing local population densities with stronger resource competition and increased levels of density-dependent emigration (Poethke *et al.*, 2003). This example shows that evolutionary or plastic responses in dispersal traits are severely influenced by changed climatic conditions.

A recent study by Hof *et al.* (2011) sheds new light on the prevailing concept of climate change. By investigating the speed of global warming the IPCC concludes, that "it is very likely that the global warming of $4 - 7\,^{\circ}\mathrm{C}$ since the Last Glacial Maximum (21,000 BP) occurred at an average rate about 10 times slower than the warming of the 20th century" (IPCC, 2007, p.435). Hof *et al.* (2011) reviewed, however, a study by Steffensen *et al.* (2008) showing that near the end of the last glacial period (14,000 BP) temperature increases of almost 4 °C yr^{-1} occurred. Despite these dramatic changes there was no large biological extinction event, except for some large mammal and European tree species. The authors address the question, why biodiversity at that time could cope with such strong changes. They hypothesize that populations could have been able to find shelter in so-called 'microclimatic pockets' (i.e. small areas of favorable conditions in an unfavorable environment) allowing for survival without the need of tracking the changing climate. However, this is no good news as the landscape nowadays is highly fragmented and hence a large amount of these pockets do not exist anymore. These findings impose a very important implication for dispersal evolution under climate change: on the one side we can expect stronger selection in favor of dispersal than during past climate changes due to the lack of microclimatic pockets. However, on the other side the increased habitat fragmentation leads to higher costs of dispersal and thus implies selective pressures against dispersal.

1.2.3 Density-dependent emigration

It has already been mentioned that populations (especially of insects) living in fragmented landscapes have to cope with severe demographic stochasticity. In such a stochastic world strategies are selected for that equalize population densities. One such strategy is density-dependent emigration (see Poethke & Hovestadt, 2002), which has been documented in several species (Loxdale & Lushai, 1999; Enfjäll & Leimar, 2005; Matthysen, 2005).

For a proper understanding of density-dependent emigration it is necessary to find a quantitative relationship between emigration propensity and population density (Hovestadt *et al.*, 2010). Several suggestions for such a relationship have been formulated in the past, starting with a truncated linear function provided by Travis *et al.* (1999). Poethke & Hovestadt (2002) (and similarly Ruxton & Rohani, 1998) presented an alternative approach based on the marginal value theorem (Charnov, 1976). A comparative study using evolutionary competition with alternative functions showed that individuals following the latter model indeed out competed any other strategy for most parameters (except for scenarios with very high overall dispersal rates; Hovestadt *et al.*, 2010). Based on these results I will focus on the use of the model developed by Poethke & Hovestadt (2002) throughout this thesis.

1.2.4 Dispersal evolution during range expansions

The investigation of range expansions of species can provide very helpful insights into processes leading to range borders and is — especially in the context of invasions — currently in the focus of many studies (Kinezaki *et al.*, 2003; Hughes *et al.*, 2007; Sax *et al.*, 2007; Duckworth, 2008; Phillips, in press). The evolution of dispersal at range margins during periods of expansion has been intensively studied by Ben Phillips and co-workers (Phillips *et al.*, 2008, 2010b,b, but see also Simmons & Thomas, 2004; Duckworth, 2008). They found that the dispersiveness of cane toads rapidly increased during their Australian invasion, expressed in e.g. longer legs allowing farther movement distances (Phillips *et al.*, 2010b). This phenomenon can be explained by what they call 'spatial selection'. The individual toads that are most dispersive and travel the longest distances obviously appear with the highest probability beyond the current range margin. Given enough time and recurrent colonization events this ecological filter of individuals leads to a strong phenotypic shift in mean dispersal ability at the range margin. This has led to more than fivefold increases in range shift velocity of the cane toads since the invasion began (Phillips *et al.*, 2010a). However, it is still not clear whether this process relies on mutations occurring at the range margin or 'simply' selects from the already existing variability of phenotypes.

It should be noted that in populations subject to strong founder effects kin structure becomes strongly pronounced. As kin selection is known to be an important determinant of the evolution of higher dispersal, one could argue that the increased kin structure during invasions is a major driving force for selection of increased dispersal. First exemplary simulations involving shuffling of kin similar to Poethke *et al.* (2007) revealed that kin or higher-level selection effects may be the major driving force for increased dispersal during range expansions (see also Travis *et al.*, 2009). However, these mechanisms have to be investigated in more detail to get a clear picture of the relevant selective pressures affecting dispersal during range expansions (Kubisch *et al.*, in prep.).

1.3 Single-species concepts for range formation

Classically, range borders were seen as the outcome of processes defining a single species' distribution. In 2003 Holt reevaluated the ideas of Robert MacArthur and developed a framework for the evolutionary ecology of range limits (Holt, 2003). He defined three issues relevant for investigating range border formation: niches, spatial variation, and dispersal. Furthermore he states that most if not all mechanisms affecting the niche limits of species again interact with dispersal. As dispersal itself is subject to intense selective pressures that depend on the landscape (i.e. spatial variation) it is reasonable to claim that dispersal is a key attribute relevant in the formation of range borders of single species.

In the following I will analyze more deeply the role of the landscape for the formation of range borders of species, while ignoring (for the moment) the role of biotic interactions. Geographical barriers, like e.g. coasts, are important determinants for stable ranges. However, their impact is obvious and thus I will not further discuss these mechanisms.

MacArthur already stated that "future theory will concentrate on the boundaries of species ranges as they are encountered on ecologically uniform or continuously varying terrain" (MacArthur & Wilson, 1967, as cited by Holt, 2003). This prediction is fulfilled by recent range border research, as most studies focus on the formation of range borders in smooth environmental gradients. It is typically assumed that abiotic factors basically change the ratio between colonization and extinction of populations at range margins. Where colonization equals extinction a stable border is formed (Oborny *et al.*, 2009). Hence it seems reasonable to divide the influences of environmental gradients into two classes: those affecting spatio-temporal variance and thus mainly influencing the extinction rate of local populations and those affecting habitat fragmentation and therefore mainly influencing colonization rates. Some mechanisms proposed in this chapter dealing with dispersal evolution and the formation of range borders have to my knowledge not been investigated yet. Hence these should rather be interpreted as proposed ideas than as a review of conducted studies. This shows that much work still needs to be done to better understand the key role of dispersal evolution for range formation.

1.3.1 Gradients increasing spatio-temporal variance

Many environments are highly unstable (Easterling *et al.*, 2000). This instability has direct consequences for dispersal evolution (see the description of the influences of temporal variance on dispersal at the beginning of this chapter) and can increase along gradients through several factors. In the most simple case variance increases along gradients of patch size, i.e. habitat availability. Small patches (meaning habitat patches with a small carrying capacity) lead to higher demographic stochasticity, increasing the risk of extinction (McPeek & Holt, 1992). Indeed, once patch size falls below a critical threshold, demographic stochasticity becomes too high to allow for extended population survival and local populations go extinct (Gonzalez-Guzman & Mehlman, 2001).

The variability of climatic conditions can also change along e.g. altitudinal gradients (Körner, 2007). Stronger fluctuations in climatic conditions can lead to spatio-temporal differences in growth rates. The consequence are externally driven demographic fluctuation resulting in increased extinction risk (Lande, 1998). Further, along land-use gradients also catastrophic events may occur, leading to the complete extinction of local populations (Ronce *et al.*, 2000) and thus hindering a metapopulation from further spread.

All the described examples of gradients share one common characteristic, which is of high importance for range formation: they lead to selection for increased dispersal at the range margin. These increased dispersal rates can have several consequences for species' ranges. On the one side they allow for a larger fraction of sink populations. Sink populations exist under conditions that do not allow for positive population growth but are kept populated by recurrent immigration from source populations (Pulliam, 1988). However, high dispersal at the range edge could also increase gene flow. A hypothesis widely used to explain range formation is that a higher fraction of gene flow from the core to the margin of a range than vice versa can hamper local adaptation to marginal habitat and thus lead to a stable range border (this mechanism will be described in more detail in section 1.3.4). When gradients in local conditions (e.g. temperature) are superimposed by gradients in spatio-temporal variability the effect of asymmetric gene flow could be counteracted or at least subdued by selection for reduced dispersal in the core area: the basic assumption of a net gene flow from core to margin may not hold anymore when individuals at the range core show lower dispersal due to lower variance than individuals from the range margin.

At the beginning of this section I mentioned that a too strong spatial variation of conditions can also lead to selection for decreased dispersal. Considering a spatial gradient these insights reveal a dependence of the reaction of dispersal evolution on the gradient's steepness. When the gradient is smooth enough dispersal is expected to be selected for in areas with higher spatial or temporal variance in conditions. However, when such a gradient is too steep it could behave similarly to a mainland-island situation. This means that at the 'good' end of the gradient the 'mainland' is located in an area with low demographic stochasticity and hence low dispersal rates. On the nearby 'bad' end variance is high and dispersal rates (or distances) would need to be high, too, to allow for population survival there. A consequence could thus be a contraction of the range to areas with low variance (similar to Poethke *et al.*, 2011b).

1.3.2 Gradients increasing habitat fragmentation

The fragmentation of natural habitats is of utmost importance for species' ranges and is one of the most dramatic impacts of anthropogenic disturbance (Wilcove *et al.*, 1986; Honnay *et al.*, 2002; Leimu *et al.*, 2010). Generally, habitat fragmentation is considered to be influencing two characteristics of landscape structure: the size of patches of suitable habitat and their isolation. These two parts have different influences on dispersal evolution. The potential effects of gradients of decreasing patch size have already been mentioned in the previous section.

Bonte *et al.* (in press) have argued that severe habitat fragmentation leads to increased costs of dispersal and thus results in selection against dispersal. This argument leads to quite different predictions concerning species' distributions. For example, Virgos (2001) investigated the most important factors affecting the abundance of badger populations (*Meles meles* L.) in several landscapes. They found that in unfragmented areas with high forest cover the best predictor for badger abundance was habitat suitability. However, in highly fragmented areas (forest cover below 20%) the suitability of habitat patches did only play a minor role and isolation between patches was the most predictive parameter. Similarly a study in Belgium by Baguette *et al.* (2003) revealed that habitat fragmentation led to a rapid adaptive response in dispersal behavior of the bog fritillary butterfly (*Proclossiana eunomia*) towards decreased dispersal rates. The authors concluded that dispersal mortality was the key factor driving selection against dispersal. Additionally biotic interactions can become important when dealing with the effects of habitat fragmentation. Similarly, for animal-dispersed plants seed dispersers of certain plant species may be lost in too highly fragmented habitat, reducing the plant's dispersal capabilities indirectly (Leimu *et al.*, 2010).

1.3.3 The impact of Allee effects on range formation

In classical ecological theory interactions between members of a population are mostly viewed as being negative, like e.g. competition (Courchamp *et al.*, 2010). Warder Clyde Allee was, however, more interested in positive interactions of animals, especially regarding group formation. In consequence he described a phenomenon that is now largely known as the Allee effect: the reduction of population growth rates at low population size or density (Allee, 1938). For many species Allee effects have by now been documented, although the strength of the effects as well as the underlying mechanisms are rarely clear (Kramer *et al.*, 2009).

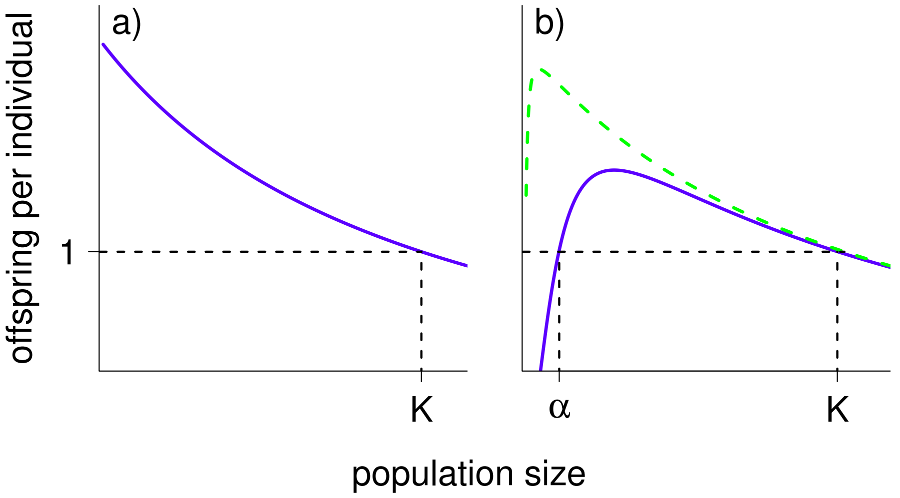

Figure 1.1: Influence of Allee effects on population growth, shown as the functional relationship between per capita offspring and population size. The shown functions are exemplary and the same as used in chapter 3. a) Logistic growth without Allee effect. b) Logistic growth with a strong (solid blue line) and a weak (dashed green line) Allee effect, respectively. The horizontal dashed line denotes the limit of one offspring per individual, below which the population size decreases. At carrying capacity (K) a stable equilibrium is found. In case of a strong Allee effect a second (unstable) equilibrium at population size α emerges.

Allee effects can be divided into two major classes: weak and strong demographic Allee effects (see figure 1.1 for exemplary functional relationships). 'Demographic effects' means here that the effect of such positive interactions between individuals at low densities can be seen at the level of population growth. Weak effects describe a decline in population growth rate for low sizes or densities, but without falling to growth rates below one. Hence, populations at low levels can still increase in size, but at a lower rate. In the case of a strong Allee effects populations go extinct when falling below the critical threshold size as population growth becomes negative (α in Fig. 1.1b).

There are many mechanisms that can lead to Allee effects. These reach from those affecting the survival of species (e.g. social foraging or defense) to genetic factors (like inbreeding depression; Courchamp *et al.*, 2010). However, one of the most general mechanisms leading to reduced growth of populations at low sizes is the difficulty of finding mates at low population size or density, which is present in all sexually reproducing species (Kramer *et al.*, 2009).

Much effort has already been invested into elucidating the role of Allee effects on biogeographical patterns (e.g. Taylor & Hastings, 2005; Kanarek & Webb, 2010; Cassini, 2011). Keitt *et al.* (2001) investigated the influence of strong Allee effects on species' invasions, based on the idea that every range of species was created by past invasions. They found that strong positive density-dependence in growth rates (at low densities) could indeed lead to the formation of stable range borders even in homogeneous environments. At the distributional margin newly colonized patches are not neighbored by enough populations to allow for sustainable population growth. Gastner and colleagues found a similar effect. The authors investigated an assumed universal law of range border geometry (Gastner *et al.*, 2009). They calculated the fractal dimension of range borders in several theoretical scenarios as well as one empirical example and found approximately the same values indicating the same geometry. However, when they incorporated Allee effects into their analysis (Gastner *et al.*, 2010) the picture changed. As a consequence of lowered colonization success at the range margin they found much more sharp transitions in patch occupancy, drastically changing the range border geometry.

Johnson *et al.* (2006) investigated the ongoing invasion of the Eurasian gypsy moth (*Lymantria dispar*) in the northeastern United States. This invasion shows an interesting progression: for longer time periods the gypsy moth's range is constrained in its extent. However, in a periodic interval (about every 4 years) the range strongly expands until a new stable position is held for another couple of years. The authors could simulate this phenomenon by including strong Allee effects and stratified diffusion, i.e. a small fraction of long-distance dispersal. They conclude that during the periods of range stasis no expansion is possible because population sizes at the range margin are too low and the Allee effect hinders the populations from further colonization. After approximately 4 years the populations have grown and provide large enough numbers of emigrants to overcome the Allee effect and allow for a period of invasion.

The selected studies highlight important influences of Allee effects on range dynamics. Especially the case of the gypsy moth invasion provides insight into the interplay between Allee effects and dispersal, a topic that will be investigated in more detail in this thesis.

1.3.4 Range formation caused by gene flow

In 1956 Haldane came up with the idea that asymmetric gene flow can lead to the formation of stable range limits (Haldane, 1956). Populations in the core of the range are of larger size than populations at the margin. Hence more individuals disperse from the core to the marginal areas than vice versa with the result of a net gene flow into this direction. Individuals from the core of a range along an environmental gradient are locally adapted to conditions there. Hence the described gene flow should result in increasing maladaptation of populations at the range margin ultimately hindering these from colonizing new areas even 'further down' the gradient.

In a review, Bridle & Vines (2007) have gathered several theoretical studies on this phenomenon as well as empirical evidence for populations subject to maladaptation because of gene flow. The mechanism behind this phenomenon has also been named 'migration load' (Garcia-Ramos & Kirkpatrick, 1997) because of its close relation to the 'mutation load', where a constant rate of mutation leads to a selective differential persisting in populations. Selective differential hereby is defined as "within-generation changes in trait frequencies or means" (Bolnick & Nosil, 2007) and hence measures a given selective pressure. Bolnick & Nosil (2007) investigated migration load theoretically, with a simulation model fitting to the natural history of walking-stick insects (*Timema cristinae*). They found evidence for a higher selective differential in marginal populations revealing a load of maladapted genes as a consequence of dispersal.

However, not all authors are convinced that range limits are indeed caused by asymmetric gene flow. Bradshaw (1984) suggested that range limits should mainly emerge as a consequence of lacking genetic variation at the range border not allowing for evolutionary adaptation to conditions there. In a review regarding adaptation to marginal habitats, Kawecki (2008) summarized theoretical and empirical studies showing that gene flow from core to margin can even foster adaptation to the range periphery. The argument is that mutations arise in the range core, where population sizes are large, and then reach the range margin by dispersal. An example is provided by the grass *Agrostis capillaris* living in zinc-contaminated areas at the margin of its range. Evidence suggests that adaptation to this harsh environment occurs only where large populations live in surrounding of uncontaminated areas, in which a high frequency of zinc-tolerant mutants occurs (Al-Hiyaly *et al.*, 1993).

Obviously it is not easy to decide on the exact influence of gene flow on adaptation to marginal habitats. Whether range expansion can be stalled by migration load might depend on the specific environmental and biotic settings. Recently, Holt & Barfield (in press) provided a model that identifies conditions, under which range expansion can be possible regardless of a net gene flow from the range core to the margin. They list factors like the initial degree of maladaptation, mutation rate, the heterogeneity of the occupied ranges, as well as sexuality and dispersal patterns. This study provides a sound foundation of mechanisms altering the effects of migration load. However, the impacts of evolution are still ignored in this study. Preliminary simulations have revealed that if dispersal evolution of a species living along an environmental gradient is allowed, predictions may indeed change. In scenarios without dispersal evolution but high emigration rates, range expansion is very slow due to the effect of gene swamping. However, when emigration rates are allowed to evolve the range expands even slower. Emigration is selected against as a consequence of the maladaptation of immigrants. Hence, there is no further gene flow and invasion into empty regions is strongly slowed down — this may give way for the evolution of local adaptation within edge populations.

1.4 Multi-species concepts for range formation

1.4.1 Antagonistic systems

Antagonistic biotic interactions can influence range limits in many different ways. For example, competition between species has been shown to lead to stable range borders over ecological time scales (Case *et al.*, 2005). This is indeed the most easy explanation of a range border, as the border just emerges, where competing species meet. Price & Kirkpatrick (2009) have shown that competition can lead to range limits that are stable over evolutionary time scales. In their model two species, of which both occupy different resource niches, meet in a landscape. When resource density of one species declines, either over space or in time, the species would principally have the potential to adapt to the other resource (i.e. shift its niche) by rapid evolution. However, as the other resource is already used by its competitor, it is this biotic interaction that ultimately limits the niche and thus the range of the species.

The formation of range limits can also be affected by predator-prey (or similarly host-parasite) interactions. Holt (2009) showed that predators can in many ways shape their own as well as their prey species' range. This is not surprising for generalist predators, since their impact on prey is density-independent. Where abundance of the predators gets too high the prey is hindered in its range expansion as the mortality becomes too high. However, for specialist predators showing density-dependent functional responses one would not expect alterations of the prey's range. As typically the population density is low at the range margin, in fact extinction of the prey-dependent predators in marginal range areas is expected. However, when space is heterogeneous in prey productivity near the range margin, there may be sites with high prey and hence also predator density. If the predator is mobile and can move efficiently between prey populations this heterogeneity could lead to predator spillover from high to low density patches. This immigration of predators could then lead to prey extinction in sparsely occupied patches and hinder the range from expanding (Holt, 1984). The same mechanism works for parasitoids, too, given high enough attack and dispersal rates (Hochberg & Ives, 1999). However, predators might also lead to the expansion of prey-ranges. If they live inside the prey's distributional area, they induce changes in the behavior of their prey if predation pressure would induce dispersal in the prey. This can increase the prey's metapopulation persistence (and hence also the predators' survival; Prakash & De Roos, 2002). However, Poethke *et al.* (2010) showed by using individual-based simulations of an aphid system that delayed predator-induced dispersal needs a substantial temporal correlation of predator presence as well as weak competition among prey to evolve.

Prey range expansion as a consequence of predation could also be a consequence of relaxed spatial gradients in prey population density. In the previous section I already explained that asymmetric gene flow from the core to the margin could severely reduce at the range margin, which ultimately constrains a given geographic distribution. However, when a predator is introduced into the prey's range core, as is typically done when applying biological control agents to invasive species, it strongly feeds on the prey in this region and consequently leads to a decline in prey density in the core area. This would also reduce gene flow to the margin, releasing the prey populations there from migration load. This could ultimately result in range expansion of both prey and predator (Holt *et al.*, 2011).

The influences of antagonistic biotic interactions are very complex and also partially counter-intuitive. A large number of theoretical studies have been conducted and several potential mechanisms have been described. There is, however, a strong lack in empirical tests of these hypotheses.

1.4.2 Mutualistic systems

Range borders in mutualistic systems are seemingly easy to understand when the mutualism is obligate for the involved species. Whenever the cooperative partner is absent, colonization of new habitats or even survival is impossible, constraining the species' range (Case *et al.*, 2005).

More complex is the problem of dispersal evolution in the face of mutualistic biotic interactions. Many studies dealing with dispersal evolution and positive interactions focus on cooperation rather than real mutualisms. However, the results should hold for all types of positive biotic interactions. It has for example been suggested that the evolution of cooperation between species can foster the evolution for increased dispersal rates. When species cooperate they increase their population size, either by increasing growth rates or decreasing mortality. Consequently, population density increases and thus local competition for resources. This competition leads to a larger benefit of dispersal (Taylor, 1992). On the other hand dispersal can also be selected against to increase the clumping of species. Without large mixing of individuals over space the probability of cooperative species to meet other cooperators is higher if they do not disperse (Doebeli & Knowlton, 1998; Killingback *et al.*, 1999).

In a recent study, Mack (in press) investigated the joint evolution of mutualism and dispersal distance in metapopulations, without considering the presence of an environmental gradient. He found a strong correlation between lower dispersal distances and higher degrees of mutualism for given environmental settings. When non-mutualism was favored by selection, dispersal distances were higher, showing that the selective force of mutualism on dispersal was stronger than that imposed by the environmental (extrinsic) conditions. Interestingly, for certain parameter combinations a coexistence of mutualists with low and non-mutualists with high dispersal distances was found. The results of this study underline the idea described above that mutualistic interactions can constrain species ranges by limiting dispersal and hence decreasing colonization of new habitats.

1.5 Range shifts under global climate change

In section 1.2.2 I have already described several consequences of global climate change for the evolution of dispersal. How these mechanisms influence shifts of ranges during the change of climate is still unclear, however. As already mentioned climate change has two major impacts: the change in mean conditions and the increase in climatic variance (Jentsch *et al.*, 2007). The potential consequences of the latter for possible range shifts has not been incorporated into models, yet (but see Battisti *et al.*, 2006; Zimmermann *et al.*, 2009). As outlined before (section 1.2), increased temporal variability in environmental conditions increases the risk for demographic extinction of populations and hence is expected to foster selection for increased dispersal. However, in this area much research needs to be done to assess the influences of higher stochasticity on ranges in any respect.

