Dispersal and eco-evolutionary dynamics in response to global change

Thesis presented by Jeroen Boeye to obtain the grade of Doctor of Science

Ghent 2015

Date of the public defence: 2 February 2015

ISBN: 978-94-6197-262-0

The Research conducted in this thesis was conducted at the Terrestrial Ecology Unit (TEREC), Ghent University, Belgium and financially supported by the Research Foundation Flanders (FWO).

Please refer to this work as:

Boeye (2015) Dispersal and eco-evolutionary dynamics in response to global change. PhD thesis, Ghent University.

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‘Feeling gratitude and not expressing it is like wrapping a present and not giving it.’

William Arthur Ward

De voorbije vier jaar zijn voorbij gevlogen. Ik heb de kans gekregen om geweldig veel bij te leren, interessante mensen te leren kennen en rond te reizen. Dit alles was niet mogelijk geweest zonder de hulp en steun van een aantal mensen.

In de eerste plaats denk ik aan mijn promotor Dries Bonte. Ik zal de kans die ik van jou gekregen heb niet snel vergeten. Ondanks je ongelooflijk drukke agenda geef je jouw doctoraatstudenten steeds de hoogste prioriteit. Dit is alles behalve evident en ik besef dat ik veel geluk heb gehad met een promotor die zich zo beschikbaar stelt en zo snel feedback geeft. Meermaals kreeg ik een verbeterde draft terug op dezelfde dag dat ik hem inzond, chapeau! Daarnaast is Dries ook nog eens gewoon een toffe collega. Dries, 1000 x bedankt!

Secondly, I want to thank all members of the jury who invested a lot of their precious time in reviewing the text. Your insightful comments and suggestions really helped to improve the work. Thank you!

Hiernaast denk ik uiteraard ook aan de andere terecers en limnologen. In de eerste plek de medeoprichters van de TEREC-dartsclub Steven en Hans. Steven, merci voor de vele schoon momenten de voorbije vier jaar. Ik denk met plezier terug aan onze waterjuffer-projectjes op stage, onze reis naar Canada en de States en gewoon alle leuke momenten op de TEREC zelf. Ik ben zeker dat ge nog een sjieke wetenschappelijke carriere voor u hebt liggen in Camebridge, Costa Rica en wie weet waar nog allemaal. Hans aka daddy Matheve, sorry dat ik u zo vaak heb laten verliezen :). Nee, serieus, merci om altijd beschikbaar te zijn voor nen babbel of een noodsituatie in het koffielokaal. Den TEREC zou niet hetzelfde zijn zonder u.

Katrien, met u valt er altijd iets te beleven. Meestal gaat er iets kapot als ge mee op stap gaat maar dat maakt die avonden eens zo legendarisch. Bedankt ook voor uw inspanning om het mijtenwerk klaar te stomen voor mijn thesis. Ik denk dat we dat samen heel goed gedaan hebben. Alex, thank you for the many laughs and free cocktails! I’m sure your story at the TEREC is not over yet, you really have a winner in you ;). Adriana, gracias por escuchar mi terrible español con paciencia. Jasmijn, je was een top thesisstudente en ik wens je veel succes met je doctoraat. Annelies, jou wens ik veel geluk toe in je huisje met zwembad, ezel, en schaap; klinkt als de perfecte plek voor een eerste reünie! Charlie, Leen, Els merci voor alle geestige momenten! Luc, Viki, Angelica bedankt voor de ondersteuning, jullie zijn de stille motor achter de TEREC maar weet dat ik jullie werk zeer appreciëer. Dirk en Lynda, bedankt voor de vele interessante gesprekken aan de koffietafel. Thank you Brambo, Bdog, Pieter, Céline, Helena, Laurence, Chrisoph, Bram Sercu, Dries

Van Loock, Alejandro, Cátia, Lander, Frederik, Carl, Liesbeth, Valérie, Lucien, Tanja and Jacob for the good times we had together.

Thank you Emanuel Fronhofer and Alex Kubisch for the pleasant collaboration, hospitality, and friendship.

Bedankt Dirk Helsen om mijn interesse in Biologie en de wetenschappen aan te wakkeren en me het zelfvertrouwen te geven om hiervoor te gaan.

Bedankt Chris en Amber, voor de talloze lekkere maaltijden en steun in goede en kwade dagen.

Bedankt Joris, Dries, Lisa en Dennis, hermanos y hermana! Zonder jullie zouden de dagen een stuk donkerder zijn.

Bedankt Familie, voor de warmte, goede raad en verbouwingshulp (Gerd = held). In het bijzonder, bedankt moemoe voor de ontelbare pistolets en zo veel meer.