In the mean time much more work has been conducted to understand the influences of gradual changes in climate on the distribution of species. Usually it is assumed that under climate change species will track the changing conditions and migrate to where they find their optimal environment. Thomas (2010) has reviewed a vast amount of empirical evidence for range shifts that are most likely a response to moving climate windows. Frequent tools used to predict these changes are "species distribution models" (often also referred to as "bioclimate envelope models"; Guisan & Zimmermann, 2000; Bakkenes *et al.*, 2002; Pearson *et al.*, 2002). These models are of purely correlative nature. Current (or past) distributions of species are statistically correlated to certain abiotic environmental characteristics. Based on this relationship future changes in distribution are inferred. Many authors assume to achieve a good estimate for a species' niche by this method. This estimation can be problematic, e.g. when source-sink dynamics or delayed extinctions come into play (Schurr, pers. comm.). Yet, species distribution models (SDMs) have been criticized for many other reasons, like their lack of incorporating species-specific dispersal abilities as well as geographic barriers, the genetic potential of species for adaptation to changing conditions and biotic interactions (see e.g. Hampe, 2004; Dormann, 2007; Lavergne *et al.*, 2010).

Criticism often comes from authors studying the qualitative influences of climate change on (meta)populations, seeking for a mechanistic understanding. Best *et al.* (2007) used a simulation model of a metapopulation under climate change to investigate the role of the type of competition (scramble vs. contest) and density-dependent emigration on the survival probability of species when their climate window shifts. They found that contest competitors are much more vulnerable to climate change than scramble competitors and this difference is further increased when density-dependent dispersal is considered. Mustin *et al.* (2009) focused on the role of spatial heterogeneity of the environment in concert with population dynamics. Their results showed that these two factors can severely impact the potential of species to track the shifting climate. One very important aspect still missing in these studies is the potential of species to evolutionarily adapt to changing conditions, a mechanism that seems to be very important in nature (Davis *et al.*, 2005). Atkins & Travis (2010) aimed to fill this gap. They also used a metapopulation model in a scenario with a shift of climatic mean conditions and allowed species to adapt within certain limits. One outcome was that even if the distribution of a species prior to climate change overlaps with the potential distribution afterward, it is not certain that the species will survive in the areas of overlap. A more applied model was provided by Anderson *et al.* (2009), who investigated the potential range shifts of two lagomorphs. They tested different degrees of dispersiveness and found that when species were modeled to be more mobile this assumption increased the velocity of shift for the northern (leading) range border, but decreased velocity for the southern (trailing) edge.

There are efforts to improve the quality of species distribution models (Jeltsch *et al.*, 2008; Thuiller *et al.*, 2008; Kearney & Porter, 2009; Pagel & Schurr, 2011). Cabral & Schurr (2010) implemented for example a process-based (mechanistic) model in combination with an observation submodel (based on the 'virtual ecologist approach' provided by Zurell *et al.*, 2010) to explain the distributions of several tree species. The process-based submodel included relevant processes like reproduction, dispersal, mortality and extinction. They parametrized the model using field data and compared the output of the observation submodel to empirical distribution data using a likelihood approach. Using this method they could discover relevant aspects mainly influencing the trees' distribution (like Allee effects or the type of density-dependent reproduction) and proved that it is possible to join mechanistic models and field data. There are plans to further develop this approach to create a type of models called 'dynamic range models', which are even planned to incorporate evolutionary processes (Schurr, pers. comm.). This will be aided by newly developed statistical methods allowing to directly fit mechanistic models to field data (see e.g. Hartig *et al.*, 2011).

1.6 Topics of this thesis

In the following chapters I will analyze the influence of evolving dispersal on the formation of species' range borders in space and time. Robert Holt formulated the hypothesis that species' ranges could contract after periods of range expansion as a consequence of evolving dispersal abilities of species (Holt, 2003). Based on thoughts of MacArthur (1972), Holt assumes that during range expansion populations should evolve higher dispersiveness (as described in section

1.2.4). This high dispersal could allow the species to occupy sink patches only supported by the high rate of immigration. However, when the expansion period is over and individuals are locally adapted, dispersal towards these sink patches is selected against. Hence, emigration at the range border decreases. Consequently, the sink populations can not be further maintained by immigration and the initial range contracts. With the study presented in chapter 2 I investigate, whether this prediction holds for all types of gradients influencing a metapopulation's dynamics. I use an individual-based metapopulation model of invasion into gradients of dispersal mortality, patch size, growth rate or population extinction probability. I find that whether such 'elastic' behavior of the range border indeed emerges depends strongly on the type of gradient and how it influences dispersal evolution.

As already described (section 1.2.3) many species disperse not randomly but use information, e.g. on population density, to decide whether to emigrate or not. Density-dependent emigration is known to severely improve a species' ability to cope with demographic stochasticity and to enhance metapopulation persistence (Hovestadt & Poethke, 2006). I thus investigate the influence of conditional versus unconditional emigration on the emergent position of the range margin along gradients in chapter 3, further assessing the influence of high variation in growth rates. Results show that conditional dispersal leads under all conditions to the formation of wider ranges than unconditional dispersal, especially when environmental stochasticity is high. The size of the effect varies, depending on whether the applied gradient increases extinction or decreases colonization rate. This difference between strategies is further increased when a strong Allee effect is considered, decreasing the potential for successful colonization of patches at the range margin.

In chapter 4 I revisit the phenomenon of elastic range boundaries, but in a different setting. As climate change is expected to increase the variance of environmental conditions I model a scenario of climate change by increasing fluctuations in growth rates. Therefore I use equilibrium simulations as well as changes faster than the evolutionary potential of species to adapt to the changing conditions. I assume density-dependent emigration and thus can build upon the findings of chapter 3. I find that in gradients of dispersal mortality and growth rate an expansion of the range for small increases in spatio-temporal variance can occur, followed by a drastic decline in range width as variability further increases. In a patch size gradient, which is itself selecting for increased emigration at the range border, no range expansion is evident, however.

Chapter 5 focuses on the role of biotic interactions for range shifts under climate change. Most attempts to predict future range shifts lack the incorporation of evolutionary adaptation of species to changing conditions. In this chapter, I firstly investigate, whether predictions of range shifts are altered if species can adapt their dispersal behavior and other life-history traits to changing conditions due to mutation. Therefore I use a similar metapopulation model as in the previous chapters but now apply a gradient in an abiotic habitat characteristic (e.g. temperature) that determines a juvenile's mortality, depending on its adaptation to local conditions. Without allowing mutation, the species indeed shifts its range in a scenario of temporal temperature increase and perfectly tracks the changing conditions. However, when evolution of temperature adaptation is allowed the metapopulation actually invades, for most tested scenarios, the whole gradient, even 'against' the direction of climate change. As rapid evolution occurs in nature this result indicates that some important factor must be missing that hinders species from spread, otherwise restricted ranges would not be found (except for those imposed by obvious physical obstacles). The solution to this 'riddle' is the incorporation of competition with another species. Assuming that initially a border exists between two species that are adapted to two different temperature ranges but are otherwise similar, I find everything from complete tracking of the moving climate window to a complete stasis of the range border (with corresponding adaptation of species to changing conditions) depending on the simulation scenario.

In the last chapter (6) I present a schematic concept of range border formation in the light of dispersal evolution. To my knowledge, such a scheme has not been developed before. This scheme has the potential to serve as a landmark describing the current state of understanding the main influences of dispersal (evolution) on range dynamics. It lines out where the largest gaps in knowledge remain.

Chapter 2

Elastic ranges emerge due to invasion into gradients[1]

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2.1 Introduction

The establishment of species' range borders is the focus of many evolutionary and ecological analyses (Holt *et al.*, 2005; Thomas *et al.*, 2006; Dytham, 2009; Gaston, 2009). Demographic processes at a range margin play an especially important role for understanding range formation and predicting a species future distribution (Holt *et al.*, 2005). Dispersal plays a key role for demographic patterns and hence for the formation of geographic ranges (Bridle & Vines, 2007; Gaston, 2009).

A well established observation during periods of range expansion is an increase in dispersiveness (Thomas *et al.*, 2001; Simmons & Thomas, 2004; Duckworth, 2008; Phillips *et al.*, 2008). This phenomenon is caused by a kind of ecological filter at the front of the travelling wave: more dispersive individuals from the most forward populations are more likely to be found in newly established habitat patches than less dispersive ones. This effect can multiply over generations as emigrants from these patches are most likely to expand the range even further (Travis & Dytham, 2002). Hence, the distribution of genotypes in newly colonized patches is shifted towards a higher emigration tendency.

The evolution of emigration at range borders has, however, not received much

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[1] This chapter has been published as: A. Kubisch, T. Hovestadt & H. J. Poethke (2010) On the elasticity of range limits during periods of expansion. Ecology 91 : 3094–3099.

attention from the side of theoreticians and ecological modelers (but see Gros *et al.*, 2006; Dytham, 2009). In a review of MacArthur's (1972) pioneering book about geographical ecology, Holt (2003) concluded, that in stable source-sink systems dispersal should be selectively disadvantageous, as a consequence of the potential fitness loss of individuals migrating mainly from source to sink populations. He argued that in such systems the source populations will have a population density less than one because of the outflow of emigrants and hence future fitness expectations for philopatric inhabitants are higher. As individuals in sink populations have a lower fitness and more dispersers emigrate from source patches than from sink habitats, the majority of migrants will move downwards in a fitness gradient. This leads to strong selection against emigration. Holt thus concluded that a species' range could shrink after the initial expansion due to selection disfavoring dispersal once (all) new suitable habitats have been colonized.

In most theoretical studies the authors do not distinguish between the effects of different types of gradients for range expansion and specifically the relevance of Holt's prediction. Gradients modelled either affected reproduction (Travis *et al.*, 2005; Brooker *et al.*, 2007; Rowell, 2009), patch size (Bahn *et al.*, 2006) or the individuals' survival probability (Antonovics *et al.*, 2006; Armsworth & Roughgarden, 2008). However, in a recent study, Dytham (2009) systematically explored selection on dispersal distance along a variety of gradient types e.g. in growth and death rate, distance dependent dispersal costs and patch size, with a focus on equilibrium conditions. He showed, that the emergent dispersal distances at range margins strongly depend on the conditions that lead to the formation of the species' ranges. Scenarios, in which the spatio-temporal variance increases along the gradient, e.g. reduction in patch size or increased habitat turnover, lead to the evolution of longer dispersal distances in the range border zone than in the core area. In contrast a gradient in dispersal costs favors lower dispersiveness at the margin than in the core. However, Dytham did not investigate the phenomenon predicted by Holt, i.e. the shrinking of ranges after initial expansion caused by selection for reduced dispersal at range margins. We expect to observe such 'elastic range boundaries' mostly in gradients, where the benefits of dispersal are distinctly larger during expansion than after establishment. These should be gradients that do not greatly affect the variance and/or extinction probability of populations once they are established. This should especially hold for a gradient in dispersal mortality (e.g. habitat fragmentation). In contrast, conditions favoring high dispersal in the margin should not lead to a decrease in emigration probability at the stable range margin and hence we expect no or just slight elasticity of the range border for these cases.

In this study, we thus more thoroughly address the conditions under which range contraction (after initial expansion) might be observed. To investigate the phenomenon we perform individual-based simulations of a spatially explicit metapopulation along four kinds of environmental gradients: (*i*) declining patch capacity, (*ii*) declining per capita growth rate, (*iii*) increasing dispersal mortality and (*iv*) increasing probability of externally enforced local extinction.

2.2 The Model

The individual-based simulations we use are applicable to annual organisms with discrete reproduction phases. Similar population models were used e.g. by Travis *et al.* (1999); Gros *et al.* (2006) or Kun & Scheuring (2006). The simulated world is a rectangular lattice, consisting of 100 stripes (x-dimension) of 50 patches each (y-dimension), i.e. a total of 5000 habitat patches. Every patch is characterized by specific environmental conditions affecting reproduction, habitat quality and inter-patch dispersal mortality. Each individual is characterized by its sex, its affiliation with a specific patch (i), and by two alleles at one locus that determine the density-independent probability to emigrate. The generation cycle is supposed to be discrete, so every individual has only once in its life - before mating and reproduction - the opportunity to disperse (details below). Local population dynamics are density-dependent according to the discrete time model developed by Hassell (1975). Every female gives, after mating with one randomly chosen male in the same patch, birth to Λ offspring, where Λ is a Poisson distributed number with patch- and time-specific mean $\overline{\Lambda}_{i,t}$. For each generation $\overline{\Lambda}_{i,t}$ is drawn itself from a log-normal distribution with mean λ and standard deviation σ. The latter determines the magnitude of environmental fluctuations, i.e. annual fluctuations in growth conditions. According to Hassell's model the newborn individuals survive with a certain probability (s), calculated as

$$s = \frac{1}{1 + a \cdot N_{i,t}}, \tag{2.1a}$$

$$\textit{with} \quad a = \frac{\lambda - 1}{K_i} \tag{2.1b}$$

$N_{i,t}$ represents population size in patch i at time t, and K_i = habitat capacity of patch i. After all individuals mature, they emigrate with their individual dispersal propensity d, which is calculated as the arithmetic mean of its two alleles at the dispersal locus. One of these alleles is inherited from each of its parent. Alleles can mutate with a probability of 0.001. In case of mutation allele values are changed by adding a random number drawn from a Gaussian distribution with mean zero and standard deviation 0.2. At the beginning of simulations, the individuals' alleles were initialized as random numbers from a uniform distribution between 0.05 and 0.15. We assume nearest neighbor dispersal, i.e. the destination patch is randomly chosen among the eight habitat patches, that surround the natal one. However, we assume a certain dispersal cost, i.e. an emigrant dies with probability μ_i. At the end of each generation we implemented the occurrence of environmental catastrophes, i.e. the populations in every patch go extinct with probability ε_i, independent of the actual population size.

Environmental gradients are applied linearly in space, starting with favorable conditions that allow the species' survival and reproduction (see standard values below). Along the x-direction of the metapopulation grid one parameter (either K_i, λ_i, ε_i or μ_i) changes linearly from standard conditions ($K_i = 100, \lambda_i = 4, \varepsilon_i = 0.05, \mu_i = 0.2$) to conditions that do not allow the persistence of populations ($K_i = 1, \lambda_i = 0, \varepsilon_i = 0.5, \mu_i = 1$). The magnitude of environmental fluctuations σ was set to 0.5 for all simulations. Such values have already been succesfully fitted to empirical data of natural insect populations (e.g. Nowicki *et al.*, 2009) and were used in other theoretical studies as well (e.g. Travis *et al.*, 1999; Poethke & Hovestadt, 2002).

To simulate range expansion only the patch stripe with the most favourable conditions at $x = 1$ was initially occupied with individuals. During the next 5000 generations, the species was allowed to expand its range. We defined the range border as the stripe containing the most forward occupied patch. Data from the five most forward patch stripes behind the range border were pooled and analysed to gain values for the mean emigration probability at the margin during the simulations (see inset in Fig. 2.1). To calculate the fraction of emigrants, the number of emigrating individuals was determined at the range border each generation and divided by the total population size before dispersal. For each parameter combination simulations were repeated 20 times each.

All graphics were generated using the R language for statistical computing, version 2.9.2 (R Development Core Team, 2009).

2.3 Results

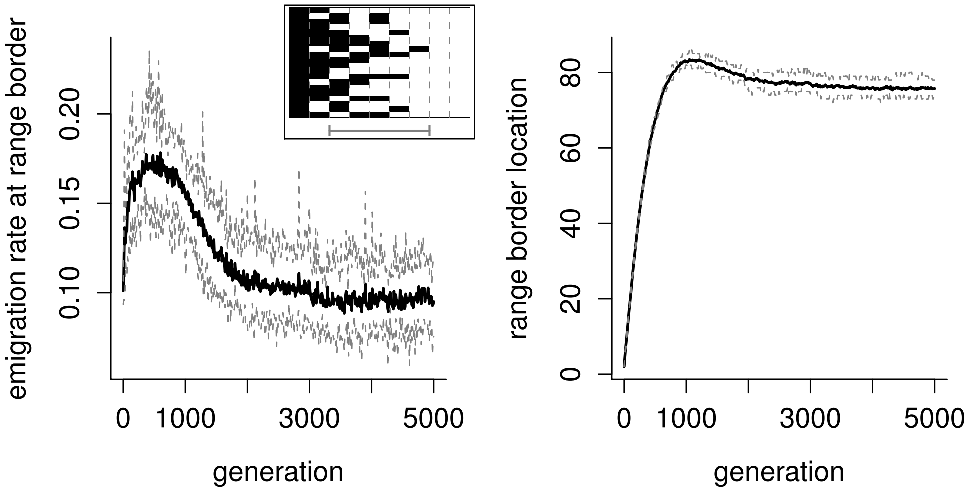

Figure 2.1: Change in mean emigration rate at the range border (left panel) and range border position in the μ-gradient (right panel) over time. Shown are the results of 20 replications, with black lines indicating the mean and grey lines the 5% - and 95% - quantiles. The schematic inlet in the left plot shows the occupancy of patches at the edge of the metapopulation's range. The grey bar indicates the zone, over which emigration rates were averaged, i.e. all patches in the y-dimension of the last five stripes of the gradient counted from the most forward occupied patch. The probability to disperse increases rapidly at the expanding wave front, showing it's maximum at approx. generation 1100, when the metapopulation achieved its maximum range. After settling into a static distribution selection leads to a decrease in emigration rate, resulting in a contraction of the range.

For all types of gradients the mean emigration probability increased during the phase of range expansion. The left panel of Fig. 2.1 shows the increase in emigration probability at the range border over time for the dispersal mortality gradient: values increase from about 0.09 at the beginning to a maximum of approximately 0.17 during invasion. Yet once the expanding front reached the areas of high dispersal mortality, emigration probability reduced again. It can be seen, that in parallel with this decrease in dispersal the range of the species contracts. The final range was formed at a position in the gradient, where dispersal mortality was 0.81. In the other gradients the range stabilized at the following values: $K = 14, \lambda = 1.13, \varepsilon = 0.33$.

In Fig. 2.2 we show the evolution of emigration rates plotted against the range border location only for the ten outermost patch stripes behind the maximum possible range. In the gradient of dispersal mortality (left top panel) emigration rates during range expansion were higher than in the range core, but fell below core values once the maximum range expansion was reached. The emigration

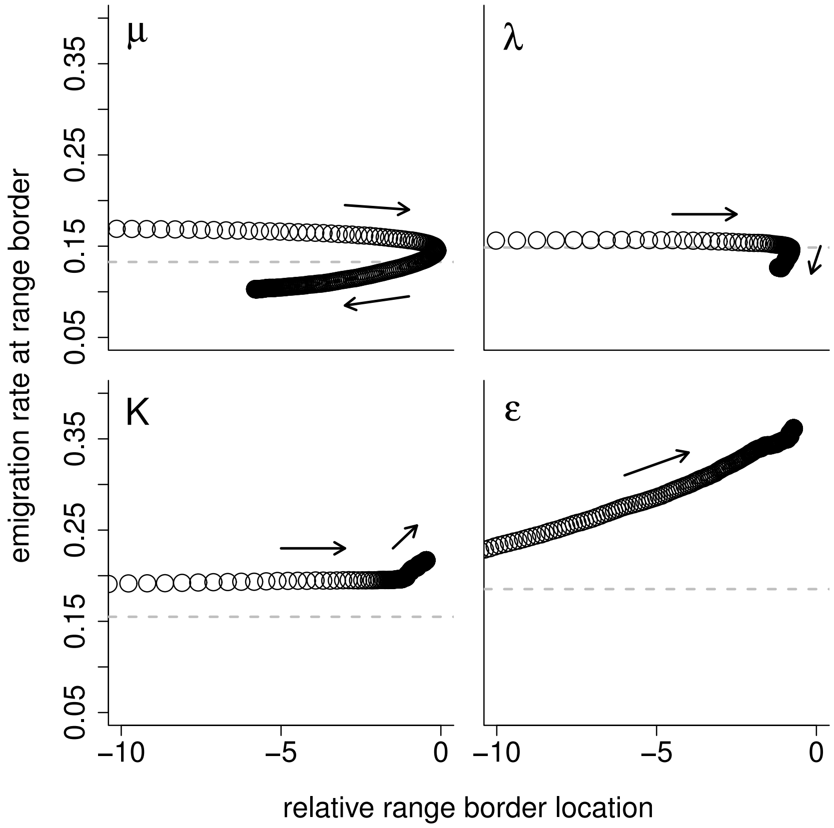

Figure 2.2: Emerging emigration probabilities in the range border zone (see inlet in Fig. 2.1) plotted against the range border location for all four gradients. The spatial location is set to zero for the maximum measured range for each case of gradient. Arrows indicate the direction of progression in time; data are plotted every 10 generations. Grey lines denote the mean emigration rate measured in the range core at the end of the simulations. The data shown are the average of 20 replicates for each scenario. To smooth the line, a moving average with a window of 50 data points was calculated.

rates in the growth rate gradient (right top panel) also decreased after range settlement, but the effect on the range border location is rather low. Again, during range expansion the emigration rate at the range border exceeded that in the core habitat, but fell below it once the expansion stalled. For the gradient in patch capacity and especially for the extinction rate gradient migration rates continued to increase over the whole simulation time (two bottom panels). We did not observe a contraction of the range for either scenario. In both cases the emigration rates at the expanding wave front exceeded those in the range core.

2.4 Discussion

We have shown that Holt's prediction about range contraction following an initial phase of expansion only holds under special circumstances. In a gradient of dispersal costs the range indeed showed strong elasticity. A growth rate gradient led to a similar, but less pronounced effect. On the other hand in simulations with gradients of patch size or extinction rate range contractions did not emerge at all, instead an ongoing increase in range size. We trace the difference across the four scenarios to the fact that in the former two (μ and λ-gradient) emigration rates evolve to lower levels at the margin compared to the core region once the range expansion is over. In the latter two, however, dispersal at the margin is maintained at higher levels, even after the expansion has stalled. We thus conclude that a decline in emigration is the precondition for the phenomenon of elastic range borders, caused by a decrease in the recolonization probability of extinct patches (as described e.g. by Holt *et al.*, 2005; Oborny *et al.*, 2009).

In the dispersal mortality and the growth rate gradient dispersal initially is highly beneficial due to the colonization of empty sites. Once established, however, populations persist well in these scenarios. After range expansion there are thus only few chances to colonize empty patches, consequently the dispersal benefit declines when the expansion phase is over and selection increasingly acts against high emigration. In comparison, in the gradient of growth rate extinctions caused by demographic stochasticity are more likely to happen than in the μ-gradient, leading to a higher patch turnover. Hence, dispersal remains more favorable and this in turn weakens the elasticity effect.

For the gradients in patch size and extinction rate the opposite is true. Both gradients lead to an increase in patch turnover due to the extinction of local populations, hence increasing the benefits of dispersal due to bet-hedging (distribution of risk; Philippi & Seger 1989; Ronce 2007). In the K-gradient this is caused by the declining patch capacity that introduces strong demographic stochasticity (Hanski & Gilpin, 1997).

The emigration rates in the K-gradient increased much more slowly than in the other case. This can be explained by a lack of mutants, necessary for fast evolution, as total population sizes simply become very small at the range margin. This is not the case in the ε-gradient. Although patches went extinct every three to four years near the final range border region (ε ca. 0.33), inhabitants of newly colonized patches have a high fitness and much offspring, leading to enough mutants to allow rapid evolution for dispersiveness.

To test the robustness of our results we ran additional simulations with different standard values for habitat capacity K (except for the K-gradient). We found that range size increases initially with patch size, yet that the effect levels of at a patch capacity of 100, where demographic stochasticity plays a little role for patch extinction. Additionally, for smaller values of K, elasticity was lower than for larger patches. Small patches specifically suffer from an elevated demographic extinction risk leading to a reduction in range size as other conditions get harsher. However, frequent extinction due to demographic stochasticity introduces an added benefit to dispersal (like externally driven extinction risk) and hence favours the maintenance of high emigration probabilities. This does not change much after the expansion phase is over and we thus observed a rather minor reduction in emigration in scenarios with low K values. As the range border elasticity directly depends on the difference between dispersal rate during range expansion and after stabilization, the range contracted less.

In our study we used nearest neighbour dispersal in a grid-based model. However, Dytham (2009) did not observe a strong effect on the evolving mean dispersal distance along various habitat gradients tested, except for a gradient that directly affected the distance specific costs of dispersal. Distances emerging would usually lead to nearest neighbour dispersal (see Bartoń *et al.*, 2009). We thus assume that simulations with evolving dispersal kernels would not fundamentally alter the conclusion we draw in this manuscript.

Range contractions are hard to detect in field studies (Thomas *et al.*, 2006) and are even harder to explain once they are found (Channell & Lomolino, 2000). However, as we showed it is possible that some of these range contractions might not be caused by temporal changes in the environment, but occur in the aftermath of historical range expansions, at least in gradients that favour lower emigration rates at the range margin than in the core area. Yet in nature, gradients are unlikely to occur independent from each other. Especially a habitat fragmentation gradient (represented by μ in our study) will frequently coincide with a decline in patch size / patch quality, what might blur the effect of the fragmentation on dispersal evolution. Nonetheless we expect the phenomenon of elastic ranges to occur in nature with increasing frequency in light of the ongoing climatic change that promotes expansion of northern range boundaries. Recent studies showed, that the changing climate is expected to have strong influences on species' range shifts, leading to an increase in invading species (Parmesan, 2006).

This study highlights the importance of investigating non-equilibrial situations in range formation processes. To be able to gain better predictions of species' future distributions in time and space and improve conservation strategies we need to focus research also on transient states, as most geographic ranges are unlikely to be in equilibrium.

CHAPTER 3

Density-dependent dispersal expands species' ranges[1]

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3.1 Introduction

Understanding the processes, which lead to the formation of a species' geographical range is of central interest in the light of shifting environmental conditions caused by global climate change or invasive species (Dukes & Mooney, 1999; Holt & Keitt, 2005; Anderson *et al.*, 2009; Walther *et al.*, 2009). This is especially true for the development of reasonable conservation management strategies (Phillips *et al.*, 2008; Tobin *et al.*, 2009).

Resulting range shifts are the outcome of interactions among habitat characterestics, demographics and dispersal. The latter is a key process in such shifts because it allows the colonization of empty, but suitable habitat patches. An important component of dispersal is emigration, which may involve behavioral

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[1] This chapter has been published as: A. Kubisch, H. J. Poethke & T. Hovestadt (2011) Density-dependent dispersal and the formation of range borders. Ecography 34 : 1002–1008.

decisions of individuals. It is well known that many species use information on patch quality for their decision to leave a patch or not (Enfjäll & Leimar, 2005; Ronce, 2007; Armsworth & Roughgarden, 2008). Especially density-dependent emigration has been investigated empirically (Conradt *et al.*, 2000; Enfjäll & Leimar, 2005; Matthysen, 2005) as well as theoretically (Travis *et al.*, 1999; Metz & Gyllenberg, 2001; Poethke & Hovestadt, 2002; Enfjäll & Leimar, 2009). Yet, there is however little knowledge about the possible influences of density-dependent emigration on the formation of species' ranges (but see Travis *et al.*, 2009).The intention of this study is to fill this gap. Specifically, we will compare the effect of density-independent and density-dependent emigration in populations exposed to an Allee effect.

Allee effects, i.e. reduced growth rates at low population densities, have long been underestimated in their importance for metapopulation dynamics, but are evident in many empirical studies (Kramer *et al.*, 2009; Courchamp *et al.*, 2010). In recent years, an increasing proportion of theoretical investigations focused on the impacts of Allee effects on biogeographical patterns (e.g. Travis & Dytham, 2002; Dennis, 2002; Kanarek & Webb, 2010). Until now it is still unclear, to what extent Allee effects may shape species' ranges and influence their position in space (but see Keitt *et al.*, 2001; Cabral & Schurr, 2010).

Allee effects have two major influences on metapopulation dynamics and hence range formation: (1) established populations can go extinct more easily if they are reduced to low population densities by adverse environmental conditions and (2) Allee effects impede the colonization of empty habitat patches.

We expect that density-dependent emigration may affect both of these consequences: firstly, it should reduce the risk of extinction as population densities less frequently fall to such low levels that an Allee effect could influence the population's growth rate (Hovestadt & Poethke, 2006); secondly, it might increase the chance of colonization by overcoming the Allee effect, because at low population densities no further emigration is expected.

Variability in population densities across space and time has been shown to intensify selection favoring dispersal, as the chance increases to migrate from high-density into low-density patches (Cadet *et al.*, 2003; Poethke *et al.*, 2007). These effects might have strong influences on the range formation of species and will increase in their importance in the future. Usually the effect of climate change is described as an increase in annual mean temperature. However, an increasing number of authors suggest that the temporal variability of climatic conditions will increase as well, leading to a higher frequency of extreme climatic events (reviewed by Jentsch *et al.*, 2007). This in turn will result in a higher spatial variability of population densities and hence should increase selection for dispersal (Poethke & Hovestadt, 2002). We thus predict that the higher temporal stochasticity occurring during climate change will have considerable consequences for shifts of species' range borders along gradients.

Gradients in environmental conditions that ultimately prevent a species from further range expansion can be categorized according to their effect on growth rate (as modeled by Travis *et al.*, 2005; Brooker *et al.*, 2007), patch size (Bahn *et al.*, 2006), extinction risk (Holt & Keitt, 2000; Oborny *et al.*, 2009), or patch connectivity (Virgos, 2001; Körner, 2007; Gastner *et al.*, 2009). Clearly, certain changes in environmental attributes could have several such effects. For example, a gradient in habitat fragmentation typically affects connectivity and patch size. In this study, we are approaching this by implementing a gradient in dispersal mortality, which results in degrading connectivity along space. Such a reduction in connectivity is especially interesting, as it directly leads to a decrease in colonization probability, allowing extinction rates to exceed colonization rates and impede a further range expansion of the metapopulation.

In this paper we use well established individual-based simulation approaches to address a number of questions: (1) How does a gradient in dispersal mortality affect the establishment of a species' range limits, (2) how is the position of the range border affected by the emigration strategy (density-independent vs. density-dependent) and a strong Allee effect and (3) how might increased environmental stochasticity, as it is predicted to accompany climate change, effect range formation for the given scenarios.

3.2 The Model

3.2.1 Landscape and individuals

Here we use an individual-based model with discrete generations (for similar systems see e.g. Travis *et al.*, 1999; Poethke & Hovestadt, 2002; Kun & Scheuring, 2006; Kubisch *et al.*, 2010). The simulated world is spatially explicit, consisting of 100 columns (x-dimension) of 50 patches each (y-dimension), providing a total of 5000 habitat patches. Each column of patches is characterized by a specific value μ_x, characterizing the dispersal mortality of emigrating individuals. This reflects the connectivity of patches in that region, i.e. habitat fragmentation. Gradients in patch size, per capita growth rate and extinction rate have been tested as well; these results are qualitatively described in the discussion.
Each individual carries different traits, i.e. its sex, its affiliation with a spe-

cific patch i and two alleles at a single diploid locus that encode the dispersal probability (either density-independent or density-dependent, see below).

3.2.2 Local population dynamics and Allee effect

Local population dynamics follow the discrete-time model of density-dependent growth provided by Hassell (1975). We extended this model by the implementation of a relative Allee effect, i.e. the effect depends on population density in relation to the patch's carrying capacity (see eq. 3.1c). Every female mates with one randomly chosen male. If no males are present no reproduction is possible. Afterwards every female gives birth to Λ offspring, where Λ is a random number drawn from a Poisson distribution with patch- and time-specific mean $\overline{\Lambda_{i,t}}$. For each patch and generation $\overline{\Lambda_{i,t}}$ is drawn itself from a log-normal distribution with mean λ and standard deviation σ. The parameter σ simulates environmental stochasticity, which we assume to be spatially correlated with a radius of one single patch. At the end of each generation every patch may go extinct with probability ε, independent of the current size of the population; ε thus represents the probability of external catastrophes. This ensures extinction and colonization processes necessary for the formation of a range border after initialization (see below).

Newborn individuals survive with a certain density-dependent probability ($s_{i,t}$):

$$s_{i,t} = \frac{b}{1 + a \cdot N_{i,t}}, \tag{3.1a}$$

$$\textit{with} \quad a = \frac{\lambda - 1}{K_i}, \tag{3.1b}$$

$$b = \frac{(N_{i,t}/K)^2}{(N_{i,t}/K)^2 + \alpha^2} \tag{3.1c}$$

with $N_{i,t}$ representing population size N in patch i at generation t and K_i being the carrying capacity. The parameter α describes the strength of the Allee effect. We assume a sigmoid increase in survival probability with the number of inhabitants in a patch (see eq. 3.1c). Individuals in a population at density $\frac{N_{i,t}}{K_i} = \alpha$ will thus have a decrease in their survival of 50 % and so the population will have a decrease in growth rate of 50 % as well.

For standard values of the model parameters see table 3.1.

Any offspring inherits one randomly chosen allele (that determines the probability to disperse) from each of its parents to allow for recombination. The alleles may mutate to form new alleles with a probability of $m = 10^{-3}$ by adding a Gaussian distributed random number with mean 0 and a standard deviation of 0.2. The dispersal alleles were initialized with a uniform distribution between 0 and 0.2 for density-independent and between 0.8 and 1 for density-dependent emigration, both leading to approximately similar dispersal rates. Other start values were tested, but did not influence the outcome of the simulations.

3.2.3 Dispersal

After all individuals mature they emigrate with a certain emigration probability d, calculated differently for the two used scenarios: (1) for density-independent emigration (DIE), d is calculated as the arithmetic mean of the individual's two alleles a_1 and a_2:

$$d = \frac{a_1 + a_2}{2} \tag{3.2}$$

(2) for density-dependent emigration (DDE), the calculation of d follows the dispersal model provided by Poethke & Hovestadt (2002), i.e. no emigration at population densities below the dispersal threshold C_{th} and a nonlinear increase in emigration propensity for densities above this threshold:

$$d = \begin{cases} 0 & \text{for} \quad \frac{N_{p,t}}{K} \leq C_{th} \\ 1 - \frac{C_{th} \cdot K}{N_{p,t}} & \text{for} \quad \frac{N_{p,t}}{K} > C_{th} \end{cases} \tag{3.3}$$

with C_{th} being the individual's threshold density, calculated as in eq. 3.2. Alternative models for density-dependent dispersal have also been suggested (e.g. Travis *et al.*, 1999; Metz & Gyllenberg, 2001; Kun & Scheuring, 2006). However, Hovestadt *et al.* (2010) compare different approaches and demonstrate that models derived from first principles (e.g. Metz & Gyllenberg, 2001; Poethke & Hovestadt, 2002) are most appropriate to describe the relation between density and emigration rate. However, the model by Metz & Gyllenberg (2001) applies to populations with continuous reproduction while that by Poethke & Hovestadt (2002) has been developed for non-overlapping generations and hence is the model of choice for our simulations.

We assume nearest neighbor dispersal, i.e. the destination patch of an emigrating individual is randomly chosen from the eight habitat patches that surround the natal patch. We assume the world to form a tube along the x-

Table 3.1: Model parameters with meanings and standard values.

parameter	meaning	value
K	habitat capacity	100
λ	per capita growth rate	2
ε	extinction rate	0.05
$\Delta_{\mu,x}$	slope of the gradient	0.008
σ	environmental stochasticity	$0-1$
α	Allee effect strength	$0, 0.05$

dimension, i.e. if an individual leaves the world in the y-dimension on one side it will enter on the opposite side. Individuals crossing the world's limits along the x-dimension are reflected into the other direction. To test the robustness of our results for different border conditions, we also implemented absorbing world limits, i.e. all individuals crossing the limits die. However, this had hardly any influence on the model outcome.

As mentioned above, dispersal incurs a cost μ calculated from the mortality values μ_x assigned to the column of the natal and the destination patch. As we assume an environmental gradient, these column-specific values for the dispersal mortality change linearly along the x-dimension of the world, measuring from $\mu_1 = 0.2$ to a maximum of $\mu_{100} = 1$. This can be translated into a steepness $\Delta_{\mu,x}$, i.e. a change of μ per x, of 0.008.

3.2.4 Simulation experiments

In order to simulate the effects of increasing spatio-temporal variability in patch quality caused by global change, we tested several values for the magnitude of environmental stochasticity $\sigma \in \{0, 0.25, 0.5, 0.75, 1\}$. We compared different outcomes of the model for all parameter combinations of the values for σ and two different values for α, describing either no ($\alpha = 0$) or a strong Allee effect ($\alpha = 0.05$). For all parameter combinations the simulations were repeated 20 times each.

Table 3.1 summarizes all relevant model parameters, their meanings and the standard values used for the simulations.

All patches are initially occupied by K individuals. During the next 2000 generations the populations were allowed to adapt their dispersal traits to the local conditions until an equilibrium state was achieved and a stable range border had been formed. We determined the range border as the column that contained the outmost populated habitat patches. We tested additional range border criteria based on patch occupancy, but did not find any qualitative changes of our results. Emigration rates at range margins were calculated as the fraction of individuals emigrating from the five patch stripes immediately preceding the range border. We calculated range core emigration rates in the same way, but for the five habitat columns of the simulated landscape that lay behind the first two columns. These first two columns were omitted from the analysis to avoid taking edge effects into account.

To compare the frequency distributions of immigrants, we additionally counted the numbers of immigrants per patch and generation for patches either lying at the range margin or in the core over the last 50 generations. For testing the robustness of our results we conducted a sensitivity analysis.

3.3 Results

Our simulation results clearly demonstrate the importance of conditional dispersal for the formation of range borders. Density-dependent emigration consistently leads to wider ranges than density-independent dispersal (Fig. 3.1, 3.2).

More interestingly increasing environmental stochasticity has a negative effect on the range under DIE, whilst we observed range border expansion into areas with even higher dispersal mortality under DDE when σ increases (Fig. 3.2 a).

An Allee effect leads to a range contraction for both dispersal strategies, but the difference in the range size becomes increasingly pronounced with growing environmental stochasticity, i.e. under DDE the influence of an Allee effect is comparatively weaker (Fig. 3.2 b).

As predicted by Cadet *et al.* (2003), in the range core both dispersal strategies show higher emigration probabilities with increasing environmental stochasticity. We observe lower emigration probabilities at the range margins than in the core (Fig. 3.3). In scenarios with DDE, higher environmental stochasticity correlates with a decrease in the emigration probabilities at the range border (Fig. 3.3 c). However, for DIE they are increased (Fig. 3.3 a). An Allee effect slightly decreases emigration at the border for both dispersal strategies, but does not qualitatively change the patterns (Fig. 3.3 b, d).

Without environmental stochasticity ($\sigma = 0$) both, the range core and the range margin, show little differences in the distribution of immigrant numbers per patch and generation between the two dispersal strategies, either with or without an Allee effect (Fig. 3.4, top row). However, slightly more events with large numbers of immigrants can be seen for DDE than for DIE. In scenarios

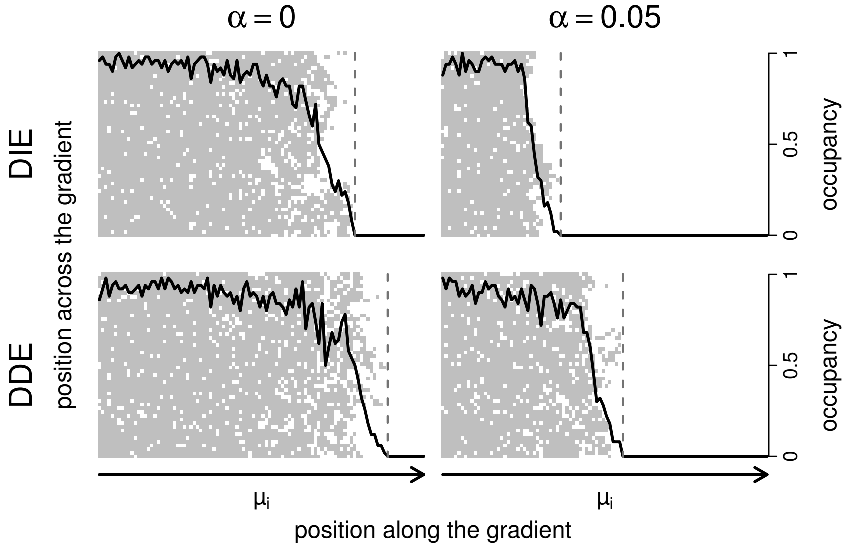

Figure 3.1: Snapshots of the metapopulation's occupancy at the end of in each case one exemplary simulation run (in equilibrium) for density-independent (DIE; top row) and density-dependent emigration (DDE; bottom row) and the two different intensities of the Allee effect (left column: $\alpha = 0$; right column: $\alpha = 0.05$). Grey squares denote occupied patches, white space unoccupied habitat. The gradient in dispersal mortality (μ) proceeds from left to right in each simulation (see x-axis). The black lines show the mean occupancy for every column of patches perpendicular to the gradient. The dashed lines indicate the location of the range border defined as the patch column containing the outmost occupied patches. $\sigma = 0.5$.

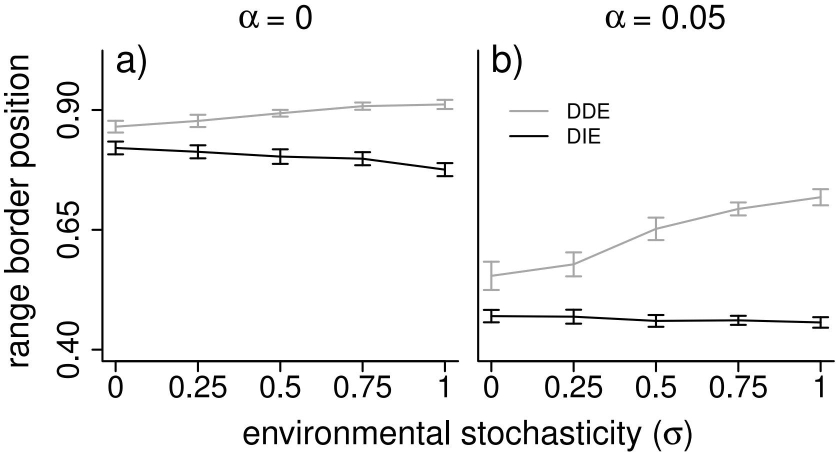

Figure 3.2: Influences of environmental stochasticity (σ) and Allee effect on the location of the range border, i.e. the value for dispersal mortality μ_x, at which the range border is on average formed. a) Strong Allee effect ($\alpha = 0$), b) weak Allee effect ($\alpha = 0.05$). Black lines: density-independent emigration, Grey lines: density-dependent emigration. Shown are the arithmetic means of 20 replicates. Error bars denote standard deviation.

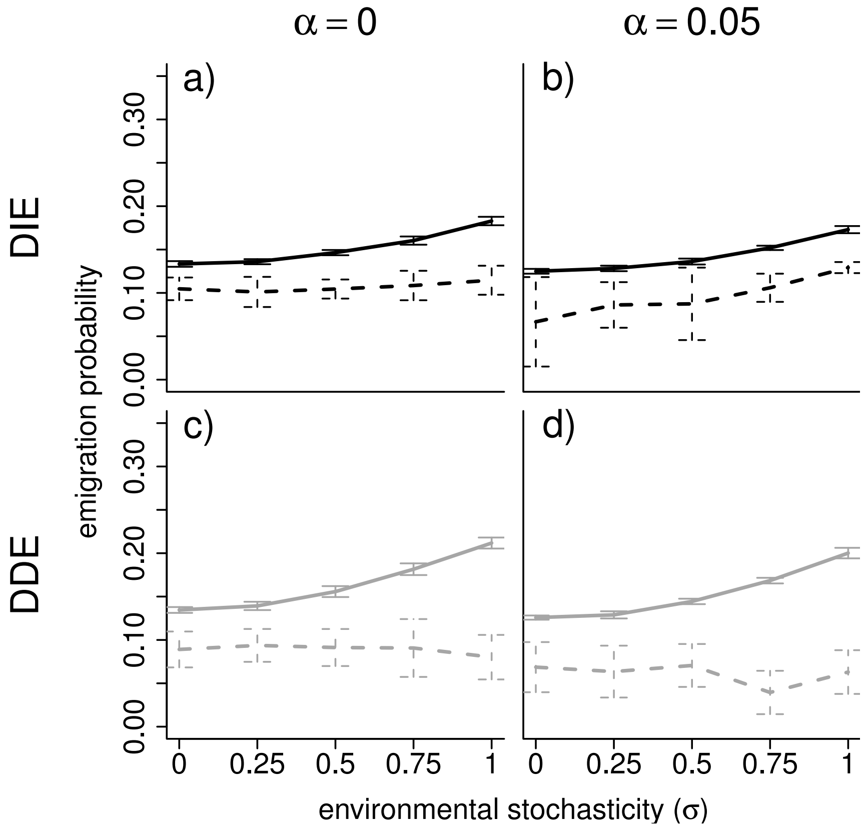

Figure 3.3: Emerging emigration probabilities at the range margin (dashed lines) and in the range core (solid lines) for all simulated scenarios. DIE: density-independent emigration, DDE: density-dependent emigration. For our definitions of core and margin see model description. Shown are the arithmetic means of 20 replicates. Error bars denote standard deviation.

with high environmental stochasticity ($\sigma = 1$; Fig. 3.4, bottom row), there are strong differences between the strategies. The distribution of immigrant numbers for DIE is slightly wider in the core, but does not change much at the range margin compared to the simulations with $\sigma = 0$. However, the frequency distribution becomes strongly leptokurtic for DDE in the core and also in the margin area, especially under a strong Allee effect: there is a high frequency of patches receiving no immigrants, but there are also many events with very high numbers of immigrants.

The sensitivity analysis showed that under all tested model parameter values the wider ranges for DDE were robust to changing conditions (see appendix).

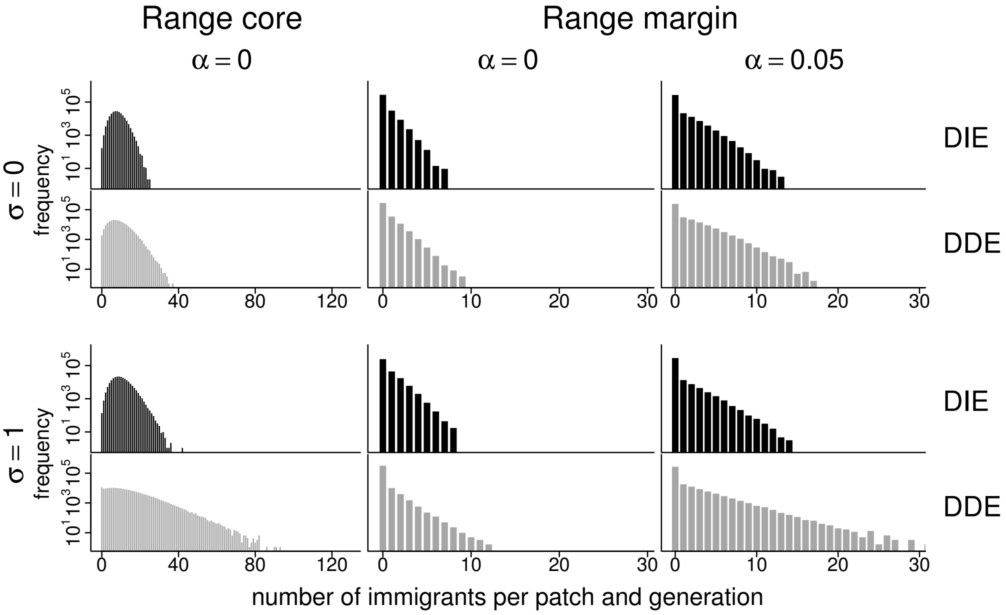

Figure 3.4: Influences of environmental stochasticity (top row: $\sigma = 0$; bottom row: $\sigma = 1$) and Allee effect strength (left and middle column: $\alpha = 0$; right column: $\alpha = 0.05$) on the frequency distributions of the number of immigrants per patch and generation arriving in the range core (left column) and range margin area (middle and right column). Grey bars: density-dependent emigration, Black bars: density-independent emigration. There is no qualitative difference in the histograms for the range core when implementing the Allee effect, hence the corresponding results are not shown. The histograms are based on one representative simulation run. Note that the y-axis is scaled logarithmic and the different classes (x-axis) for range core and margin.

3.4 Discussion

The simulation experiments above presented demonstrate that accounting for the use of environmental information in dispersal decisions can have substantial consequences for the prediction of ranges established by species living in spatial fragmentation gradients. In all simulated scenarios, density-dependent emigration (DDE) leads to wider ranges than density-independent emigration (DIE).