Bedankt vader en (vooral) moeder om ons zo goed te soigneren. Ik kan met geen woorden beschrijven hoeveel jullie ondersteuning betekent voor Jill en mij. Het aantal maaltijden, wasmanden, of ritjes naar het containerpark is niet meer bij te houden. Laat staan de gesprekken, warmte of talloze kleine attenties, bedankt, bedankt, bedankt.

Tenslotte, bedankt Jill voor uw engelengeduld en liefde. Samen gaan we er geraken!

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1

General introduction.

Jeroen Boeye.

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1.1 Caught between a rock and a hard place

Let’s assume a lineage of organisms that consistently lives and reproduces on the exact same spot. Clearly this lineage would get in trouble quite soon, local resources would deplete and there would be strong competition between the members of our theoretical lineage. Even if this population were to reach a stable state, in the long run it would be doomed due to temporal variability in both biotic- (e.g. parasitism, predation, interspecific competition,...) and abiotic effects (e.g. sea level rise,...). To avoid this ill fate, every individual organism should ‘consider’ leaving the place where it was born. This process is called dispersal and is commonly defined as any movement of individuals or propagules with potential consequences for gene flow across space (Ronce 2007). The opposite of not dispersing at all, dispersing as far as possible from the natal site, would not be a very good strategy either since dispersal itself comes with a wide variety of direct and indirect costs (Bonte et al 2012). Therefore, the challenge becomes to balance these costs and benefits in a dispersal strategy. The diversity in dispersal strategies observed in nature can be explained by the complex interplay between costs and benefits to dispersal which differ between species, populations and individuals. Finally, these costs and benefits are not constant but continuously changing, together with the environment; these changing selection pressures result in the evolution of dispersal strategies. The current, anthropogenic, changes observed in nature such as global warming and habitat deterioration speed up this process and make this an interesting and relevant time to study dispersal and its evolution.

1.2 Why is dispersal important?

Dispersal plays a key role in answering a very old ecological question, which is why species occur where they do and what limits their ranges (Kubisch et al 2014). In the long history of this question, work by Andrewartha and Birch (1954) marked a turning point where the importance of local extinctions and (re)colonisations became acknowledged. This idea was applied on oceanic island systems by (MacArthur et al 1967) who introduced the species-area relationship and thereby laid the foundations for the SLOSS (single large or several small) debate on the optimal spatial structure of conservation reserves (Diamond 1975; Tjørve 2010). In the same spirit (Levins 1969; Levins 1970) came up with the idea of a ‘population of populations’ or metapopulation. A concept that was further developed by (Hanski 1999; Hanski and Gaggiotti 2004) and is widely applied in both theoretical and conservation biology (Fronhofer et al 2012). Dispersal is central in this framework; not only because it affects extinction and (re)colonization probabilities but also because of its many, often subtle, ecological effects; On a multi-species level it affects species-interactions, be it of the predator-prey (Holt et al 2011; Pillai et al 2012; Travis et al 2013b), competitive (Durrett and Levin 1998; Lanchier and Neuhauser 2006; Abrams 2007), mutualistic (Yamamura et al 2004; Travis et al 2005) or host-parasite type (Chaianunporn and Hovestadt 2012a; Chaianunporn and Hovestadt 2012b).

Within species dispersal interacts with population genetics (Short and Petren 2011; Fronhofer et al 2011; Kubisch et al 2013), intra-specific competition (Lambin et al 2001; Entling et al 2011) and landscape effects (Brachet et al 1999; King 2002; Bonte et al 2006). The landscape's structure is particularly interesting as it not only affects the dispersal strategy but also the stability of coexistence between two competing specialist species; this is the topic of our work in chapter 2.

In recent decades dispersal has become a hot topic in light of two of the main factors of global change, i.e. habitat fragmentation and global warming. Rapid habitat loss and fragmentation challenges populations to persist and remain connected (Fahrig 2003) while global warming forces populations to quickly adapt or track their preferred conditions through space (Visser 2008). Moreover, the negative interaction between both effects makes them even more troublesome (Warren et al 2001; Travis 2003).

Glossary

Evolutionary rescue:
The idea that evolution might occur sufficiently fast to arrest population decline and allow population recovery before extinction ensues .

Diapause:
A physiological state of reduced growth, development and physical activity with very specific initiating and inhibiting conditions used as a mechanism to survive predictable, unfavorable environmental conditions.

Dispersal kernel:
The probability distribution of the distance traveled by an individual.

Spatial sorting:
An evolutionary mechanism that in contrast to classic natural selection sorts individual through space rather than through time. This mechanism is especially powerful at expanding range fronts.