It is well known that increasing environmental and demographic stochasticity, and hence, variation in population density between habitat patches, leads to selection for dispersal (Cadet *et al.*, 2003; Poethke *et al.*, 2003, 2007). In our results (Fig. 3.3) the emerging emigration rates in the range core increased accordingly with higher σ. This is due to the effect that more individuals will emigrate from high-density habitat patches that have a greater chance of arriving in less densely populated patches. However, the evolving emigration probabilities were higher in the range core than at the margin as a consequence of local adaptation to the dispersal mortality gradient, which is similar to the results of Dytham (2009).

More significantly, the simulations predict a range expansion with increasing σ under DDE, but range contraction under DIE. One reason for this difference can be found in the extinction risk, which is different between both dispersal strategies (Hovestadt & Poethke, 2006): at low population densities, which are especially likely to occur at the range margin, individuals may still leave a sparsely populated patch under DIE, while this does not happen under DDE. At low densities populations have a higher chance of survival and growth in scenarios with DDE than with DIE. This is particularly relevant in the case of strong environmental fluctuations, as these induce great variability in population sizes. Furthermore we found strong differences in the distributions of the number of immigrants per patch and generation for the two dispersal strategies (Fig. 3.4). These show that – especially in the range core – higher values of σ lead to only a slightly higher variance in the distribution of immigrants under DIE (just because of the higher variance in population sizes), but to a strongly leptokurtic distribution under DDE. This is due to the fact that there are much more 'bad' years without any emigrants because of low population densities below the dispersal threshold. In addition, years of exceptional favourability may see events of 'mass dispersal' where emigration can occur in very high numbers. Hence an increase in σ leads to an increase in the number of events with many emigrants especially under DDE; this allows successful patch colonization even in regions with high dispersal mortality. This in turn allows for the formation of a wider range as less colonization events and less dispersal are necessary to maintain the borders of the metapopulation.

An Allee effect has negative effects on range expansion in both dispersal scenarios but obviously more in the DIE scenario. This is due to the fact that the Allee effect increases the extinction risk once a population has fallen to a low density. As already discussed this is more likely to happen if environmental stochasticity σ is high and more likely to occur under DIE than under DDE. Yet, more importantly, Allee effects influence the colonization probability of empty patches. In marginal populations with high dispersal mortality, immigrant numbers are generally low and successful colonizations occur rarely under the presence of an Allee effect. As a consequence, the benefit of dispersal is lower in these scenarios (Travis & Dytham, 2002): if an individual is unlikely to successfully reproduce in an empty patch then it is better for it to stay at home. In all scenarios, contractions in range sizes and lower emigration rates were observed, when we incorporated the Allee effect (Fig. 3.3, right panel). As the number of surviving emigrants decreases along the gradient, the Allee threshold can only be overcome closer to the range core, where dispersal mortality is relatively low.

More specifically an Allee effect leads to a sigmoid (and, as such, non-linear) increase of colonization probability with increasing numbers of immigrants in stochastic environments (Taylor & Hastings, 2005). As marginal populations are only sparsely populated, this means that every additional immigrant leads to a disproportional increase in the probability of successful colonization (at low densities the progression of the colonization probability curve is exponential). This explains the increased discrepancy between range size for the two dispersal scenarios: the 'boosted' dispersal events caused by the leptokurtic distribution of the number of immigrants in the DDE-scenario can result in rare events of mass immigration that allow for the colonization of patches despite of the Allee effect.

From an emigrating individual's perspective the more skewed distribution emerging in the DDE scenario implies that it will very probably be among a large group of immigrants upon arrival. This increases its probability to reproduce successfully in the new patch. For example in the simulations with $\sigma = 1$ and $\alpha = 0.05$ approximately 16.3% of the immigrants in the DDE scneario arrived in groups of more than five and hence had a good chance to overcome the Allee effect. In contrast less than 5.2% of the immigrants were in such large groups under DIE.

As the Allee effect fundamentally leads to a contraction of the range, the range border falls into regions where more emigrants disperse successfully. Consequently the differences in the distributions of immigrants among DIE and DDE remain thus more pronounced. Hence, the colonization success is lower for DDE with an Allee effect than without, but increasingly higher than for DIE. The difference in the geographic range between species following either the non-informed (DIE) or the informed dispersal strategy (DDE) becomes larger.

Gradients in habitat fragmentation are common in nature (Körner, 2007) and the effects of fragmentation have been well studied theoretically (e.g. Gastner *et al.*, 2009) and empirically (Virgos, 2001; Coulon *et al.*, 2010; Magle *et al.*, 2010). In this study we focussed on patch connectivity representing one aspect of habitat fragmentation. However, one can expect that increasing habitat fragmentation has further consequences, like lower growth rates, smaller patches or a higher frequency of environmental catastrophes. We ran additional simulations with gradients in these parameters (i.e. K , λ and ε) and the results showed that scenarios with DDE led to wider ranges than those with DIE in ll environmental settings. However, the influence of the Allee effect on the difference between the two tested emigration strategies was smaller in gradients of K and λ, as in these scenarios the absolute population sizes were lower at the range margin and hence the diverging distributions of migrants were less pronounced. The gradient in extinction rate (ε) nearly showed the same results like the one in dispersal mortality, as population sizes are still high at the range border.

Some authors have shown that Allee effects are expected to have strong influences on the geometry of species ranges. Keitt *et al.* (2001) as well as Gastner *et al.* (2010) conclude that the lower colonization probability caused by an Allee effect leads to a sharpened edge of the range and thus may stabilize dynamically fluctuating ranges. In this study we did not investigate range border sharpness, but we would hypothesize that density-dependent emigration could counteract this effect, as it increases the colonization efficiency of species. However, whether this assumption holds, is in need of further research.

The role of information-based dispersal, especially density-dependent emigration, for the formation of range borders has rarely been investigated before. We show that an Allee effect can lead to smaller ranges, but that it also increases the importance of acquiring and using current information about population density for dispersal decisions for an individual and range formation. Additionally, we show that increasing environmental stochasticity, as it is predicted to increase during climate change, might even lead to range expansions, if populations follow a density-dependent dispersal strategy. As individuals of many species are likely to incorporate information about their natal patch into their movement decisions (Matthysen, 2005; Ronce, 2007), these findings suggest that the appropriate choice of the dispersal model is of crucial importance when modeling the future distribution of species under global change.

3.5 Appendix

3.5.1 Sensivity Analysis

We tested the robustness of the results presented in this paper by conducting a sensitivity analysis for all relevant model parameters. We changed every parameter by ± 20 % and analyzed the difference between range border positions for DDE and DIE (i.e. position in the DIE - scenario subtracted from the position in the case of DDE) for $\sigma = 1$ and either with or without an Allee effect. Sensitivity was calculated as the relative change of the named difference divided by

Table 3.2: Results of the sensitivity analysis for a change of ± 20 % of the relevant model parameters. Given is the difference in range border positions (DDE-DIE), i.e. positive values indicate wider ranges in the case of density-dependent emigration. The numbers in brackets denote the sensitivity of this difference for the given parameter. For a decrease of λ and $\alpha = 0.05$ the populations in the DIE scenario went extinct. σ=1. For detailed information see text.

		$\alpha = 0$	$\alpha = 0.05$
K	$+$	$0.13\ (-0.29)$	$0.25\ (-0.16)$
	$-$	$0.18\ (-1.76)$	$0.28\ (-0.47)$
λ	$+$	$0.10\ (-1.18)$	$0.23\ (-0.47)$
	$-$	$0.20\ (-2.35)$	$-$
ε	$+$	$0.14\ (\pm 0)$	$0.46\ (+4.06)$
	$-$	$0.13\ (+0.29)$	$0.21\ (+0.90)$
$\Delta_{\mu,x}$	$+$	$0.13\ (-0.04)$	$0.26\ (+0.08)$
	$-$	$0.13\ (+0.29)$	$0.26\ (\pm 0)$

the relative change of the according parameter. The results are shown in Table 3.2.

The results show that for all tested scenarios DDE led to wider ranges than DIE. However, the influences of the parameters were different. Habitat capacity proved to have a negative influence on the difference between range border positions (all sensitivity values are negative). This can be explained by the fact that higher population sizes lower the risk of demographic extinction and hence the benefit of DDE is less pronounced. Higher values for λ weaken the effect, too. As higher growth rates lead to faster population growth after colonization even in the case of DIE the demographic extinction risk is lowered and as a consequence the difference between the dispersal strategies is getting smaller.

Because of the negative impact of these two parameters we hypothesized that extreme values might lead to the range difference vanishing. Therefore we also tested the sensitivity of the effect to such values by changing K to 1000 and found that the range difference was nearly not detectable without an Allee effect but was still present with an Allee effect included. We conclude that increasing K to large values aligns the predicted range borders for the two strategies. As the Allee effect in our model depends on the population density, the influence of big values for K is comparably small. Changing λ to 5 only led to a slightly positive difference between the range border positions for the two strategies, hence an alignment of the range borders occurs for large values of λ, too.

A higher extinction risk ε clearly has a positive influence on the difference between range border positions. It increases the importance of colonizations and hence stresses the benefits of DDE.

The steepness of the gradient has hardly any influence on the results and is thus not of further importance.

Chapter 4

Elasticity revisited: climate change and conditional dispersal[1]

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4.1 Introduction

Climate change is expected to crucially influence the ranges of species and is in the focus of many recent biogeographical studies (Opdam & Wascher, 2004; Brooker *et al.*, 2007; Anderson *et al.*, 2009; Mustin *et al.*, 2009; Atkins & Travis, 2010). Mostly climate change is associated with a gradual temporal change in mean climatic conditions ('trends' in terms of Jentsch *et al.*, 2007). However, there is consensus emerging that increasing variance of conditions, not the change in mean conditions, will be of outstanding importance for distributional patterns of species (Easterling *et al.*, 2000; Jentsch *et al.*, 2007, 2009; Van De Pol

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[1] This chapter has been published as: A. Kubisch & H. J. Poethke (2011) Range formation in a world with increasing climatic variance. Evolutionary Ecology Research 13 : 159–169.

et al., 2010). How such an increase in environmental fluctuations will ultimately influence the formation or change of range borders and their position in heterogeneous landscapes remains an unsolved question (but see Battisti *et al.*, 2006; Hochkirch & Damerau, 2009; Zimmermann *et al.*, 2009).
Many species exist in spatially structured populations (e.g. due to habitat fragmentation; Hanski & Gilpin, 1997). Stable range borders in such landscapes are formed, where colonization of empty patches equals extinction of occupied ones along gradients that affect survival (Holt & Keitt, 2000; Guo *et al.*, 2005; Holt & Keitt, 2005). Consequently it is either a too high risk of extinction or a lack of colonizers that impedes further spread of populations and dispersal is a key mechanism that affects both of these processes. If an increase in environmental fluctuations leads to an increase in local extinctions, it is assumed that increasing variance of conditions will lead to a contraction of range borders. However, dispersal is known to play a pivotal role for range formation processes and for the prediction of potential range shifts (Holt, 2003; Best *et al.*, 2007; Huntley *et al.*, 2010) and it is known that environmental fluctuations strongly influence dispersal rates (Cadet *et al.*, 2003; Poethke *et al.*, 2007). Thus, increasing dispersal may counteract the effect of increased extinction.

It is clear that conditional dispersal (i.e. the use of information about the current environment) has strong consequences on the persistence and structure of metapopulations (Ims & Hjermann, 2001; Ronce, 2007; Armsworth, 2009). It has also been found empirically that conspecific population density is an important cue that triggers emigration (Conradt *et al.*, 2000; Enfjäll & Leimar, 2005). We recently investigated the consequences of such density-dependent dispersal for range border formation (Kubisch *et al.*, 2011), and found that conditional emigration leads to wider ranges than unconditional dispersal. This effect becomes more pronounced with increasing environmental stochasticity caused by a shift in the distribution of emigrant numbers. When individuals of a population emigrate positively density-dependent, they will more likely not emigrate in ‘bad’ years with low population densities and leave their patches in higher numbers in ‘good’ years when growth rates are high and competition in their natal patches is increased. However, we did not investigate a further increase of this variance, especially in comparison between different gradients, which finally lead to range border formation.

In the present study we want to further these investigations by focusing on the effect of climatic variance on dispersal evolution and range border formation in different kinds of gradients. We used a spatially explicit (i.e., grid based) individual-based modeling approach to simulate a metapopulation of a species with discrete (non-overlapping) generations living in a spatial gradient of environmental conditions. We applied gradients in either patch isolation by increasing dispersal mortality, patch quality by decreasing per capita growth rate, or patch size by decreasing habitat capacity.

Our objective was to test whether (i) higher environmental stochasticity leads to a consistent contraction of the range and (ii) how the resulting patterns depend on the landscape (i.e., type of gradient) and its influences on range border formation.

4.2 The Model

4.2.1 Landscape

We used an individual-based model of a metapopulation with discrete generations that has been used similarly in other theoretical studies as well (Travis *et al.*, 1999; Kun & Scheuring, 2006; Kubisch *et al.*, 2010). The model world was spatially explicit and consisted of $x \cdot y = 100 \cdot 50 = 5,000$ habitat patches arranged on a rectangular grid. To investigate range border formation, we implemented habitat gradients by assigning to each column of patches (i.e. all patches that share one x-coordinate) certain values for important habitat characteristics and let these values change in x-direction. We modeled an isolation gradient by increasing dispersal mortality from $\mu_{x=1} = 0.2$ to $\mu_{x=100} = 1$ (i.e., at the 'good' end of the gradient, 20 % of all migrants survive, whereas at the other end of the gradient, no migrants survive). To simulate a patch quality gradient, per capita growth rate (see below) was decreased from $\lambda_{x=1} = 4$ to $\lambda_{x=100} = 0$. Patch size (regarding the number of individuals that can reproduce successfully in the patch due to, e.g., the amount of resources) was varied by decreasing local carrying capacity from $K_{x=1} = 100$ to $K_{x=100} = 1$. In every scenario conditions at the 'bad' end of the gradient did not allow further spread of the metapopulation. For an illustration of the model world and range border formation see Fig. 4.1.

4.2.2 Individuals

Each individual was characterized by its sex, its specific position in the model world and two alleles (c_1, c_2) at one locus, which determined its threshold density for emigration (see below). When an individual was born, its alleles were randomly inherited one from each parent and they mutated with a certain mutation probability ($m = 10^{-4}$) by adding a random number drawn from a normal

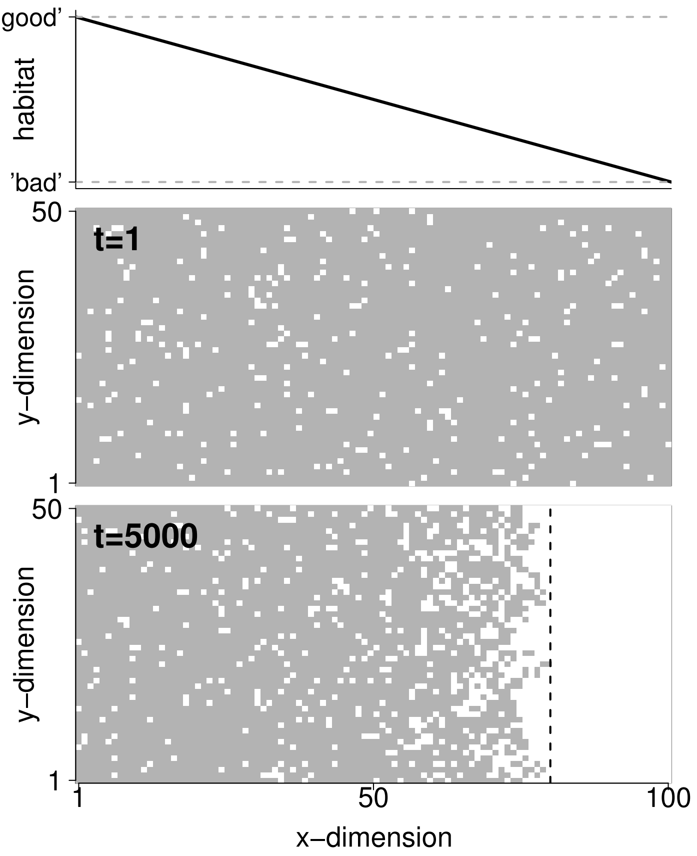

Figure 4.1: Illustration of the simulation model. The upper panel shows schematically the progression of the habitat gradients, leading from 'good' conditions ($\mu_{x=1} = 0$, $\lambda_{x=1} = 4$, $K_{x=1} = 100$, respectively) at the left end to 'bad' conditions not allowing metapopulation survival ($\mu_{x=100} = 1$, $\lambda_{x=100} = 0$, $K_{x=100} = 1$, respectively) at the right end of the world. The middle panel shows a snapshot of a simulation (dispersal mortality gradient, $\sigma = 0$) after one generation. Grey squares denote occupied habitat patches, white space unoccupied habitat. At the end of the simulations (after 5000 generations) a stable range border was formed (lower panel; the dashed line shows the absolute range border position R)

distribution with mean 0 and standard deviation 0.2.

4.2.3 Population dynamics

Local population dynamics in each patch followed the discrete time model provided by (Hassell, 1975). After mating with one male chosen at random from the local population every female gave birth to Λ offspring. Λ was a random number drawn from a Poisson distribution with patch- and time specific mean $\bar{\Lambda}_{x,y,t}$. To simulate climatic fluctuations the latter was drawn from a log-normal distribution with column-specific mean λ_x ($\lambda = 2$, if not considered as gradient) and standard deviation σ. Hence, σ determined the magnitude of environmental stochasticity expressed in temporally fluctuating growth rates. Lastly, the survival probability for newborn individuals (s) was finally calculated by

$$s = \frac{1}{1 + a \cdot N_{x,y,t}} \tag{4.1}$$

with $a = \frac{\lambda_x - 1}{K_x}$, $N_{x,y,t}$ being population size N in the patch at coordinates x, y at generation t and K_x representing the carrying capacity of all habitat patches in column x of the world ($K = 100$ if not considered as gradient).

4.2.4 Dispersal

Offspring, which survived density-dependent population regulation, could emigrate from their natal patch. Emigration probability (d) was calculated according to the density-dependent dispersal model by Poethke & Hovestadt (2002):

$$d = \begin{cases} 0 & \text{for} \quad \frac{N_{x,y,t}}{K_x} \leq C_{th} \\ 1 - \frac{C_{th} \cdot K_x}{N_{x,y,t}} & \text{for} \quad \frac{N_{x,y,t}}{K_x} > C_{th} \end{cases} \tag{4.2}$$

where C_{th} represents the genetically determined threshold population density of every individual, calculated as the arithmetic mean of its two dispersal alleles ($C_{th} = (c_1 + c_2)/2$). Hence we assumed no emigration at all, if the population density lay below that threshold and an asymptotic increase towards one in emigration probability, if it lay above. This model is based on the marginal value theorem and has been shown to be most appropriate for modeling density-dependent dispersal in metapopulations with discrete generations (Hovestadt *et al.*, 2010).

Emigrating individuals died during the migration process with a certain dispersal mortality μ_x ($\mu_x = 0.2$ if not considered as gradient). We assumed nearest neighbor dispersal, i.e. the target patch for an emigrating individual was randomly drawn from the eight patches that surrounded its natal habitat. To avoid edge effects we modeled periodic boundary conditions in the y-direction, meaning that an individual that crossed the world's limits along the y-direction re-encountered it on the opposite side. When it would have left the world in the x-direction it was reflected back from the edge. The three columns of patches at the very ends of the world have hence been left out of the analysis. We tested absorbing border conditions as well, but these had no qualitative influence on our results.

4.2.5 Environmental catastrophes

Severe environmental fluctuations were modeled by implementing a random probability of local patch extinctions ($\varepsilon = 0.05$). This increased the rate of extinction and colonization events and facilitated range border formation after initialization of the simulations (see below).

4.2.6 Simulation experiments

We initialized the simulation experiments with all patches being occupied by K ($K = 100$ for all patches) individuals each (equal fractions of males and females). Alleles coding the dispersal behavior of individuals (c_1, c_2) were initialized as uniform random numbers drawn from the interval ($0 \leq c_i \leq 1$). Simulations were run for 5000 generations which proved to be enough time for evolutionary adaptation to local conditions and hence the emergence of stable range borders. The position of the range border did not change for most scenarios after approximately 1000 generations.

Environmental stochasticity (σ) was varied in the range of $\sigma \in 0, 0.5, 1, 1.5, 2, 2.5, 3$. For each parameter set we ran 25 independent replicate simulations, which have proven to be enough to determine the central tendency of the simulations (see standard deviations of the results in Fig. 4.2, 4.3).
We defined the range border R as that column (in x-direction) of patches along the gradient, where the outermost populated patch was located. Additional range border definitions (i.e., determining the range border as the column, where patch occupancy fell below 0.5 or 0.05, respectively) have been tested, but had no qualitative influence on the results. The results of single simulation runs were the mean range border locations of the last 500 generations of simulation.

We also measured the relative range expansion r_{exp}, which we defined as the change of the range border location along the gradient for a certain increase of environmental stochasticity. Therefore we divided the relative change of range border location Δ_R/R by the change in environmental stochasticity Δ_σ:

$$r_{exp} = \frac{\Delta_R/R}{\Delta_\sigma} \tag{4.3}$$

Positive values of r_{exp} indicate an expansion of range size for increasing environmental stochasticity, whereas negative values denote a contraction of the range if σ was increased the given amount.

4.3 Results and Discussion

4.3.1 Range border formation in the different gradients

In general we see that high environmental stochasticity led to a strong contraction of the range for every simulated landscape (i.e., type of gradient; for the relative range border changes see Fig. 4.2, for the absolute locations see Fig. 4.3a-c). However, in the dispersal mortality gradient lower degrees of environmental fluctuations ($\sigma < 1$) led to a wider range (Fig. 4.2a, 4.3a). A slight expansion of the range area was also evident for the growth rate gradient for low values of stochasticity, but to a considerably lesser degree (for $\sigma < 0.5$; Fig. 4.2b, 4.3b). In the gradient of carrying capacity no wider ranges emerged, only range contraction was found for increasing environmental fluctuations (Fig. 4.2c, 4.3c).

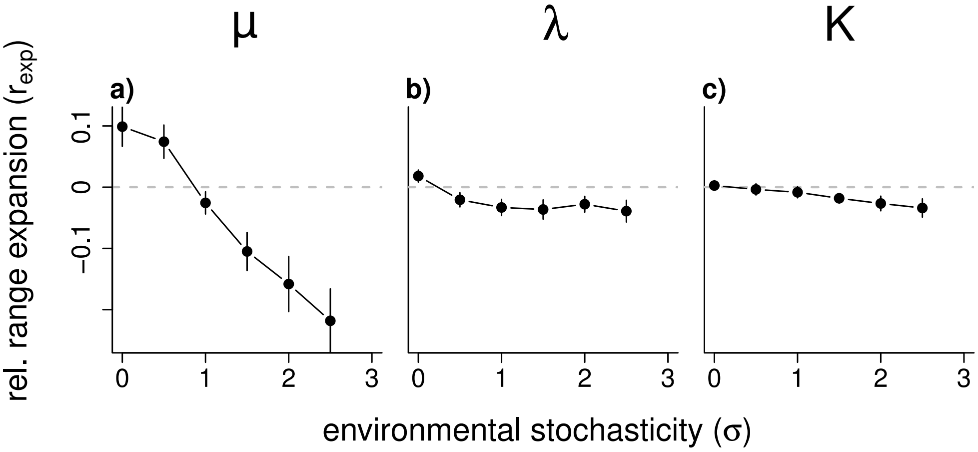

Figure 4.2: Effects of increasing environmental stochasticity (σ) on range border formation in gradients of (a) dispersal mortality (μ_x), (b) per capita growth rate (λ_x) and (c) habitat capacity (K). The range border was defined as the x-position of the outermost populated patch and the relative range expansion (r_{exp}) describes the change of the border location for increasing σ at a given value by 0.5. Positive values indicate range expansion for higher σ, negative values range contraction. Shown are the means of 25 replicate simulations, error bars denote standard deviation.

The different reactions of the populations in these different types of gradients to an increase in environmental stochasticity may be explained by factors limiting distribution of a species in concert with the specific effects of density-dependent dispersal (Hovestadt *et al.*, 2010). Results show that in all tested gradients the mean emigration rate in the range margin area (defined as the five columns of patches immediately preceding the absolute range border) increased with increasing environmental stochasticity, though the effect was more pronounced in gradients of habitat quality (λ) and patch size (K) (Fig. 4.3d-f).

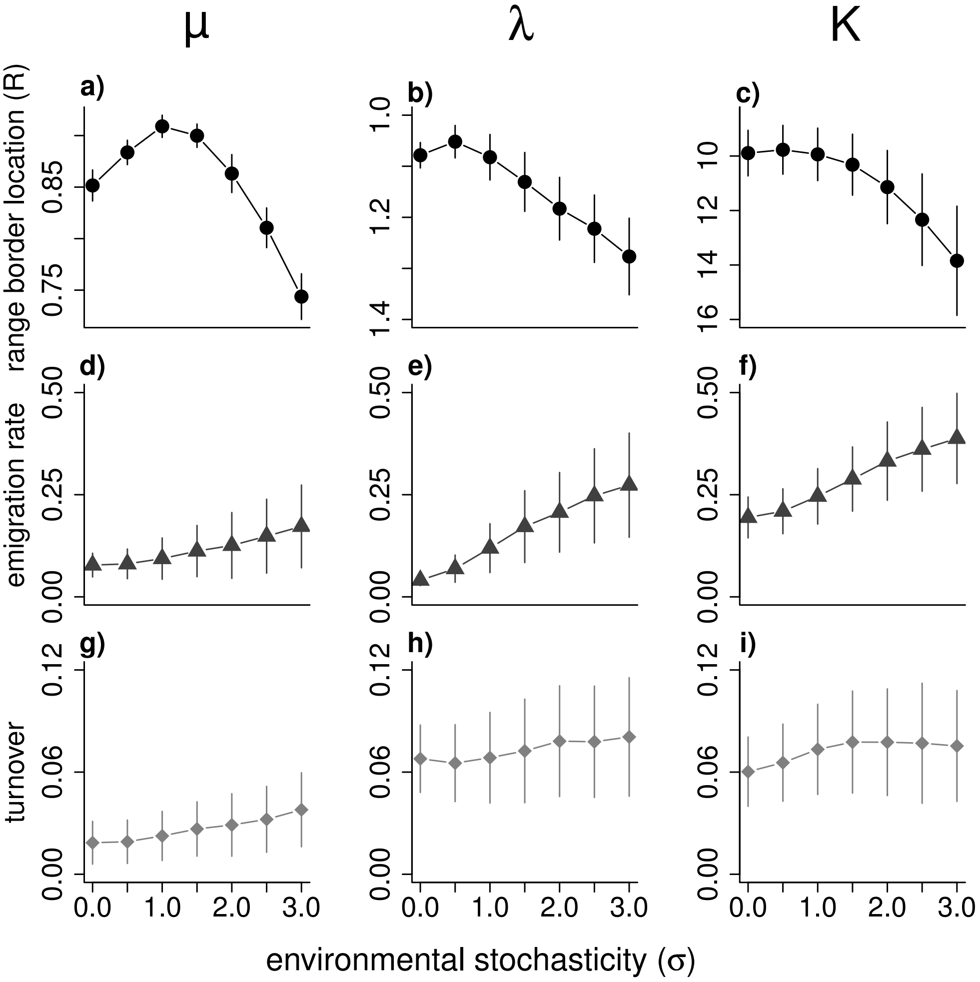

Figure 4.3: Effects of increasing environmental stochasticity (σ) on the absolute range border location (R, a - c), emigration rates in the range margin area (d - f) as well as turnover rate at the range margin (g - i) for gradients in dispersal mortality (μ), per capita growth rate (λ) and carrying capacity (K). Range border was defined as that position in the gradient (expressed in the gradual changing parameter value) at which the outermost patch was populated (see Fig. 4.1). The range margin area contained the five columns preceding the range border (including the column of the range border). Shown are the arithmetic means of 25 replications, error bars denote standard deviation.

It is well known that increasing environmental variation leads to selection for higher emigration rates, because it increases spatio-temporal variability of population density and thus the probability of dispersing from high to low density habitats (Cadet *et al.*, 2003; Poethke *et al.*, 2007). Especially in the case of density-dependent dispersal increased temporal fluctuations of the environment result in a more skewed distribution of emigrants (Hovestadt *et al.*, 2010; Kubisch *et al.*, 2011). In years with low growth rates population densities are low and few individuals emigrate. In good years with high rates of growth, population densities are high and mass emigrations may occur. Together with the increased dispersal rates at the range margin, the increased probability of mass emigration induced the described initial range expansion in the isolation (μ) and habitat quality (λ) gradient, because it increased colonization probability. In the dispersal mortality gradient it was the lack of colonizers which ultimately determined the limit of the range and hindered the populations from further spread.

In the habitat quality (λ) gradient low reproductive rates at the range border resulted in low mean population density. Particularly with density-dependent dispersal the low density patches at the range border produced fewer emigrants and suffered from an increased risk of extinction (compare the higher patch turnover, i.e. the relative number of patch extinctions and colonizations per time step, between this scenario and the dispersal mortality gradient in Fig. 4.3g,h). Thus, emigration rates were lower in this gradient than in the gradient of dispersal costs. In the habitat capacity gradient the range border was largely determined by the high demographic extinction risk in small patches (4.3i; Hanski & Gilpin, 1997), which can also be seen in the initially higher emigration rates (Fig. 4.3f). Further increasing variability in growth rates enhanced selection for dispersal, which resulted in an increase of patch recolonization, but it also increased the rate of patch extinction caused by increasing demographic stochasticity. Hence, no remarkable range expansion was observed in this scenario (Fig. 4.2c, 4.3c).

Poethke *et al.* (2003) pointed out the twofold effect of increasing environmental variation. They showed in their Fig. 2 that increasing environmental variance lowers the risk of extinction due to the rescue effect caused by selection for higher emigration rates. However, increasing stochasticity also proved to heighten the population extinction risk. The same effect occurred in our present study: in each of the simulated landscapes high environmental stochasticity strongly increased population-level extinction risk up to levels that could not be compensated by dispersal. Consequently the ranges contracted in every gradient and the range margin formed in areas nearer to the range core, where either dispersal mortality was lower, growth rates were higher or patches were bigger, all factors lowering the risk of extinction.

Our results clearly demonstrate that the effect of increased environmental stochasticity on the range of a species depends on the factors that limit its distribution so far and on the relative amount of environmental stochasticity already experienced at the range margin. When a further spread of the species is prevented by limited dispersal – either because high dispersal mortality selects against high emigration rates or because low spatio-temporal variability of population density (low environmental variance σ) does so – increased environmental variance may promote range expansion. These results support and help explain previous findings about expanding ranges after weather extremes (Battisti *et al.*, 2006; Hochkirch & Damerau, 2009). However, when environmental fluctuations are already high and population sizes at the range margin are stochastic due to fluctuations in growth rate or small individual numbers a further increase will dominantly result in increased extinction risk leading to a retraction of the range border into regions with more favorable conditions.

4.3.2 Range border formation under non-equilibrium conditions

So far we have not considered the time scale of climate change. We have focused solely on equilibrium conditions and assumed that the change of environmental conditions is much slower than the evolution of adapted dispersal rates. However, populations need time to adapt to changing conditions. To account for this we have run additional simulation experiments for the dispersal mortality gradient where we analyzed different temporal gradients (i.e. different values of the annual increase $\Delta_{\sigma,t}$ of environmental fluctuations σ, Fig. 4.4).

Results of this experiment suggest that for steep temporal gradients the initial positive range expansion was delayed in its occurrence and damped in its extent. This was caused by the fact that evolution needs time - both the occurrence of beneficial mutations as well as their spread in the population due to natural selection needed time that was missing in these scenarios. The faster environmental stochasticity increased (Fig. 4.4b; line types in Fig. 4.4a show the range border positions for the corresponding progressions of σ over time) the less that better-adapted dispersal phenotypes could occur by mutation and increase in frequency by selection in the time of increasing σ a certain amount. Hence the populations' ability to adapt to the new conditions was constrained and the effects of dispersal on the range border location were reduced. The time lag in the evolution of emigration rates persisted for further increasing values of environmental stochasticity. In this case even the contraction of the range was mitigated, as dispersal rates were still quite high and allowed for persistence of the populations at higher values of dispersal mortality (i.e. deeper in the gradient) than in the quasi-equilibrium case of the slowest climate change.

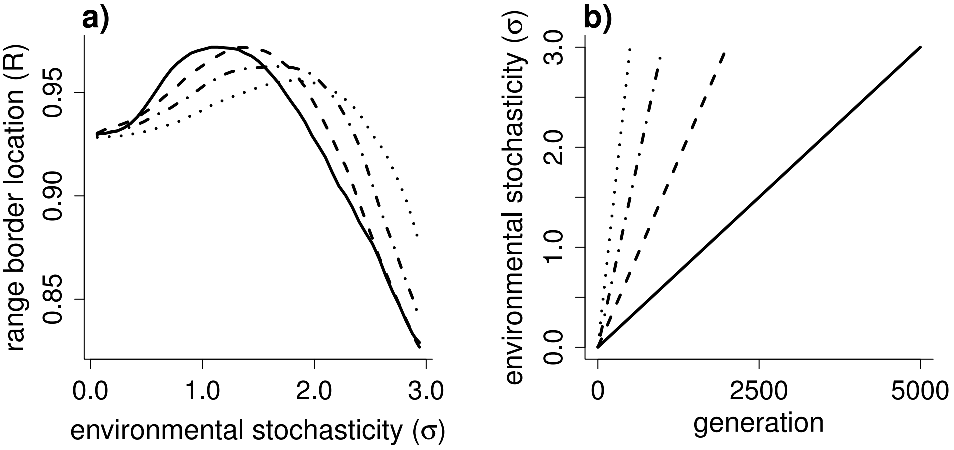

Figure 4.4: To test the influence of time on the shown results, we exploratory tested a temporal increase of environmental stochasticity during simulation time for the isolation gradient (dispersal mortality increasing along space). Shown are (a) the absolute range border position and (b) the corresponding temporal increase of environmental stochasticity (σ) over time. The number of time-steps for an increase of σ from 0 to 3 determined the speed of the change. Different line types denote the corresponding changes of σ over 5000 (solid), 2000 (dashed), 1000 (dot-dashed) and 500 (dotted) generations. Shown are the arithmetic means of 25 replications. To smooth the line a moving average with a width of 10 data points was applied.

Interestingly, the mean population density at the margin was hardly influenced by the rate of increase (not shown), because in years with low growth rates the higher extinction probability was counteracted by the characteristics of density-dependent emigration (i.e., no emigration occurring at low densities; Hovestadt & Poethke, 2006). Of course in the long run, adaptation would take place and the range would contract.

4.3.3 Conclusions

With the present study we show that increasing extreme environmental events (e.g., weather) can promote range expansion to a certain degree. However, this type of range expansion would be restricted to cases where the range border of a metapopulation is predominantly determined by decreased colonization rates of patches (i.e., when dispersal at the margin is disfavored). If, on the other hand, extinction risk at the range border is already high, either from the quality of the landscape (e.g., low patch quality or patch size) or by high environmental stochasticity, no range expansion is expected. Instead, the range would be expected to contract as the frequency of extreme events increases.

When accounting for non-equilibrium conditions, the speed of global change may determine the possibility of populations to adapt evolutionarily to the changing world. Hence the steepness of the temporal gradient has a strong influence on our findings. The faster the frequency of extreme events increases, the more delayed and less strong the range might react.

Our results underline the importance of understanding the factors that ultimately lead to the formation of range borders of species for the ability to draw appropriate predictions of future range shifts. The time scale of predicted changes also is of pivotal importance and should not be underestimated.

CHAPTER 5

Biotic interactions and the prediction of range shifts[1]

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5.1 Introduction

In the face of potential ecological and societal impacts of global climate change there is an increasing interest in forecasting future distributions of species, both in theory (Brooker *et al.*, 2007; Mustin *et al.*, 2009; Huntley *et al.*, 2010) and practice (Thomas, 2010; Jankowski *et al.*, 2010). Species will not only need to

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[1] This chapter is in revision as: A. Kubisch, T. Degen, T. Hovestadt & H. J. Poethke (in revision) Biotic interactions and the prediction of range shifts. Global Ecology and Biogeography

cope with a more or less gradual change in climatic conditions leading to shifts of certain climatic areas (Walther *et al.*, 2002) but possibly also with higher variance in climatic conditions (reviewed by Jentsch *et al.*, 2007).

It has been proposed that species distributions will change according to changing climatic conditions. Corresponding evidence was recently found for a mammal species in Europe, the bat *Pipistrellus nathusii*, having adapted its geographic range in accordance with changing climatic conditions (Lundy *et al.*, 2010). Walther *et al.* (2002) have reviewed further empirical evidence for climate-induced range shifts in several taxa. However, they did also conclude that the responses of species to the changing climatic conditions were strongly dependent on their dispersal abilities, as e.g. butterflies matched the changing climate much better than alpine plant species.

'Bioclimate envelope models' (BEMs; also referred to as species distribution models) have become standard tools to predict range shifts in response to environmental changes (Guisan & Zimmermann, 2000; Bakkenes *et al.*, 2002; Pearson *et al.*, 2002; Adams-Hosking *et al.*, 2011). These models are based on statistical correlations between current (or past) species distributions and certain habitat parameters, i.e. on the identification of a species niche. Based on the species specific niche and knowledge about future distributions of environmental conditions predictions of range shifts are inferred. However, BEMs have been criticized as too simplistic and for not taking into account several aspects that are likely to influence species' ranges (and their shift). Among these are the dispersal abilities of species, dispersal barriers and habitat fragmentation, the genetic variability of species and the potential for local adaptation, or the role of biotic interactions (Pearson & Dawson, 2003; Hampe, 2004; Dormann, 2007; Beale *et al.*, 2008; Lavergne *et al.*, 2010).

Efforts have been taken to improve predictive models (Jeltsch *et al.*, 2008; Thuiller *et al.*, 2008; Kearney & Porter, 2009) but to our knowledge it is still mostly ignored that the dispersal capacity and particularly the dispersal tendency of species is not a fixed trait but subject to potential evolutionary change. It has been shown that the dispersal behavior of species may quickly evolve in response to changed environmental conditions (Parmesan, 2006; Hochkirch & Damerau, 2009). Thus, it may be misleading to extrapolate from observed dispersal behavior under stable conditions to the dispersal tendency (evolving) under changing conditions (Lavergne *et al.*, 2010).

However, it is not only the dispersal tendency that may show a fast evolutionary response to global change. There is increasing evidence that evolution of many different traits can occur much more rapidly than expected, making the discrimination between 'ecological' and 'evolutionary time-scales' obsolete (Hairston *et al.*, 2005; Reusch & Wood, 2007). Rapid evolution may result in adaptation of populations to changing environmental conditions (Parmesan, 2006; Pearman *et al.*, 2008). Jump & Penuelas (2005) have reviewed studies investigating the genetic diversity of species and potential evolutionary responses of plant populations under climate change. They conclude that in fragmented habitats changing climatic conditions could overwhelm populations as they could not track suitable conditions by dispersing, thus increasing the importance of possible evolutionary adaptation to the new conditions. Another very important factor for the formation of range borders are interactions with other species (Case & Taper, 2000; Bridle & Vines, 2007) but such interactions are largely ignored in BEMs (Beale *et al.*, 2008).

We thus conclude that to fully understand the possible influence of climatic change on the range (shifts) of species we must necessarily take into account potential evolutionary processes and the interaction between species. Only models that include these processes will allow to predict, whether a species will mostly track its currently preferred climatic conditions (as assumed in BEMs), adapt locally, or simply go extinct as it has neither the dispersal capacity to follow its preferred range nor the genetic diversity to adapt. To investigate the key processes that determine the balance between these different reactions to changing environmental conditions, we have developed an individual-based metapopulation model of either one or two competing species living along a large-scale temperature gradient and exposed to gradual climatic change. In a set of different simulation scenarios we aim at assessing the influence of evolutionary processes on the validity of predictions based on bioclimate envelope approaches.

5.2 The Model

5.2.1 Landscape and individuals

We are using a spatially explicit individual-based metapopulation model of a sexually reproducing insect species with discrete generations. The model has already been successfully applied in theoretical studies (Travis *et al.*, 1999; Kubisch *et al.*, 2010; Fronhofer *et al.*, 2011) and fitted to empirical data (Poethke *et al.*, 1996; Amler *et al.*, 1999). The simulated landscape consists of 125 columns (x-dimension) of 50 patches each (y-dimension), i.e. 6250 habitat patches in total. Every column of patches is characterized by its specific abiotic habitat conditions τ_x. For the sake of simplicity τ_x will be interpreted as 'mean temperature' throughout this manuscript. However, it may represent any other environmental condition that is systematically influenced by global change. This mean local temperature will be used for the determination of local adaptation of individuals. To simulate a large-scale habitat gradient τ_x changed linearly from $\tau_{x=1} = 0$ to $\tau_{x=125} = 5$ along the x-dimension, i.e. by $\Delta_{\tau,x} = 0.04$ degrees when moving one step in x-direction.

Local populations (communities) are composed of individuals that are characterized by several traits: (1) the species it belongs to (in the two-species scenario), (2) its sex, (3) two alleles at one locus coding for the individual's emigration probability (see below), and (4) another two alleles at a locus coding for the individual's 'habitat preference', i.e. the environmental conditions (temperature τ) under which the individual survives best (see below).

5.2.2 Local population dynamics and survival of offspring

Local population dynamics follows the discrete time model of Beverton & Holt (1957). After mating with a randomly chosen male from the patch of residence every female gives birth to $2 \cdot \Lambda$ offspring. Subsequently all adults die, that is we simulate annual organisms. At each of the two loci (dispersal propensity and temperature preference) newborn individuals inherit one randomly chosen allele from each of its parents. During transition from one generation to the next an allele may mutate with a probability of $m = 10^{-4}$. Mutations are simulated by adding a random number drawn from a Gaussian distribution with mean 0 and standard deviation 0.2. In scenarios without evolutionary adaptation to environmental conditions only the dispersal alleles were allowed to mutate.

To allow for inter-individual variation in reproductive success individual offspring numbers Λ are drawn from a Poisson distribution with mean $\overline{\Lambda_{x,y,t}}$. Spatio-temporal variation in $\overline{\Lambda_{x,y,t}}$ allows to model spatial and temporal variation in environmental conditions. Thus $\overline{\Lambda_{x,y,t}}$ is drawn for each patch x, y and generation t from a log-normal distribution with mean λ and standard deviation σ. Throughout the simulations we assume a maximum net reproductive rate of $\lambda = 2$ and a strength of spatio-temporal environmental fluctuations of $\sigma = 0.5$. Newborn individuals survive to reproductive age with probability s, which depends on a density-dependent component s_1 due to competition and density-independent component s_2 related to local adaptation, i.e.

$$s = s_1 \cdot s_2 \tag{5.1a}$$

$$\textit{with} \quad s_1 = \frac{1}{1 + \frac{\lambda - 1}{K} \cdot \sum\limits_{i=1}^{2} N_{i,x,y,t}} \tag{5.1b}$$

$$s_2 = \exp\left(-\frac{1}{2} \cdot \left(\frac{\tau_{opt} - \tau_x}{\eta}\right)\right) \tag{5.1c}$$

As we assume symmetric competition for identical resources, density-dependent survival s_1 is determined by the sum of individuals of the two species $N_{1,x,y,t}$ and $N_{2,x,y,t}$. Density independent survival depends on adaptation to local conditions, i.e. on the difference between the genetically encoded optimal temperature τ_{opt} ($\tau_{opt} = \frac{l_{a,1}+l_{a,2}}{2}$, with $l_{a,1}$ and $l_{a,2}$ giving the 'values' of the two corresponding alles) of an individual and local temperature conditions τ_x. η describes the niche width or 'tolerance' of both species. Thus we assume different environmental niches for all individuals. However, this allows for our simple approach of niche evolution. The niche of the whole species must be seen as the cumulative result of all individual niches.

Using equation 5.1a we assume that density-dependent mortality $(1-s_1)$ acts before mortality due to maladaptation to local conditions $(1-s_2)$. It might also be reasonable to assume that the survival due to local adaptation of offspring is decreased in early phases of life, before density regulation through competition takes place. Hence we have also tested scenarios with local (mal)adaptation acting on the fecundity of females rather than on the survival probability of offspring. However, this did not qualitatively alter the results though the extinction risk of the metapopulation was slightly increased.

5.2.3 Dispersal

Surviving offspring may disperse. Individuals disperse with probability d that is determined by the two alleles ($l_{d,1}$,$l_{d,2}$) it carries at the dispersal locus ($d = \frac{l_{d,1}+l_{d,2}}{2}$). If an individual emigrates it will die with probability μ, which accounts for various costs that may be associated with dispersal in real populations, like fertility reduction or predation risk. We assume nearest-neighbor dispersal, i.e. successful dispersers settle in one of the eight surrounding habitat patches. To avoid edge effects along the gradient we wrap the landscape into a tube along the x-dimension. Hence, if an individual leaves the world in y-direction during dispersal, it will reenter the simulated world on the opposite side. However, if it leaves the world in the x-direction, it is lost from the simulation.

5.2.4 Simulation experiments

Simulations are initialized with a clear spatial separation of species. In the two-species scenario the colder half of the world (from $x = 1$ to $x = 62$) is exclusively occupied by the cold adapted species and the warmer half of the gradient (from $x = 63$ to $x = 125$) by the more warm adapted one. In the single-species scenarios we initialize simulations with the warm adapted species only. Its distribution is initially restricted to the warmer half of the gradient (from $x = 63$ to $x = 125$) while the colder half is kept free of individuals. At the beginning of simulations, dispersal alleles ($l_{d,i}$) are randomly drawn from the interval $0 < l_{d,i} < 1$. Local populations are initialized with optimally adapted individuals, i.e. preference alleles were initialized according to the local temperature τ_x.

Simulation experiments covered a time span of 3000 generations. To establish equilibrium conditions mean temperature τ_x in patches remained constant during the first 2000 generations. In the single species scenarios individuals were confined to stay in the warmer half of the gradient during this time. During the following 1000 generations global change is simulated by gradually increasing the temperature τ_x of every patch by one degree in total ($\Delta_{\tau,t} = 0.001$ degrees per generation). We also tested more rapid or slower changes in mean temperature but this did not change simulation results qualitatively. It is important to keep in mind that the numeral values of the temporal change are not comparable with real world predictions. The impact of climate change on the species in our simulations depends rather on the ratio between the temporal and the spatial variation in temperature.

To investigate the influence of habitat connectivity on range shift we vary dispersal mortality from $\mu = 0$ to $\mu = 1$ in 101 equidistant steps. We performed simulations for species with a narrow niche ($\eta = 0.1$) and those with a wide niche ($\eta = 0.5$), equivalent to a decrease of survival probability of about $\Delta_\mu = 0.08$ (for the narrow niche) and $\Delta_\mu = 0.003$ (for the wide niche) when dispersing one patch away from the optimal habitat, respectively. As shallower gradients would have qualitatively the same effect as wider niches, we did not vary the gradient's steepness.

Table 3.1 summarizes all relevant model parameters, their meanings and the standard values used for the simulations.

Table 5.1: Model parameters with meanings and standard values.

parameter	meaning	value
K	habitat capacity	100
λ	per capita growth rate	2
σ	environmental stochasticity	0.5
m	mutation rate	10^{-4}
$\Delta_{\tau,x}$	slope of the temperature gradient	0.04
μ	dispersal mortality	$0-1$
η	niche width	$0.1; 0.5$
$\Delta_{\tau,t}$	annual temperature increase	0.001

5.2.5 Analysis

At the end of the simulation we calculated the range border position of a species i as that position in x-direction, where the fraction of occupied patches (I) fell below $I = 0.05$. In the two-species scenario this value was estimated independently for each species and the arithmetic mean of the two border positions defined the range border between the two species. Alternative definitions (incidence below 0.5, 0.1, 0) did only marginally alter the results presented here. If species would exactly track the shifting temperature conditions (perfect envelope matching), the range border should follow changing temperature conditions and always lay in that landscape zone (in x-dimension) where temperature conditions are similar to those at the border before the onset of climate change (i.e. in generation 2000). We calculated the deviation (ϕ) between this predicted ($R_{pred,t}$) and the realized range border position ($R_{real,t}$) as:

$$\phi = \frac{R_{real,3000} - R_{pred,3000}}{R_{pred,3000} - R_{real,2000}} \tag{5.2}$$

Thus, for $\phi = 0$ the range shift ideally matched the prediction. For $\phi < 0$ it lacked behind the prediction and for $\phi > 0$ the range shifted even faster than predicted.