Allee effect:
The positive correlation between local population density and individual fitness that can occur in small populations also known as 'undercrowding'. An ultimate cause can be inbreeding.

Kin-competition:
Competition with closely related individuals. This is more costly than standard intra-specific competition since not only the individual itself is affected but also those individuals sharing the same genes.

1.3 Dispersal evolution

Dispersal traits have repeatedly been shown to be heritable (Saastamoinen 2008) and evolve (Bowler and Benton 2005; Ronce 2007; Clobert, Baguette, Benton 2012). This has to be taken into account when making predictions on species responses to environmental changes, especially since the feedback between ecology and evolution can occur rapidly (Stockwell et al 2003; Carroll et al 2007). Changes in the landscape's structure are a factor driving rapid dispersal evolution (Bonte and Lens 2007; Cheptou et al 2008; Hanski and Mononen 2011). Given the current process of anthropogenic habitat loss and fragmentation we can expect selection for less and shorter distance dispersal as the cost to disperse increases (Travis and Dytham 1999; Murrell et al 2002b). In a worst case scenario this could bring numerous species on the path of evolutionary suicide as has been observed in *Centaurea corymbosa*; a rare, endemic plant species that has entered a spiral of decreasing dispersiveness leading to the isolation of the remaining sub-populations in a very small area (Colas et al 1997). However, to the majority of species the spatiotemporal variation in fitness will be sufficient to promote dispersal (Heino and Hanski 2001). Furthermore, our changing world also creates certain selection pressures promoting dispersal (Kokko and López-Sepulcre 2006). Important examples are the positive selection pressures on dispersal at range fronts during range shifts and expansions. These two phenomena may have different origins (range shifts are most often associated with tracking preferred environmental conditions while expansions are more associated with invasive species), if the rate of environmental change is high enough the dynamics that happen near the expanding range front are quite similar. At this location an evolutionary process called spatial sorting may take place (Shine et al 2011). Since more dispersive individuals are more likely to reach the empty habitat near expanding range fronts they will occur in these areas in relatively high frequencies. Consequently, these high dispersive individuals will produce offspring more dispersive than the population average (i.e. the Olympic village effect (Phillips et al 2008)). Since this spatial sorting process repeats over several generation a fast evolution of high dispersive individuals can be expected near the expansion front. However, the strength of spatial sorting depends on the amount of standing genetic variation on dispersal traits in the population (Boeye et al 2013). A famous example of this phenomenon can be found in the invasion of the cane toad (*Bufo marinus*) in Australia, where toads near the range front tend to move more often, farther, and follow straighter paths than toads from old populations (Phillips et al 2006; Phillips et al 2008; Brown et al 2014). Apart from traits related to movement and dispersal, several life-history traits (e.g. developmental speed) are expected to evolve in response to range expansions. In chapter 5 we study this interesting phenomenon in the two-spotted spider mite (*Tetranychus urticae*) which underwent a recent northward expansion.

The significance of evolution as an important driving process of range expansions is currently recognized by both empirical (Thomas et al 2001; Phillips et al 2006; Phillips et al 2008; Léotard et al 2009) and theoretical work (Garcia-Ramos and Rodriguez 2002; Travis and Dytham 2002). Results from a simulation model developed by (Phillips 2011) suggest that recent range shifts could even promote the formation of stable range edges because more dispersive individuals experience environmental gradients more intensively; a different model suggests that when dispersal costs at range margins become too high, selection against dispersal may eventually induce range contraction (Kubisch et al 2010). However, high dispersal rates are known to evolve at range borders and to induce evolutionary rescue in theoretical studies (Travis et al 2009; Bonte et al 2010; Fronhofer et al 2011). This is something we explore in chapter 4 where we study the effects of different rates of climate change on the evolution of dispersal distances in a population shifting its range. We investigated whether these changes could increase the capability of the population to deal with habitat fragmentation (i.e. evolutionary rescue).