5.3 Results and Discussion

5.3.1 Single species systems without creation of new genotypes by mutation

To explore the dynamics of range borders in more detail we first restricted our simulation experiments to single-species systems. We initialized the simulations

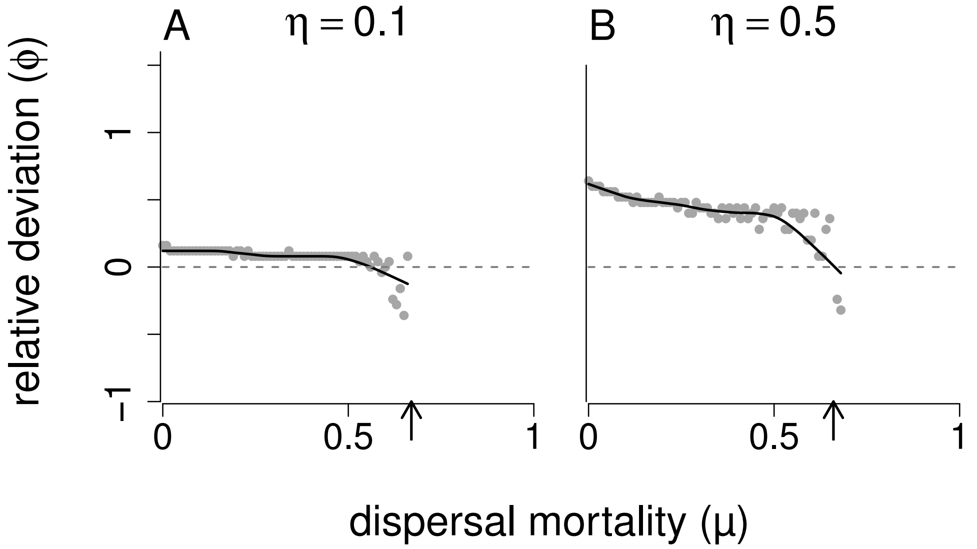

Figure 5.1: Influence of dispersal mortality on the response of a single-species system without evolutionary adaptation to temperature change. The x-axes show the relative deviation ϕ between predicted (see text) and realized range border at the end of the simulated period ($t = 3000$); positive values indicate that the range border lies in front, negative values that it lags behind the predicted border (for details see model section). Results of 101 simulation runs for different dispersal mortalities ($\mu = 0, 0.01, 0.02, \ldots 1.0$) with a) narrow niche width ($\eta = 0.1$) and b) wide niche width ($\eta = 0.5$). Arrows below the x-axis indicate the critical dispersal mortality, above which the system (ultimately) goes extinct (for details see model section); corresponding ϕ-values were thus omitted. Lines were fitted using the lowess-algorithm provided by Cleveland (1981).

with one species occupying (and until the onset of global temperature increase (generation 2000) restricted to) the warmer half of the world and kept the other half free of individuals. All cells were filled with individuals optimally adapted to local conditions. For further details see model section.

In a first set of simulations we did not allow mutations of the temperature trait while mutations at the dispersal locus are allowed. Thus, the spectrum of temperature traits remains restricted to those genotypes initially introduced into the population. These single species scenarios yield only two principle outcomes. With low dispersal mortality (μ) the species initially increases its range slightly (indicated by the small positive deviation from the predicted range) and then follows the predicted shift (Fig. 5.1). Alternatively, beyond a certain critical value for dispersal mortality ($\mu > 0.7$) the metapopulation completely collapses and the species goes extinct. The initial increase in range depends on niche width (η) and is small for a narrow niche (Fig. 5.1a) and larger in the wide niche scenario (Fig. 5.1b). This shift is due to the fact that the species is - for the first 2000 generations - restricted to a range of optimal habitat conditions, while -

due to their tolerance (niche width) - populations could persist also in certain non-optimal (but initially inaccessible) habitat further down the gradient. The moment this restriction is released (in generation 2001) these new habitats are quickly colonized. Apart from this artifact and as long as dispersal cost (μ) does allow sufficient dispersal rates, the range shift observed during the time span with climate change is indeed fully congruent with predictions from envelope models.

Certainly, this scenario of incomplete range filling is rather artificial, but it is necessary to understand the following scenarios and their implications. In our scenario after complete range filling the marginal populations are partially sink populations. Pagel & Schurr (2011) refer to this fact and conclude that BEMs tend to overestimate the ecological niches of species due to the accidental incorporation of sink habitats.

Without the creation of 'new' genotypes by mutation dispersal is the only possibility of populations to track the changing environmental conditions during climate change. As long as gene flow is sufficiently large, the population can in fact track changing conditions infinitely. Yet, if dispersal mortality (μ) becomes too high two reasons prevent tracking of optimal adequate conditions: First, high dispersal mortality eliminates a large fraction of dispersers and second,it selects against dispersal thus limiting the number of emigrants. Both factors combined ultimately prevent gene flow of adapted types at a rate large enough to track environmental change and hence average fitness decreases (maladaptation increases) until the whole metapopulation finally collapses (see Fig. A1 for metapopulation sizes). Note that this process takes some time depending on the strength of gene flow. In the long run we would thus expect that for all cases where the species was not able to track climate change anymore ($\phi < 0$) populations would ultimately collapse, creating a sharp transition between either complete envelope matching or complete extinction. The critical cost of dispersal (μ) that allows metapopulation survival is approximately identical for the narrow and the wide niche scenario.

In summary, in the single-species system without mutation the prediction of the climate envelope basically holds as long as dispersal remains sufficiently high; this will be the case as long as no strong dispersal barriers exist and costs of dispersal are not too high.

5.3.2 Single species systems with creation of new genotypes by mutation

Up to a certain dispersal risk the realized range shift in the single-species scenario described above matched the bioclimate envelope prediction, i.e. the species manages to track the change in environmental conditions by dispersal. So far we ignored the creation of new genotypes (resulting in better adapted phenotypes) by mutation at the locus determining the temperature preference. However, it is likely and indicated by empirical evidence that new and better adapted genotypes could emerge by mutation (Thompson, 1998; Reznick & Ghalambor, 2001). In fact, negating this possibility may appear highly implausible if we on the other hand assume that dispersal traits may evolve in response to changing habitat conditions; a proposition supported by considerable evidence (Hill *et al.*, 1999; Parmesan, 2006; Phillips *et al.*, 2010b). Hence we performed a second set of simulation experiments allowing the alleles coding for the optimal temperature to mutate, too (see model section), i.e. we consider a scenario where the dispersal trait and habitat adaptation can jointly evolve due to mutation.

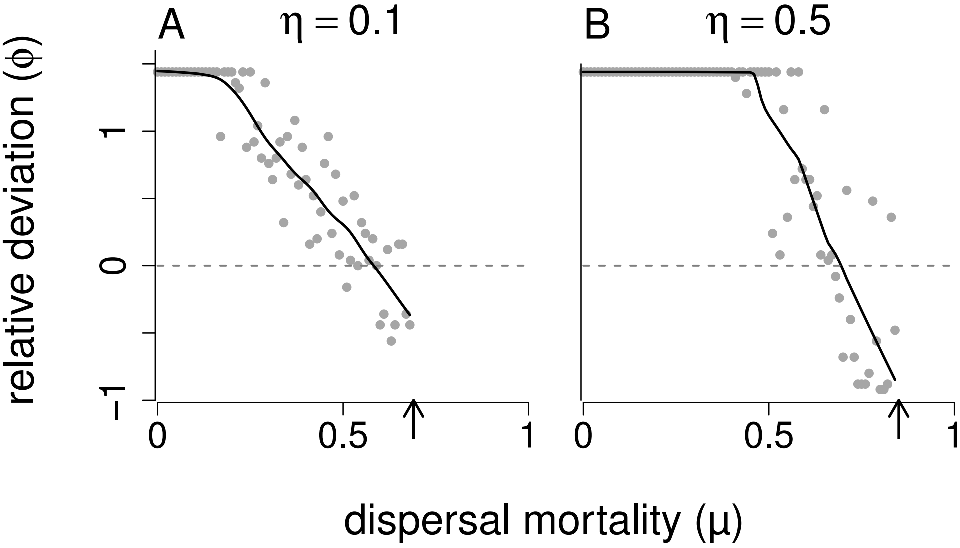

Figure 5.2: Influence of dispersal mortality on the response of the single-species system with evolutionary adaptation to temperature change. Further details as in Figure 1.

Results for these simulations considerably differ from those of the previous one. For highly connected patches (low μ) the species now simply invades the whole gradient. It thus manages to evolve – in spite of the ongoing temperature increase – even cooler adapted individuals at the rapidly advancing front (but also 'hotter adapted' types at the 'warm end' of the initial range). This implies that evolutionary change is more rapid than environmental change. Evolutionary adaptation explains the large range expansion that is only restricted by the limits of the simulated landscape (Fig. 5.2a,b). For intermediate dispersal cost species expand their range still faster than predicted ($\phi > 0$). However, range expansion is slower and the landscape is not completely filled. Nevertheless, given enough time these metapopulations would invade the whole simulated landscape, too. Finally, for the scenario including wide niches ($\eta = 0.5$) survival of metapopulations becomes possible over a wider range of dispersal mortality (compare Fig. 5.1b and 5.2b) while the system collapses at about the same dispersal mortality (μ) than in the previous scenario if the niche is narrow (compare Fig. 5.1a and 5.2a). Niche width affects the ability to persist locally and selection against non-optimal genes, respectively against being in the wrong habitat, becomes weaker as the niche becomes wider (the tolerance becomes larger). This may allow adaptation to changing conditions even under circumstances where gene flow becomes very weak and thus allows persistence even in very isolated habitats.

With mutational change of habitat (temperature) preference, the envelope approach thus becomes inappropriate for single species systems. No matter whether we introduce climate change or not, without dispersal barriers evolutionary adaptation would principally allow that a species extends its range along the whole gradient. However, if adaptability or dispersal are insufficient to match the rate of changing habitat conditions, the species will go extinct anywhere.

5.3.3 Range shifts in a two-species system

The invasion of the whole world in the above scenario is only possible because we deliberately imposed and maintained the presence of 'empty space' before the onset of climate change. However, habitats and landscapes are rarely free of other species and interactions with competitors, predators or parasites are important mechanisms that shape the distribution of species (Gaston, 2009; Price & Kirkpatrick, 2009). We thus introduced a second species into the simulations, locally adapted to the cooler half of the gradient, but otherwise identical to the first species (for details see model section). In the following we restrict our analysis to the case of competing species.

In the two-species scenario we neither found the initial range expansion nor any range shift faster than predicted by the envelope model. Instead, with increasing dispersal cost (μ) we witness an increasing lag in the range border

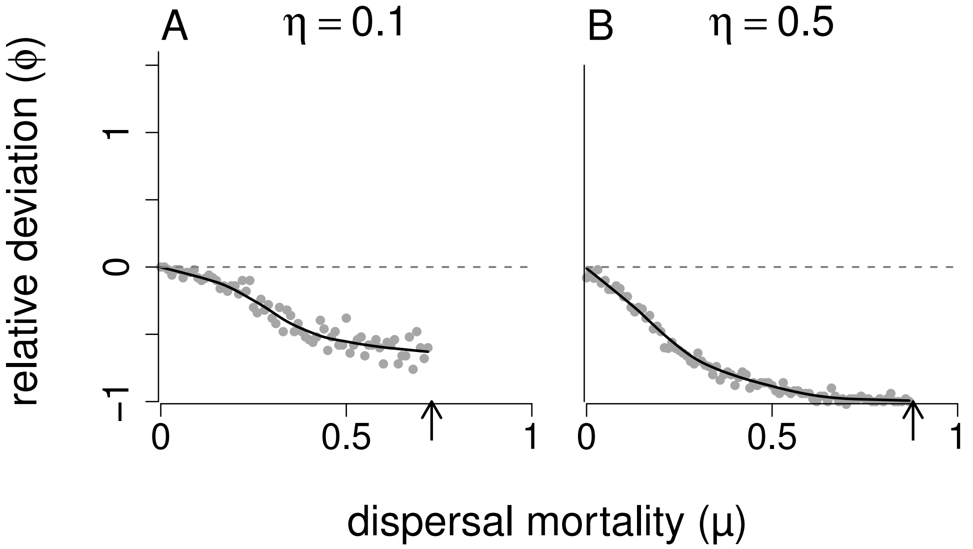

Figure 5.3: Influence of dispersal mortality on the response of the two-species system with evolutionary adaptation to temperature change. Further details as in Figure 1.

compared to predictions (Fig. 5.3). This corresponds to a gradual shift from tracking changing environmental conditions by dispersal to local adaptation due to mutation. For very low dispersal costs ($\mu \to 0$) the realized range shift nearly matches the prediction of the climate envelope because preadapted individuals of the generally 'warm adapted' species move forward according to the progressing climate change and replace the (increasingly) poorly adapted second species. However, as dispersal mortality becomes larger and correspondingly gene flow becomes lower the competition with better adapted immigrants decreases and the retreating species increasingly gets the time and chance to adapt to changing conditions as adequate mutants emerge. Consequently, the shift of the range border increasingly lags behind predictions (see Fig. A2 showing the balance between these two processes). The lag is more pronounced in the scenario with wider niche for the reasons already outlined above – if individuals are generally more tolerant to a deviation from ideal conditions, genetic diversity will be larger locally, providing a larger pool of variants from which better adapted individuals can be selected as environmental change progresses. Further, the selective pressure on dispersal induced by the change in environmental conditions is weaker for the tolerant species (having a narrower niche is similar in effect to a faster change in environmental conditions) and evolved dispersal is consequently lower in the scenario assuming a wide niche (see Fig. A3). The critical value of μ, at which the system collapses is, however, not affected by the introduction of a second species (compare Fig. 5.3 and Fig. 5.2) and there is indeed no reason why it should. Despite the fact that the rate of range shift is predominantly determined by the interaction between the species, the extinction probability for the system as a whole depends only on the ability to cope with the changing conditions. As long as species do only differ in their temperature preference this does, however, not depend on the number of species in the system.

5.3.4 Conclusions: Predicting future range shifts of species

Our results show that predictions of future range shifts based on bioclimate envelope models would indeed work well if populations could not adapt to local conditions and if they would exist independent of other species. A lot of studies indeed base their predictions on observations of single species distributions (Bakkenes *et al.*, 2002; Montoya *et al.*, 2009; Adams-Hosking *et al.*, 2011). Yet as soon as we allow adaptation of species to changing conditions by mutation, the single species scenario becomes quite useless. If interactions with other species are ignored, the focal species is expected to either expand its range unlimited, as long as no dispersal barriers are in its way, or to go extinct. In the first case we would not have an explanation for the limited range of the species to begin with. In the second it is hard to perceive why the species exists at all.

Yet the world is typically not empty but occupied by other, competing species. When generating predictions concerning the response to climate change we thus must account for the interactions with other species. Several authors have already stressed the importance of biotic interactions for predicting future distributions (Hampe, 2004; Araújo & Luoto, 2007; Dormann, 2007), but a mechanistic model integrating interactions was still lacking. Our results show that when considering more than one species it becomes unclear, whether realized range shifts will match predictions generated by simple climatic envelope models. The degree of range shift is always dependent on the balance between tracking the changing conditions by dispersal (gene flow) or adapting to them due to rapid evolution (mutation). In any specific case this balance will be affected by many different factors like the rate of climatic change, the connectivity of habitats, the steepness of the habitat gradient, the tolerance (niche width) of a species to temperature change (or habitat changes associated with it), the effective population size, generation time, mutation rate, mating system and so forth. Factors that promote the maintenance or emergence of local genetic diversity will tip the balance in favor of local adaptation and consequently of static range borders, while factors that promote dispersal will lead to a shift of range borders more in line with the predictions of simple envelope models. To determine the influence of mutation rate on our results we tested a lower rate ($m = 10^{-5}$). The evolutionary response of the species was slightly dampened in the consequence but the qualitative behavior of the system was equal leading to the same conclusions.

Jankowski *et al.* (2010) have investigated the formation of elevational ranges between neotropical songbirds and found that competitive interactions, especially aggressive interspecific behavior, restricts the ranges of these bird species. They predict that in scenarios of temperature increase dominant competitors should shift their ranges upwards the elevational gradients and thereby constrain the remaining habitat for other species. These nice empirical results fit our hypotheses very well and we have shown that these mechanisms would work even in the absence of such asymmetry in competitive ability.

Price & Kirkpatrick (2009) have shown that interspecific range borders – as we modeled them in our two-species system – are evolutionary stable under a broad range of conditions. In their discussion they concluded that it might be possible that the geographic range of a species becomes narrower in climate change scenarios, although it would have the genetic potential to adapt to the changing conditions, only because of competition with another species inhabiting the warmer end of the world. We have shown in Fig. 5.3 that this hypothesis holds for a wide range of parameters. Even if the species adapted to the 'colder' side of the gradient would be able to invade the whole world (similar to our results in Fig. 5.2) when alone, it cannot because it has to cope with another species, that is pre-adapted to the warmer conditions. We do not provide results for a two-species system without mutational creation of new genotypes at the locus for temperature adaptation because it is obvious that such a model would not lead to predictions different than those provided by the corresponding single species scenario.

In our simulations we only considered competition between species. One very interesting and important starting point for future studies would be to test the validity of BEMs for more complex types of interactions, like mutualistic, parasitic, or predator-prey systems, in a similar approach. However, we are convinced that these systems will rather lead to more dramatic deviations from the prediction of simple envelope models than our model of two competing species (see e.g. Merrill *et al.*, 2008).

Future attempts to predict range shifts during global climate change should avoid looking at single species, only, but try to include interactions with other species, the possible adaptive potential of species, as well as the configuration of the landscape. It is very important to keep in mind that species can track changes or adapt to them - but typically they do so in the presence of other pre-adapted and competing species.

5.4 Appendix

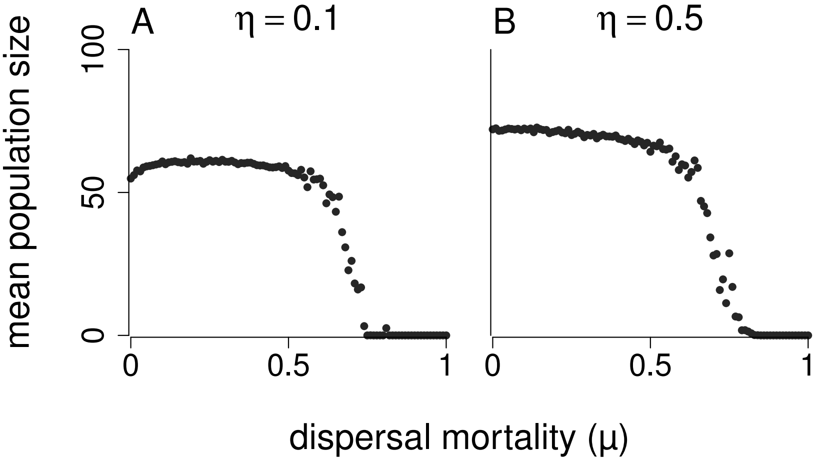

Figure A1: Mean population sizes for the single-species scenario without mutations of local adaptation. Shown are the averaged population sizes of all occupied patches for every simulation run (dispersal costs μ varied in 101 equidistant steps in the interval $[0; 1]$). a) narrow niche width ($\eta = 0.1$), b) wide niche width ($\eta = 0.5$).

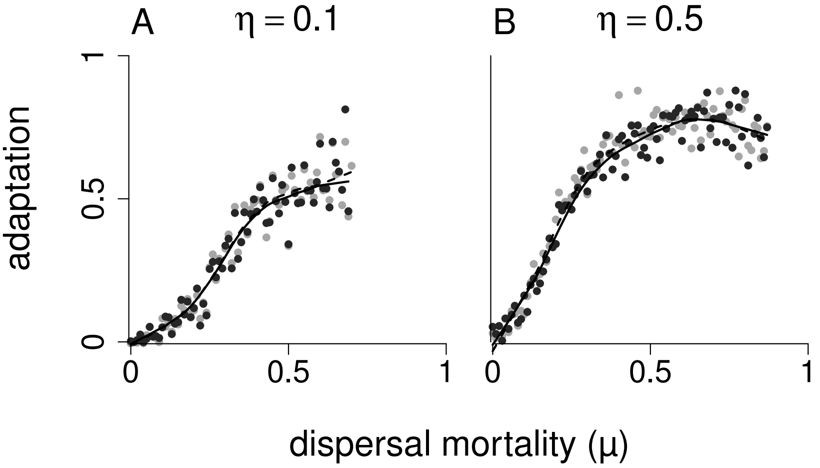

Figure A2: Evolved adaptation for the two-species scenario. Shown is the difference between the individuals' mean optimal temperatures τ_{opt} at the beginning and end of climate change, normalized to the temperature increase (see main text). The higher the values the more the species' adaptation deviated from the temperature at the predicted range margin. Dark grey dots: warm-adapted species, light grey dots: cold-adapted species. a) narrow niche width ($\eta = 0.1$), b) wide niche width ($\eta = 0.5$). Lines were fitted using the lowess-algorithm provided by Cleveland (1981).

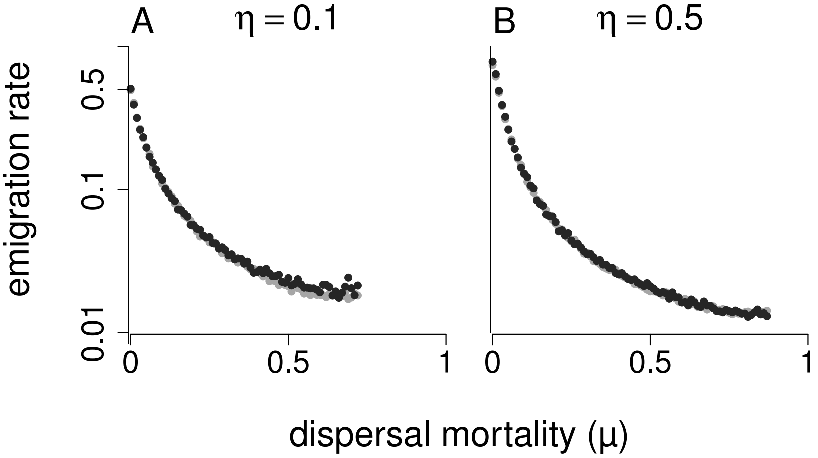

Figure A3: Evolved emigration rates for the two-species scenario. Shown are the arithmetic averages of the emigration rates for both species (dark grey dots: warm-adapted species, light grey dots: cold-adapted species). a) narrow niche width ($\eta = 0.1$), b) wide niche width ($\eta = 0.5$). Note the log-scale of the y-axis.

CHAPTER 6

A concept for range formation in the light of dispersal evolution

The previous chapters make clear that the formation of range borders strongly depends on dispersal. Emigration of individuals from their natal patches, the transition across probably unfavorable landscapes as well as (successful) establishment and reproduction in new patches are key mechanisms without which no species would have been able to spread in space. This has been formulated most explicitly by Keitt *et al.* (2001), stating that all ranges of species are the result of historical invasions.

However, until now a concept describing the interactions between dispersal and the formation of (stable) range borders has never been formulated, although a large number of studies have contributed to this topic (e.g. Case & Taper, 2000; Bahn *et al.*, 2006; Dytham, 2009; Phillips, in press). By creating a framework for the evolutionary ecology of species' ranges with a stronger focus on evolutionary processes, Robert Holt (2003) pushed the science of range formation into a new direction. In his paper, Holt went deep into the role of dispersal evolution. Many new mechanisms have been described since then (see sections 1.3 and 1.4). However, the exact interplay between dispersal and other abiotic and biotic factors as well as their consequences for ranges have not been put together, yet (but see the general review of range border research provided by Gaston, 2009).