1.4 The cost of staying and the cost of dispersal

In general, dispersal is favoured as long as individuals have a higher inclusive fitness when they move away from their natal habitat (Frank 1986; Metz and Gyllenberg 2001; Poethke and Hovestadt 2002; Dytham 2003; Bowler and Benton 2005). Therefore, spatio-temporal variance in fitness is necessary to make investments in dispersal attractive and this variance will shape the selection pressures on dispersal traits. There are a number of costs that reduce the fitness in the natal habitat. The most important ones are inter- and/or intraspecific competition for resources (Lambin et al 2001), kin-competition (Hamilton and May 1977; Comins 1982; Kisdi 2004), inbreeding (Perrin and Goudet 2001) and the spatio-temporal variability of resource availability (Levin et al 1984; Travis and Dytham 1999; Gandon and Michalakis 2001; Hof et al 2012). The costs of dispersal can be divided into four types, i.e. energetic costs, time costs, risks costs and opportunity costs. Bonte et al (2012) divided these costs over the three stages of dispersal i.e. (pre-)departure, transience and (post-)settlement (Clobert et al 2009). Before and during departure both energy and risk costs are involved; these energy costs are preparatory investments to increase the movement capacity of the individual while some of the risk costs are the higher probability to be predated or to settle in unsuitable habitat. During the transience phase an energy cost has to be paid to maintain basic life functions (especially relevant for passive dispersal) while active dispersers will also have to pay the cost to realise movement. Finally, during and after settlement individuals can face all four cost types, i.e. the risk to be predated or end up in poor habitat, the energetic cost to actively settle (e.g. anchoring in marine plankton (Olivier and Retière 2006)), the time cost to select optimal habitat and the opportunity costs of decreased survival, reproductive success, decreased social rank or Allee effects.

1.5 **Individual-based modelling**

‘All things are difficult before they are easy’

Thomas Fuller

Ecologists are drawn to computer models because they allow them to simulate complex systems and unravel the inner mechanisms by repeating different scenarios over long timescales. Individual-based models (IBMs) are particularly popular because they allow biologists to model in an intuitive, object oriented way. Typically, a blue print of an individual is created which holds the capacity to store traits relevant for the model in mind (e.g. age, sex, dispersal rate...). This blue print or ‘object’ can then be personalised for each separate individual. Next, relevant procedures are created to simulate population dynamics (e.g. reproduction, survival, movement...). Stochasticity can easily be imbedded within these procedures by sampling random numbers to determine the outcome of a process (e.g. dispersal and mortality rate). This is an advantage of IBMs compared to analytical models which are usually deterministic. Once a population of reproducing individuals is initialized the model will run independently and data can be extracted. The incorporation of evolution only requires a mutation procedure on traits passed on from parent to offspring. To create a spatially explicit model a landscape ‘object’ should be made with characteristics such as the dimensions of the landscape and local habitat qualities. Once space is incorporated and offspring are produced close to their parents kin-competition becomes present by default (Poethke et al 2007). This is not the case in analytical models where the multi-generational effects of kin-competition are hard to incorporate. Finally, it is possible to visualize the population to actually see the modelled dynamics in action.

IBMs are increasingly popular among ecologist. Grimm et al. (2006) state that ‘IBMs are important both for theory and management because they allow researchers to consider aspects usually ignored in analytical models: variability among individuals, local interactions, complete life cycles, and in particular individual behaviour adapting to the individual’s changing internal and external environment’. However, they have the disadvantage of being complex and are hard to validate, reproduce and analyze (Grimm 1999; Grimm et al 2006). Therefore, efforts have been made to create standard procedures for IBMs (Grimm et al 2006; Grimm et al 2010) and develop methods to validate and optimize their fit to empirical data (Wiegand et al 2003). ‘Pattern oriented modelling’ (Grimm 1994; Grimm et al 1996; Wiegand et al 2003) aims to aggregate significant ecological information and scales into a model and allow a better determination of parameter values by systematically comparing observed and simulated patterns. After optimizing the fit between these two, secondary predictions of a higher quality can be made. In chapter 5 we applied this approach.

All code for this thesis was written in the Python programming language (version 2.7.2) except for the work in chapter 4 which was created in Delphi with the Pascal language. The Python code is publicly available through: https://github.ugent.be/jboeye/Phd-code.

1.6 Modelling movement and dispersal

1.6.1 The struggle for optimal complexity

During the creation of a model though decisions have to be made on the level of detail to incorporate in the simulation. It is tempting to include high levels of detail in every model but this requires proper parameterization and increases the computational load. On the other hand, models with very little detail tend to ignore important behaviour, processes or influences and therefore produce generic results that cannot be applied to a specific study system. Therefore the appropriate implementation of movement and dispersal in a model depends on the study system and goal in mind; this explains the diversity of approaches used in the literature (see Table 1). Models on passively dispersing organisms clearly don't need complex movement behavioural rules, although zoochory may form an exception (D'hondt et al 2012). When dealing with complex movement behaviour and/or small temporal and spatial scales one can wonder whether it is still appropriate to summarize this movement as a simple dispersal process. There is a growing consensus that incorporating movement behaviour into the dispersal phase more explicitly can provide an added value to models and several efforts have been made to create a framework for doing so (Travis et al 2012; Baguette et al 2014). Movement ecology is an expanding field and technological advances in tracking devices that become ever smaller and bring in huge amounts of high quality data promise this field a bright future (Jeltsch et al 2013). However, when dealing with large populations over large spatial and temporal scales simplifications of this complex behaviour are unavoidable in which case we have to focus on the partition of movement contributing to actual dispersal i.e. the distance between natal site and site of reproduction. Depending on the spatial scale dispersal can be modelled as a local or a global process. In certain cases it can be appropriate to combine both local and global dispersal in a single model, an example can be found in Bonte et al. (2010) where a dispersal polymorphism in spiders (crawling or ballooning) was studied. In this case the spatial scale in mind must be restricted to a magnitude of kilometres to make the assumption hold that aerial dispersal (ballooning) results in global dispersal. A final example comes from chapter 5 where we also model aerial dispersal by an arachnid, since the spatial scale in this model spans about 1000 km we assume aerial dispersal to be a local process modelled as nearest neighbour while local movement (crawling) is ignored.