In this chapter I want to summarize important processes influencing dispersal evolution and range formation that have emerged largely from theoretical studies. Within this thesis I take a metapopulation perspective at range formation of species, i.e. I consider the real landscape modelled by a network of patches, which are interconnected by dispersal. Of course, geographic range borders can result from dispersal barriers, such as coasts. However, this mechanism is trivial and will thus be ignored in the following. Instead I focus on range borders, which are formed along smoothly changing landscapes, like temperature gradients along mountain slopes, gradients in moisture or in other abiotic factors like salinity or soil PH, which often occur in nature (Körner, 2007). In such a gradient extinction probability will necessarily increase with increasing hostility of the environment. The range ends, where extinction rates are balanced by colonizations from occupied patches inside the range (Oborny *et al.*, 2009). Thus dispersal is a key process that determines the range of a population. It leads to an increase in colonization probability, may stabilize small populations by the rescue effect, but may also increase the extinction rate of small populations by a further loss of individuals (Fig. 6.1; Hovestadt & Poethke, 2006).

Landscape-level mechanisms

Dispersal can be subdivided into three stages: emigration, transition and immigration into new patches. When looking at single stages it becomes clear that the landscape shows strong influences on dispersal. Habitat fragmentation — in terms of patch isolation — increases the costs of dispersal (Bonte *et al.*, in press), thereby decreasing the probability of immigration. Thus it directly decreases the probability of successful colonization and causes range contraction.

Temporal variance in environmental conditions leads to substantial differences in population densities between patches. This can affect the extinction risk of local populations, as more patches with low population sizes occur, which can go extinct by means of demographic stochasticity. Temporal variance thus basically has a negative impact on species' ranges (chapters 3 and 4 of this thesis).

However, dispersal is a very plastic and rapidly evolving trait (Hill *et al.*, 1999; Parmesan, 2006; Phillips *et al.*, 2010b). When the evolution of dispersal is considered, the described mechanisms acting at the landscape level have indirect influences on the ranges of species by shaping dispersal evolution (shown by the dashed arrows in Fig. 6.1). Habitat fragmentation is a major determinant of dispersal evolution (Honnay *et al.*, 2002; Virgos, 2001; Leimu *et al.*, 2010, chapters 2, 3 and 4). As in highly fragmented habitats dispersal is very costly (in terms of e.g. mortality or fertility reduction), selective pressures are acting in favor of reduced dispersal rates. Thus, patch isolation decreases colonization probability also indirectly.

The effect of temporal variance in conditions on dispersal evolution depends on its synchrony between patches. When, e.g. caused by large-scale climatic fluctuations, temporal variance is spatially correlated (and thus synchronous), the extinction risk in areas with unfavorable conditions is highly increased, not showing large impacts on dispersal. However, when the temporal variance in conditions is asynchronous between patches, higher dispersal rates are selected for. As the general chances of emigrants to arrive in more favorable than the natal habitat increase (Poethke & Hovestadt, 2002; Cadet *et al.*, 2003; Poethke *et al.*, 2007, chapters 3 and 4 of this thesis), emigrants gain on average a fitness increase. Thus, like habitat fragmentation, the effects of temporal variance are twofold, shaping species ranges directly via the increased risk of population extinction and indirectly via dispersal evolution.

High spatial variation in conditions leads to selection in favor of lower dispersal rates. Considering a world with large and small patches, a mainland-island scenario emerges (Fronhofer *et al.*, in revision). In large patches the demographic extinction risk as well as kin structure are basically lower than in small patches. As more individuals live in large patches in such a scenario than in a comparable amount of small patches, dispersal is on average detrimental, because more individuals would migrate from a larger to a smaller patch than vice versa. Consequently, a selective pressure for lower dispersal emerges (see also Hastings, 1983). Similarly, Poethke *et al.* (2011a) showed that partial improvement of the habitat, implemented by increasing the size of a fraction of patches in a metapopulation, leads to a decrease in dispersal rates. When overall dispersal is lower, small patches, which are in need of recurrent immigration due to the higher demographic extinction risk, are not populated anymore. Thus, the authors showed that increasing spatial variance in conditions, imposed e.g. by a conservation management action, can lead to a decrease in metapopulation size.

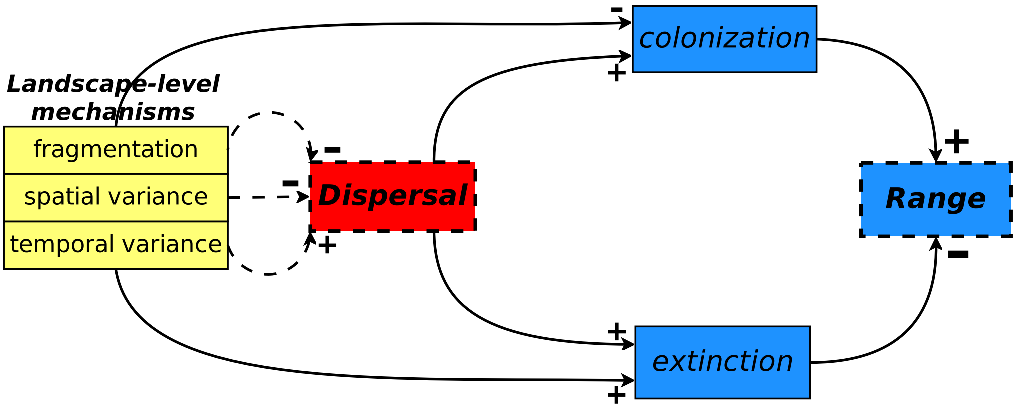

Figure 6.1: A schematic representation of the interrelations between colonization and extinction in shaping a species' range as well as the impacts of dispersal and landscape-level mechanisms. Dispersal takes a central role, as it affects colonization and extinction, which together determine the position of the range border along a gradient. Landscape-level mechanisms can either directly change extinction and colonization rate or evolutionary act on dispersal. The algebraic sign at the end of an arrow denotes, whether an element has a positive or negative influence on another element. Solid arrows denote direct (ecological) effects, whereas dashed arrows denote evolutionary impacts.

Population-level mechanisms

So far we have accepted that dispersal is able to evolve. However, when dispersal strategies are assumed to be evolvable it is reasonable to also assume that adaptation to local conditions should be an evolvable trait.

Adaptation to local conditions basically hinders populations from spread into new habitats (Fig. 6.2; Kawecki, 2008). However, dispersal has a negative effect on local adaptation, because of maladapted genes arriving in populations and depressing the degree of local adaptation (often referred to as 'migration load'; Garcia-Ramos & Kirkpatrick, 1997). It has been argued that asymmetric gene flow from the densely populated core to the sparsely populated margin especially hampers adaptation to marginal habitat and thus strongly decreases colonization and prevents further spread (Haldane, 1956; Bridle & Vines, 2007).

However, genetic diversity is also expected to positively affect a species' ability to colonize new habitat (Fig. 6.2; Bradshaw, 1984). Dispersal increases the genetic diversity in a given population (Parmesan, 2006). Hence, some authors are not convinced by the hypothesis that many range edges are formed by asymmetric gene flow and rather argue that low genetic diversity hinders populations from spread (Al-Hiyaly *et al.*, 1993; Kawecki, 2008).

Allee effects are very widespread in nature and found across many taxa (Courchamp *et al.*, 2010; Kramer *et al.*, 2009). By the reduction of population growth at low densities the probability of successfully colonizing habitats is drastically reduced, because immigrants usually arrive in low numbers (except for the special case of density-dependent emigration, see chapter 3). But Allee effects have a second effect: reduced or even negative growth rates at low densities may also result in an increased risk of local extinction when population sizes are low, e.g. due to temporal variance in environmental conditions (Fig. 6.2).

Other population-level mechanisms like sexual reproduction are able to influence the genetic patterns of range formation. When individuals reproduce sexually, including genetic recombination, genetic diversity is increased and thus colonization is favored (Holt & Barfield, in press).

We have seen in chapter 3 that conditional dispersal has important consequences for shaping species' ranges. Colonization can be increased using such a conditional dispersal strategy, as immigrants arrive in higher numbers due to a change in the distribution of emigration and immigration numbers (see Fig. 3.4 on page 42).

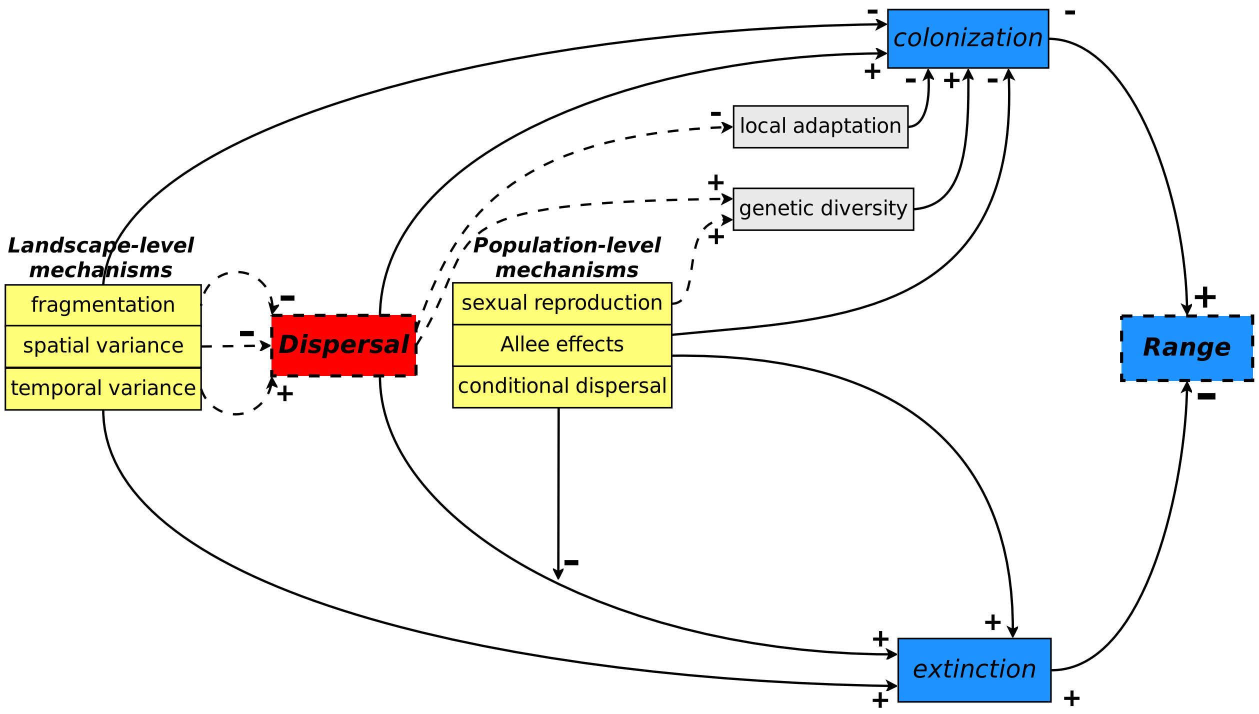

Figure 6.2: A schematic representation of the interrelations between colonization and extinction in shaping a species' range, extended by genetic and population-level mechanisms. Genetic attributes like local adaptation or genetic diversity are directly affected by dispersal evolution and shape the colonization potential of species. Other population-level mechanisms like sexual reproduction either affect the latter or directly shape colonization and extinction, as in the case of Allee effects and conditional dispersal. The algebraic sign at the end of an arrow denotes, whether an element has a positive or negative influence on another element. Solid arrows denote direct, ecological effects, whereas dashed arrows denote evolutionary impacts.

Additionally, populations are less likely to go extinct due to demographic stochasticity compared to unconditional dispersal strategies, as less (or even no) emigrants leave populations with low density (Hovestadt & Poethke, 2006).

It needs to be mentioned that dispersal can also be conditional on several other characteristics like sex ratio, patch quality or the presence of predators. However, the effects of such conditional strategies on range formation are largely unknown, thus they are ignored in this concept.

Community-level mechanisms

The major innovation of the presented concept for range border formation is the explicit incorporation of evolutionary processes. If the view on evolution is not solely focused on dispersal (as was done already by Holt, 2003), but also on the evolution of local adaptation, we face a problem, which we investigated in chapter 5. We saw that when dispersal and local adaptation to abiotic conditions were evolving traits, our simulated species was able to invade the whole world. No range border was formed by asymmetric gene flow in these simulations, because of selection for lower dispersal rates due to the fitness-decreasing effect of immigrating into another location in the environmental gradient. Hence no asymmetric gene flow from the core to the margin emerged. We thus concluded that when species live along gradients of environmental characteristics to which they could adapt, their distribution must be constrained by the presence of other species. In a scenario of competition (e.g. for resources), every species limits the area of suitable habitat for the other, lowering the other species' colonization probabilities (Fig. 6.3). Price & Kirkpatrick (2009) showed that interspecific range borders between competing species can be stable even over evolutionary time-scales.

Similarly, for mutualistic interactions a lack of colonization can be important, especially when the interaction is obligate for at least one of the partners. In this case a species' presence is constricted to the range of its interaction partner (Killingback *et al.*, 1999; Mack, in press), thus also implying a selective force for lower dispersal rates (Fig. 6.3; Mack, in press). However, it has also been argued that strong cooperative interactions lead to high local population densities and thus high competition, resulting in selection for increased dispersal rates (Taylor, 1992).

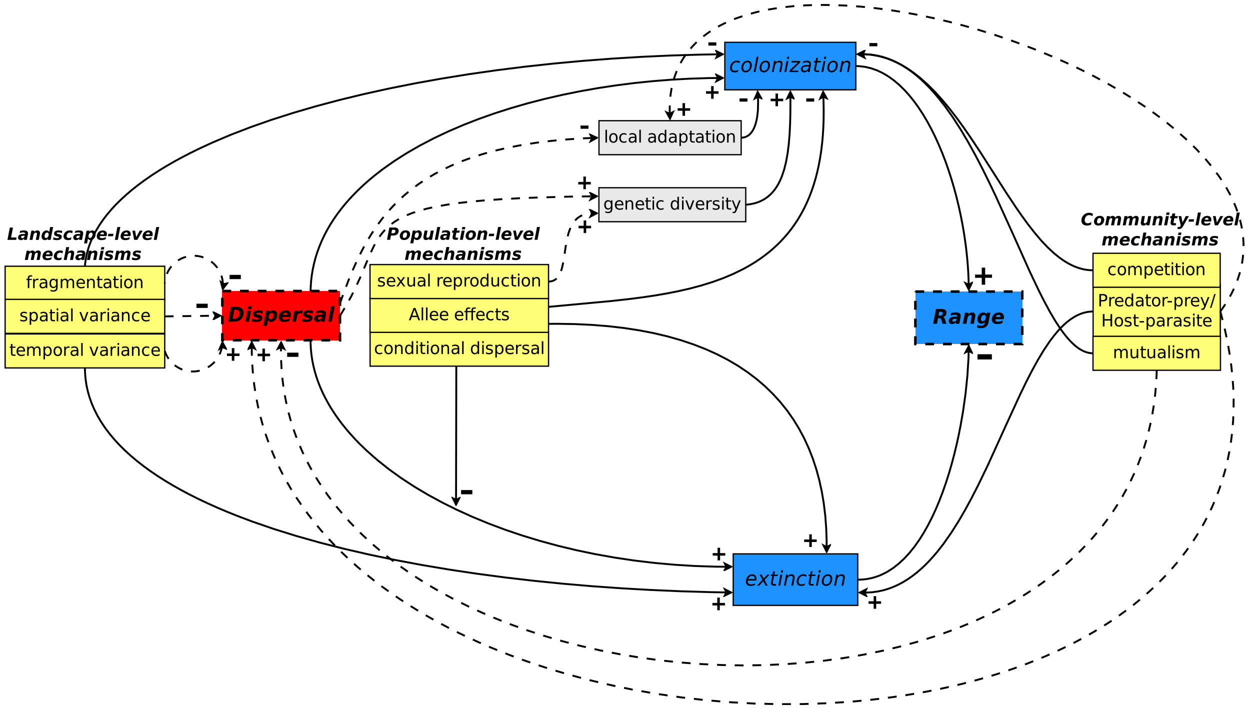

Figure 6.3: A full schematic representation of the interrelations between colonization and extinction in shaping a species' range, including mechanisms acting on the levels of landscape, populations and communities. The latter have the potential to either directly shape colonization abilities or the extinction risk of local populations, but also act on dispersal evolution and local adaptation. The algebraic sign at the end of an arrow denotes, whether an element has a positive or negative influence on another element. Solid arrows denote direct, ecological effects, whereas dashed arrows denote evolutionary impacts.

The situation is different for predator-prey or host-parasite interactions. When the density of predators (or parasites) is too high, local populations of prey (or hosts, respectively) can go extinct (Fig. 6.3). Thus, the fraction of suitable habitat for a given prey species can be restricted by the presence of the according predator, constraining its range (Holt, 2009).

Predation also can induce fleeing behavior of prey and thus select for increased emigration (Prakash & De Roos, 2002). An additional effect was recently shown by Holt *et al.* (2011), who investigated the impact of predation on the gene flow of prey across ranges. They found that predation in the range core can lower a gradient in prey population densities across their range and thus weaken a given asymmetric gene flow from range to core. Accordingly, the prey could be able to spread in space, if its range margin was set by migration load (Fig. 6.3).

Conclusions

The described concept illustrates the role of dispersal for the formation of species' ranges. It demonstrates the manifold impacts of mechanisms at the level of landscape, population and community, which act on either the colonization ability or extinction risk of populations at the range margin. The explicit view on evolutionary impacts is novel and should not be underestimated in its relevance for range formation processes.

However, the concept also hints at some points that seem not to be sufficiently investigated to be correctly evaluated according to relevance. Future research topics should focus more thoroughly on the impacts of dispersal strategies, which depend on different characteristics like e.g. the local sex ratio. Additionally, not much is known about evolutionary interactions in community systems and their implications for range dynamics.

The majority of studies in this topic are of theoretical nature. The lack of empirical studies can probably be explained by the large effort that is necessary to investigate such large-scale patterns (Gilman, 2006) and the still low availability of useful genetic data (Fournier-Level *et al.*, 2011; Hancock *et al.*, 2011; Savolainen, 2011). However, a new class of models is emerging, called 'dynamic range models'. Proposed and developed by Frank Schurr and colleagues, these models might provide a framework capable of testing the mechanisms provided here for real world populations (Schurr, pers. comm.). They can be used to fit mechanistic simulations to data collected in the field. If successful, this approach could allow researchers to test the qualitative influence of several processes, like conditional dispersal, Allee effects or biotic interactions, on existing range patterns. Thus it could be possible to draw conclusions on the importance of certain mechanisms for shaping the ranges of species. However, there is still much work needed until this direct link between theory and empiry can be created.

Summary

Understanding the emergence of species' ranges is one of the most fundamental challenges in ecology. Early on, geographical barriers were identified as obvious natural constraints to the spread of species. However, many range borders occur along gradually changing landscapes, where no sharp barriers are obvious. Mechanistic explanations for this seeming contradiction incorporate environmental gradients that either affect the spatio-temporal variability of conditions or the increasing fragmentation of habitat. Additionally, biological mechanisms like Allee effects (i.e. decreased growth rates at low population sizes or densities), condition-dependent dispersal, and biological interactions with other species have been shown to severely affect the location of range margins.

The role of dispersal has been in the focus of many studies dealing with range border formation. Dispersal is known to be highly plastic and evolvable, even over short ecological time-scales. However, only few studies concentrated on the impact of evolving dispersal on range dynamics. This thesis aims at filling this gap. I study the influence of evolving dispersal rates on the persistence of spatially structured populations in environmental gradients and its consequences for the establishment of range borders. More specifically I investigate scenarios of range formation in equilibrium, periods of range expansion, and range shifts under global climate change.

By reviewing the work of Robert MacArthur, Holt (2003) developed a framework for the evolutionary ecology of species' ranges. He considered the role of evolving dispersal and formulated some potential mechanisms for the emergence of range borders that have not been thoroughly investigated, yet. One of these mechanisms is based on dispersal evolution after periods of range expansion. It is well known that dispersiveness of populations increases during periods of range expansion due to an ecological filter effect ('spatial selection'; Phillips *et al.*, 2010b). Individuals, which are most dispersive (i.e. show the highest mobility) have a higher probability to colonize patches outside the current range. Consequently, an ongoing series of founder effects at the expanding front leads to a strong shift in the phenotypic (and genetic) composition of marginal populations towards high mean dispersiveness. Holt argued, however, that once expansion comes to a halt, e.g. because of changes in the environment, dispersal rates should decrease again. He concluded that emigrants leaving the marginal populations after the expansion period should end up in sink patches, where population growth rates are too low for sustainable growth. Thus, dis-

persal at the range margin should be selected against, leading to the demise of these sink patches and thus to range contraction. In chapter 2 I investigate, whether such a behavior of 'elastic range boundaries' indeed emerges. I created an individual-based simulation model of a metapopulation invading habitat gradients of different type. These gradients can affect dispersal mortality (habitat isolation or fragmentation), habitat capacity (patch size), growth rate (patch quality), or external extinction rate (environmental catastrophes). I find contracting ranges in the aftermath of expansion periods only for landscapes, in which dispersal at the range margin is selected against in equilibrium. Thus, for increasing dispersal mortality and — to a much lower extent — for decreasing growth rates the ranges show the elastic behavior predicted by Holt. However, for gradients in patch size and extinction probability dispersal rates at margins do not decline nor do ranges shrink after an initial expansion. With this study I can show that there are strong interactions between the landscape structure, respectively the type of gradient, and dispersal evolution, and these interactions can qualitatively alter range dynamics.

It is well known that a large number of species use information about population density for their dispersal decision. A vast amount of empirical evidence exists for such density-dependent emigration. Such "informed" dispersal strategies have also been thoroughly studied using theoretical approaches. I wanted to study the effect of such density-dependent emigration on the formation of range borders compared to density-independent (random) dispersal - still the standard assumption in most models. For this purpose, in chapter 3 I use an extension of the simulation model used in chapter 2, i.e. I implemented the density-dependent dispersal rule developed by Poethke & Hovestadt (2002) that has been proven to be the most appropriate rule for a time-discrete setting (Hovestadt *et al.*, 2010). For all tested scenarios and parameters wider ranges emerge for density-dependent emigration than for unconditional dispersal. This effect is stronger when spatio-temporal variance in population densities is higher due to environmental stochasticity in growth rates. I further test the influence of an Allee effect that decreases colonization probability. I find smaller ranges for all scenarios when an Allee effects is implemented. However, with density-dependent emigration the impact of an Allee effect is smaller than with density-independent emigration. This reduced impact is caused by a change in the distribution of emigrant numbers. In years with low population densities, a certain fraction of individuals still emigrates under unconditional dispersal. This further reduction of population size increases the already present risk of extinction due to demographic stochasticity. However, when emigration depends on density, no dispersal occurs for low density, thus reducing extinction risk. However, mass emigration events occur when population densities are high. Conditional dispersal hence reduces extinction risk for established populations and leads to less frequent immigration events. However, when dispersal occurs the numbers of immigrants are higher. These results increase the probability of overcoming even strong Allee effects. The results of this chapter highlight the possibly strong interactions between species-specific traits and landscape attributes.

In chapter 4 I extend the previous work: I use the same simulation model with density-dependent emigration included and focus on the role of environmental stochasticity in shaping the range dynamics of the species. Recent research on global climate change has revealed that not only mean conditions will change over time, but especially their variance will increase (Jentsch *et al.*, 2007). I investigate, how such an increase in environmental variance will affect the expansion of ranges. I therefore ran simulations with different magnitudes of spatio-temporal variation in growth rates. In gradients of dispersal mortality an elastic behavior of different type than in chapter 2 emerges, due to the above described characteristics of density-dependent emigration. Initially an increase in environmental stochasticity leads to an expansion of the range, as I already found in chapter 3. However, further increasing spatio-temporal variance severely increases extinction risk due to demographic stochasticity and leads to range contraction. I find only slight initial range expansion in a gradient of growth rate and no increase at all in a patch size gradient. The results depend on whether the range border is primarily determined by the lack of colonization or by high extinction risk. This shows again very clearly that landscape effects on dispersal evolution strongly influence range dynamics and are thus of major importance for our understanding of species' distributional constraints.

However, if variance increases faster than dispersal strategies can evolutionary adapt, results might change. Therefore, I performed additional simulations, where I annually increased spatio-temporal variance at different rates. When populations do not have enough time to adapt their dispersal behavior to the changing conditions, the described effects are dampened. The initial range expansion in the mortality gradient, but also the strong contraction for higher degrees of stochasticity are less pronounced when the changes occur more rapidly. Apparently the time-scale of global change is another important determinant for the interplay of evolution and range dynamics.

When predicting climate change impacts on ranges, a commonly used approach is 'bioclimate envelope modelling' (BEM; also referred to as 'species distribution modelling'). With these models future range shifts are predicted, based on statistical correlations between current (or past) distributions of species and certain habitat characteristics. This approach is widely used, although a lot of criticism has accumulated. Many authors remarked that usual BEMs ignore important factors like geographic dispersal barriers, species-specific dispersal abilities, biotic interactions, or the (genetic) potential for adaptation. In chapter 5 I focus on the role of evolutionary changes in dispersal and local adaptation for the accuracy of range predictions based on a BEM approach. For this purpose I implemented a new type of gradient: along the landscape a habitat characteristic (e.g. temperature or humidity) changes, that affects individual survival probability based on the individual's phenotype. Every individual carries a genetic locus coding for its optimal environment (I call it 'temperature' for easier interpretation). Survival probability of offspring is determined by the match between its natal patch temperature and its genetically encoded optimum. I simulate global climate change by annually increasing the temperature in every habitat patch by a certain value. By occupying only a part of the virtual landscape at initialization of simulations I can investigate the shift of the initial range border. The simulated shift can be compared to predictions of a BEM approach, assuming that the species would perfectly track the changing conditions. If evolution of the habitat trait is not allowed, simulation results indeed agree well with BEM predictions. However, when evolution of local adaptation is allowed, the species invades the whole landscape (or goes extinct if habitat fragmentation is high), regardless of the direction or magnitude of climate change. As it is known that evolution occurs and still not all species are found everywhere, an important determinant of the range border must be missing. I thus include a second species occupying half of the gradient, competing with the first one for resources. I find that for this scenario of an interspecific range border, the accuracy of the range shift depends on landscape factors. When the habitat is fragmented and thus dispersal mortality is high, selection against emigration occurs and the species mostly adapt locally to the changing conditions. In these scenarios the realized range shift lags behind the prediction of BEMs. When dispersal costs are low, however, the range shift tracks the prediction leading to a range contraction of the cold-adapted species, although it could adapt to the changes in the absence of the other species. This chapter makes clear that biotic interactions may play a predominant role for range border formation in nature.

In the last chapter I summarize the findings of this thesis and further studies by developing a concept of range formation in the light of dispersal evolution. This concept is based on the assumption that colonization and extinction are the most relevant and basic processes that shape species' ranges. I classify further mechanisms and factors, which influence dispersal evolution and range dynamics, according to whether they act at the level of the landscape, populations, or communities. The concept reveals a lack of research regarding impacts of conditional dispersal (e.g. dependent on the local sex ratio) and community dynamics with respect to evolution. Focussing more on these topics could help to at least qualitatively improve predictions on how anthropogenic influences like land use or large-scale processes like global climate change will affect species' ranges and thus the composition of communities in the future.

Zusammenfassung

Die Frage nach den Ursachen für die Ausbildung von Verbreitungsgrenzen ist ein zentrales Thema ökologischer Forschung. Dabei wurde die Bedeutung geographischer Barrieren als natürliche Grenzen der Ausbreitung von Populationen früh erkannt. Jedoch findet man oft auch in sich graduell ändernden Landschaften, in denen keine Barrieren zu finden sind, sehr scharfe Verbreitungsgrenzen. Mechanistische Erklärungen hierfür unterscheiden zwischen solchen Umweltgradienten, welche entweder die Variabilität der biotischen und abiotischen Umgebung in Raum und Zeit oder die Fragmentierung von Habitat beeinflussen. Dabei wird die spezifische Lage der Verbreitungsgrenze von weiteren Mechanismen beeinflusst, wie Allee-Effekten (d.h. verringerte Wachstumsraten bei kleiner Populationsgröße oder -dichte), zustands- bzw. kontextabhängigem Dispersal und biologischen Interaktionen.

Dispersal, das heißt Ausbreitung im Raum mit potentiellen Konsequenzen für den Genaustausch zwischen Populationen, stand im Fokus vieler Studien, die sich mit der Ausbildung von Verbreitungsgrenzen beschäftigt haben. Es ist bekannt, dass das Ausbreitungsverhalten von Populationen sehr variabel ist und selbst innerhalb kurzer Zeit evolvieren kann. Trotzdem haben sich erst wenige Studien mit den Folgen der Evolution des Ausbreitungsverhaltens für biogeographische Muster befasst. Die vorliegende Dissertation verfolgt das Ziel, diese Lücke zu füllen. Ich untersuche den Einfluss evolvierender Emigrationsraten auf das Überleben von räumlich strukturierten Populationen, sowie dessen Konsequenzen für die Etablierung und Dynamik von Verbreitungsgebieten. Dafür ziehe ich verschiedene Szenarien heran. Diese bilden die Verbreitung von Arten im Gleichgewicht, während Phasen der Expansion des Verbreitungsgebietes, sowie im Kontext des globalen Klimawandels ab.

Robert Holt (2003) entwickelte auf der Grundlage früherer Arbeiten von Robert MacArthur ein Konzept für die evolutionäre Ökologie von Verbreitungsgrenzen. Dabei ging er ausführlich auf die Rolle der Ausbreitung sowie der Evolution des Ausbreitungsverhaltens ein und formulierte Hypothesen, die teilweise bis heute nicht umfassend untersucht wurden. Eine seiner Beobachtungen betrifftteher ausbreitungsstarker Individuen die Evolution des Dispersal nach Phasen der Invasion. Der Anstieg der Ausbreitungsfähigkeit von Populationen während Invasionsereignissen ist ein umfassend untersuchtes Phänomen. Als Ursache ist ein ökologischer Filter-Effekt beschrieben („räumliche Selektion"; Phillips *et al.*, 2010b). Mechanistisch bedeutet dies, dass diejenigen Indi-

viduen einer Population, welche die höchste Mobilität aufweisen, auch mit einer höheren Wahrscheinlichkeit neue Habitate außerhalb des bisherigen Verbreitungsgebietes kolonisieren. Als Konsequenz wiederkehrender Gründer-Effekte [1] kommt es zu einer immer stärkeren Verschiebung der phäno- und genotypischen Zusammensetzung peripherer Populationen zugunsten eher ausbreitungsstarker Individuen. Holt argumentiert dabei, dass nach Beendigung einer Expansionsphase der spezielle Vorteil einer Neubesiedlung nicht mehr gegeben sei und sich Grenzen oft in Zonen etablieren, in denen Ausbreitung mit hohen Kosten verbunden ist. Die einsetzende Selektion auf niedrigere Emigrationsraten sollte entsprechend zu einer gewissen Kontraktion des Verbreitungsgebiets führen. Ich untersuche in Kapitel 2, ob sich ein solch elastisches Verhalten der Verbreitungsgrenzen in verschiedenen Habitatgradienten zeigen lässt. Dafür entwickelte ich ein individuenbasiertes Simulationsmodell einer Metapopulation, die sich im Raum ausbreitet. Ich etabliere räumliche Gradienten in Dispersalmortalität (Habitatfragmentierung), Habitatkapazität (Habitatgröße), Populationswachstumsrate (Habitatqualität) oder Extinktionsrate (Umweltkatastrophen). Ich finde ein elastisches Verhalten im Sinne Holts nach Perioden der Ausbreitung nur in Landschaften, die verringerte Emigration am Rand des Verbreitungsgebietes begünstigen. Demzufolge zeigt sich eine sekundäre Verkleinerung des Verbreitungsgebietes nach Expansion in Gradienten ansteigender Dispersalmortalität und — in weit geringerem Maß — in Gradienten mit sinkenden Wachstumsraten. In Gradienten der Habitatgröße oder Extinktionsrate steigt die Emigrationsrate auch nach der Expansionsphase an der Grenze der Verbreitung weiter an. Diese Ergebnisse demonstrieren die starken Wechselwirkungen zwischen Dispersalevolution und Landschaftsstruktur, sowie deren Einflüsse auf die Dynamik von Verbreitungsgrenzen.

Es ist von vielen Arten bekannt und theoretisch gut begründet, dass sie für die Emigrationsentscheidung Informationen über die aktuelle Populationsdichte nutzen. Ich wollte deshalb wissen, welche Einflüsse dichteabhängige Emigration auf die Ausbildung von Verbreitungsgrenzen in Gradientensystemen hat. Die Ergebnisse in Kapitel 3 basieren auf einer Erweiterung des Simulationsmodells, welches auch schon in Kapitel 2 genutzt wurde. Ich implementierte eine dichteabhängige Emigrationsregel, die von Poethke & Hovestadt (2002) entwickelt wurde und sich als angemessen für ein zeitdiskretes Szenario erwiesen hat (Hovestadt *et al.*, 2010). In allen Simulationen finde ich weitere Verbreitungsgebiete im Falle der dichteabhängigen Strategie im Vergleich zu unkondi-

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[1] Beschreibt das Phänomen, dass Populationen, die von wenigen Individuen neu gegründet wurden, nur über einen kleinen Teil des ursprünglichen Genpools verfügen.

tionellem Dispersal. Dieser Effekt wird verstärkt, wenn die lokalen Populationsdichten stärkere Varianz aufweisen. Ich teste weiterhin den Einfluss von Allee-Effekten, welche für viele Arten nachgewiesen wurden und die Kolonisationswahrscheinlichkeit leerer Habitate drastisch reduzieren. Für alle Szenarien und Emigrationsstrategien resultieren verkleinerte Verbreitungsgebiete bei Vorhandensein eines starken Allee-Effektes. Der Vorteil der Informationsnutzung für die Ausbreitung wird jedoch in Relation zur dichteunabhängigen Emigration verstärkt. Die Erklärung für die beobachteten Phänomene finde ich in der Verteilung der Anzahlen von Emi- beziehungsweise Immigranten, die von der Ausbreitungsstrategie beeinflusst werden. Auch in Jahren mit geringen Populationsdichten verlässt im Falle von unkonditioneller Emigration ein Teil der Individuen ihr Habitat, während dies bei dichteabhängiger Ausbreitung nicht der Fall ist. Diese zusätzliche Reduktion der Populationsgrößen erhöht das bereits vorhandene Risiko der Extinktion aufgrund demographischer Stochastizität. Bei der dichteabhängigen Strategie kommt es zu Massenemigrationsereignissen in Jahren hoher Populationsdichten. Dies erhöht die Wahrscheinlichkeit, die für ein positives Populationswachstum nötige Allee-Schwellendichte zu überwinden. Dichteabhängige Ausbreitung führt also zu selteneren Migrationsereignissen, aber wenn es sie gibt, treten die Immigranten in größeren Zahlen auf. Die Ergebnisse dieser Studie heben hervor, welche starken Interaktionen zwischen artspezifischen Eigenschaften und der Landschaftsstruktur bestehen.

In Kapitel 4 nutze ich das selbe Simulationsmodell wie bisher, inklusive dichteabhängiger Ausbreitung, und fokussiere mich auf die Rolle der Umweltstochastizität für die Position von Verbreitungsgrenzen. Aktuelle Ergebnisse der Klimawandelforschung belegen, dass sich nicht nur mittlere Bedingungen ändern werden (Temperaturerhöhung), sondern dass auch die Varianz der Umweltbedingungen zunimmt (Jentsch *et al.*, 2007). Deshalb war ich an der Frage interessiert, wie sich ein solcher Anstieg der Umweltstochastizität auf die Ausdehnung von Verbreitungsgebieten auswirkt. Ich führte Simulationen mit mit unterschiedlich starker raum-zeitlicher Varianz lokaler Wachstumsraten durch. In einem Gradienten der Dispersalmortalität finde ich ein elastisches Verhalten von anderer Natur als jenes, dass in Kapitel 2 beschrieben wird. Ein gewisses Ausmaß an Umweltstochastizität führt zu einer Vergrößerung des Verbreitungsgebietes, wie bereits in Ansätzen in Kapitel 3 beschrieben. Bei einer weiteren Erhöhung der Varianz ist jedoch eine drastische Verkleinerung des Verbreitungsgebietes als Folge des deutlich gestiegenen Extinktionsrisikos zu beobachten. Dieses „elastische "Verhalten der Verbreitungsgrenze zeigt sich nur leicht im Falle eines Gradienten der Wachstumsrate. In einem Habitatgrößengradienten ist hingegen keine Expansion für geringe Varianzen evident. Die Ergebnisse sind abhängig davon, welche Faktoren zum Entstehen der Verbreitungsgrenze führen. Dies unterstreicht erneut die Bedeutung der Einflüsse der Landschaft auf die Evolution von Dispersal und deren Konsequenzen für biogeographische Muster.

Für Prognosen zu den Auswirkungen globaler Klimaveränderungen sind diese Simulationen jedoch nur bedingt geeignet, denn sie basieren auf einem Gleichgewichtsansatz. Es ist nicht klar, ob Arten in sich verändernden Landschaften die Zeit haben werden, die sie für eine Anpassung ihrer Strategien an die neuen Verhältnisse brauchen. Um den Einfluss schneller Klimaveränderungen zu untersuchen, führte ich weitere Simulationen durch, in denen ich die Varianz der Wachstumsraten in jeder Generation um einen gewissen Betrag erhöhte. Dieser Betrag definiert somit die Geschwindigkeit der Zunahme an Stochastizität. Ein schneller Anstieg der Varianz bedeutet, dass sich die Metapopulation kaum noch in ihrem Ausbreitungsverhalten anpassen kann. Dies hat zur Konsequenz, dass die beschriebenen Effekte geschwächt werden. Sowohl die anfängliche Expansion, als auch die Kontraktion des Verbreitungsgebietes sind schwächer als in den Gleichgewichtssimulationen. Offensichtlich ist die zeitliche Skala des Klimawandels also ein weiterer wichtiger Parameter für die Dynamik von Verbreitungsgrenzen.

In Forschungszweigen, die sich mit den Folgen des Klimawandels beschäftigen, werden häufig sogenannte "bioclimate envelope"-Modelle (BEMs, auch als "species distribution models" bezeichnet) eingesetzt. Diese Modelle berechnen die Verschiebungen von Verbreitungsgebieten im Klimawandel auf der Grundlage korrelativer statistischer Methoden. Dabei wird die aktuelle (oder vergangene) Verteilung von Arten im Raum mit verschiedenen Habitatfaktoren korreliert. Soweit Daten über die zukünftige Veränderung jener Faktoren vorhanden sind, werden entsprechend Schlüsse über zu erwartende Verschiebungen der Verbreitung geschlossen. Dieser Ansatz wird weiterhin häufig genutzt, obwohl zunehmend Kritik geäußert wird. Viele Autoren haben bereits angemerkt, dass übliche BEMs wichtige Faktoren ignorieren, wie etwa geographische Dispersalbarrieren, artspezifische Dispersalfähigkeiten, biotische Interaktionen, oder das genetische Anpassungspotential von Arten.

In Kapitel 5 untersuche ich die Rolle von evolutionären Anpassungen in Dispersal und lokaler Anpassung für die Verlässlichkeit von BEM-Vorhersagen. Dafür implementierte ich einen neuen Typ von Gradient: entlang einer räumlichen Dimension verändere ich eine Habitatcharakteristik (z.B. Temperatur), welche die Überlebensfähigkeit der Individuen definiert. Die Wahrscheinlichkeit, die Adultphase zu erreichen, wird in diesem System basierend auf dem Grad der Übereinstimmung zwischen der genetisch codierten Optimaltemperatur eines Individuums und der vorherrschenden Habitattemperatur berechnet. Klimawandel simuliere ich als annuellen Anstieg der Temperatur in jedem zur Verfügung stehenden Habitat. Da ich nur einen Teil der virtuellen Landschaft zu Beginn der Simulation mit Populationen besetze, kann ich — entsprechend einem BEM-Ansatz — die erwartete Verschiebung des Verbreitungsgebietes berechnen. Ohne Evolution der Habitatanpassung stimmen Simulationsergebnisse und BEM-Prognose gut überein. Wenn Evolution der lokalen Anpassung erlaubt ist, expandiert die Metapopulation jedoch in die gesamte simulierte Landschaft, unabhängig von der Richtung des Klimawandels. Da aber bekannt ist, dass Evolution stattfindet und trotzdem nicht alle Arten überall zu finden sind, muss ein entscheidender Faktor in den Simulationen fehlen. Deshalb führe ich eine zweite Art ein, die die zu Beginn unbesetzte andere Hälfte der Welt besiedelt. Beide Arten konkurrieren um Ressourcen und Raum und es gibt eine stabile interspezifische Verbreitungsgrenze. Für dieses Szenario stellt sich heraus, dass die Differenz zwischen erwarteter und realisierter Verbreitungsverschiebung abhängig von Eigenschaften der Landschaft ist. Ist das Habitat fragmentiert und die Dispersalmortalität hoch, evolvieren geringe Dispersalraten, die ein Mitwandern der Verbreitungsgrenze mit den Temperaturbedingungen verhindern. Als Konsequenz müssen und können sich die Arten lokal anpassen. Sind die Kosten der Ausbreitung jedoch gering, wandert die Verbreitungsgrenze mit, da Dispersal in diesem Fall die schnellere Quelle für die Etablierung vorteilhafter Gene ist. Dies bedeutet, dass die kaltadaptierte Art zurückgedrängt wird, obwohl sie grundsätzlich das Potential hätte, sich an die veränderten Bedingungen anzupassen. Die möglicherweise dominante Rolle biotischer Interaktionen für die Bildung natürlicher Ausbreitungsgrenzen wird mit diesem Kapitel verdeutlicht.

Im letzten Kapitel fasse ich die Ergebnisse dieser Dissertation zusammen und entwickle ein Konzept für die Ausbildung von Verbreitungsgrenzen im Lichte der Dispersalevolution. Dieses Konzept basiert auf der Annahme, dass Kolonisation und Extinktion die wichtigsten und grundlegendsten Prozesse für die Ausbildung von Verbreitungsgrenzen darstellen. Ich gruppiere alle weiteren Mechanismen und Faktoren entsprechend der Ebene, auf der sie wirken. Dies umfasst die Landschafts-, Populations- oder Gemeinschaftsebene. Das Konzept zeigt wichtige Forschungsansätze auf, vorrangig bezüglich des Einflusses von konditioneller Emigration (abhängig beispielsweise von dem lokalen Geschlechterverhältnis) und evolutionärer Wechselwirkungen in Artengemeinschaften. Eine Fokussierung zukünftiger Studien auf diese Themen könnte es — zumindest qualitativ — ermöglichen, vorherzusagen, wie anthropogene oder klimatische Veränderungen die Zusammensetzung von Arten in Ökosystemen verändern werden.

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List of Publications

Fronhofer, E.A., Kubisch, A., Hilker, F., Hovestadt, T. & Poethke, H.J. (in revision). Why are metapopulations so rare? *Ecology.*

Kubisch, A., Degen, T., Hovestadt, T. & Poethke, H.J. (in revision). Biotic interactions and the prediction of range shifts. *Global Ecology and Biogeography.*

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Kubisch, A., Hovestadt, T. & Poethke, H.J. (2010). On the elasticity of range limits during periods of expansion. *Ecology*, 91, 3094–3099.

Hovestadt, T., Kubisch, A. & Poethke, H.J. (2010). Information processing in models for density-dependent emigration: A comparison. *Ecological Modelling*, 221, 405 – 410.

Conferences and talks

Conference contributions

Kubisch A., Degen T., Hovestadt T., Poethke H. J. (2011) Biotic interactions and the prediction of range shifts. *Poster presented at the 12th Congress of the European Ecological Federation in Ávila, Spain.*

Kubisch A., Degen T., Hovestadt T., Poethke H. J. (2011) Evolution and its consequences for predicting interspecific range shifts. *Talk given at the 41st Annual Meeting of the GfÖ in Oldenburg, Germany.*

Kubisch A. (2011) Biodiversity from a theoretical ecologist's point of view. *Talk given at the Interdisciplinary study days ('Biodiversity - Concept and Value') at the German Reference Center for Ethics in the Life Sciences (DRZE) in Bonn, Germany.*

Fronhofer E. A., Kubisch A., Hovestadt T., Poethke H. J. (2010) Genetic Linkage and the Evolution of Dispersal Polymorphisms. *Talk given at the 40th Anniversary Meeting of the GfÖ in Giessen, Germany.*

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

Fronhofer E. A., Kubisch A., Hovestadt T., Poethke H.-J. (2010) Stray or Stay? Evolution of dispersal polymorphisms can be triggered by a mobility-fertility trade-off. *Poster presented at the 95th Annual Meeting of the Ecological Society of America in Pittsburgh, PA, USA.*

Kubisch A., Hovestadt T., Poethke H.-J. (2009) On the influence of environmental variation on dispersal evolution and its consequences for species' ranges along gradients. *Talk given at the 39th Annual Conference of the GfÖ in Bayreuth, Germany.*

Becker P., Kubisch A., Hovestadt T., Poethke H.-J. (2009) Interaction of dispersal and local adaptation in environmental gradients in a changing world. *Poster presentation at the 39th Annual Conference of the GfÖ in Bayreuth, Germany.*

Invited talks

Kubisch A. (2010) Ranges along gradients - influences of dispersal evolution. *Seminar Komplexe Systeme und Modellierung, Institute for Chemistry and Biology of the Marine Environment (ICBM), University of Oldenburg, Germany.*

Organization

Dolos K., Fronhofer E. A., Kubisch A. (2011) 6th Workshop of the Young Modellers in Ecology. *Ecological Fieldstation Wallenfells, University of Bayreuth, Germany.*

Authors' Contributions

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

Chapter 2: Kubisch A, Hovestadt T & Poethke HJ (2010) On the elasticity of range limits during periods of expansion. Ecology 91: 3094–3099

The study was designed by A. Kubisch and H. J. Poethke. The simulation program was developed by A. Kubisch. The detailed planning of the simulation parameters and experiments was performed by all authors. A. Kubisch analyzed the results and created a first draft of the manuscript. All authors contributed equally to further revisions. Relative contributions:
A. Kubisch: 70 %
T. Hovestadt: 10 %
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Chapter 3: Kubisch A, Poethke HJ & Hovestadt T (in press) Density-dependent dispersal and the formation of range borders. Ecography.

The study including experiments was designed by A. Kubisch and T. Hovestadt. A. Kubisch developed the simulation program, conducted the experiments, analyzed the results and created a first draft of the manuscript. All authors contributed equally to further revisions. Relative contributions:

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Chapter 4: Kubisch A & Poethke HJ (2011) Range border formation in a world with increasing climatic variance. Evolutionary Ecology Research 13: 159–169.

The concept of the study was developed by A. Kubisch. The final study including experiments was designed by A. Kubisch and H. J. Poethke. A. Kubisch developed the simulation program, created and analyzed the results and wrote a first draft of the manuscript. Both authors contributed equally to further revisions. Relative contributions:
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Chapter 5: Kubisch A, Degen T, Hovestadt T & Poethke HJ (under review) Biotic interactions and the prediction of range shifts. Global Ecology and Biogeography.

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Danksagung

Ich danke in besonderem Maße Achim und Thomas, die immer ein offenes Ohr für mich haben, mir stets gute Ratschläge geben (sei es bezüglich Forschung, Essen oder Wein) und trotz achtsamer Führung mir die Freiheit gelassen haben, meine Interessen zu verfolgen. Auch Björn möchte ich danken, für viele interessante und witzige Gespräche, sowie die Übernahme des Zweitgutachtens dieser Dissertation.

Weiterhin bin ich meinen Kollegen und Freunden Emanuel, Georg, Eva, Jana & Martin, Elli & Michi, Tobi, Henrik, Zak, Gita, Mirjana und Klara, dem Zoo III - Team und und und... dankbar für schöne Jahre mit jeder Menge Abwechslung, neuen Ideen, tollen Feiern, spannenden Kickerrunden, Poker- und Kochabenden und viel Zeit zum Reden und Spaß haben.

Allem voran aber danke ich für die Liebe meiner Frau und besten Freundin Franzi. Ohne sie wäre ich nicht da, wo ich heute bin und dabei so glücklich, wie ich es sein darf.

Danke auch an meine Familie, die immer hinter mir steht, mich stets unterstützt und zum Lachen gebracht hat. Dieser Dank gilt besonders meinem Bruder André, mit dem ich immer wieder auf's Neue feststellen kann, wie besonders das Leben ist.

Außerdem gebührt mein Dank allen weiteren Kollegen, die ich getroffen und kennen gelernt habe, sowie Nick Cave, Johnny Cash, Pearl Jam etc., die mich immer treu begleitet haben.