1.6.2 Techniques to model dispersal

In the most basic, analytical, population dynamics model the dispersal process can be incorporated on the population level as the number of immigrants (I) and emigrants (E) that is added to and subtracted from the local population size:

$$N_t = N_{t-1} + B - D + I - E$$

Here N_t is the population size at time t and B is the number of births while D is the number of deaths. In a real-world situation where all individuals in a population are monitored this approach is quite straightforward to keep track of the current population size and dynamics. Individuals undertake certain actions, events happen, and we observe. However, in our modelled, virtual world nothing happens unless we implement it. As a consequence, we can't simply obtain a relevant number of immigrants or emigrants. We have to calculate these numbers somehow. A first step is to realise that the number of births, deaths and emigrants depend on the population's size. We thus have to shift from working with independent numbers to numbers that stand in proportion to the population size. The easiest way to achieve this is to assume that there are certain probabilities connected to each event or behaviour. These probabilities can then be implemented as a rate (i.e. a number between 0 and 1) which is multiplied with the population size to obtain the number of individuals that execute the action coupled to this rate. Examples are birth, mortality, immigration, and emigration rates which ideally are parameterized with empirical data. The combination of these different rates will then determine the population dynamics. However, this rate-based model still has one major issue; the population will either crash or keep growing exponentially. This can be resolved by imposing a form of regulation such as density dependence; we only have to insert a density dependence factor (1-(N/K)) where K is the carrying capacity. When the population size is lower than K this model will perform logistic growth, if the population size is higher it will decrease towards K.

An update of the simple population dynamics equation to include rates rather than absolute numbers, and density regulation results in:

$$N_t = N_{t-1} + (b - m - e)(N_{t-1}(1 - \frac{N_{t-1}}{K})) + I$$

In this equation b, m, and e are the birth, mortality and emigration rate respectively. In certain scenarios the emigration and/or immigration probabilities will depend on environmental conditions such as local density or resource abundance (Hovestadt et al 2010). However, we cannot calculate an immigration rate in this equation because we have no idea of the population dynamics outside of this particular population. To achieve this we have to incorporate space and start looking at multiple connected populations (i.e. a metapopulation). By coupling a spatial explication to an emigration and/or immigration event we take modelling dispersal to a new level.

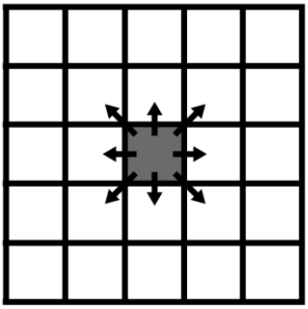

Figure 1: Visualization of nearest neighbour dispersal, the individuals from the central, gray, patch can disperse into the 8 adjacent cells.

In a spatially explicit model emigration could be implemented on the individual level and be coupled to a simple form of movement from the natal patch such as nearest neighbour dispersal (see Figure 1). Alternatively a fixed dispersal distance can be used or, finally, a distribution of probabilities to disperse a certain distance, i.e. a dispersal kernel (see Figure 2). Such a kernel can be parameterized with actual data (e.g. from seed capture experiments) or a certain functional shape can be assumed. Using a particular function for a kernel holds the benefit that with one or two function parameters a variety of shapes and thus dispersal strategies can be obtained. This allows a much more realistic incorporation of dispersal (distance) into models. Moreover, it is possible to allow function shapes to evolve, thereby optimizing the kernel shape. However, using this method optimal kernel shapes will always be restricted by the assumed function (Dieckmann et al 2006). In chapter 3 we studied the optimal kernel shapes in response to local densities and three environmental scenarios. We use a novel technique that allows the dispersal kernel to optimize without assuming a certain functional shape a-priori.

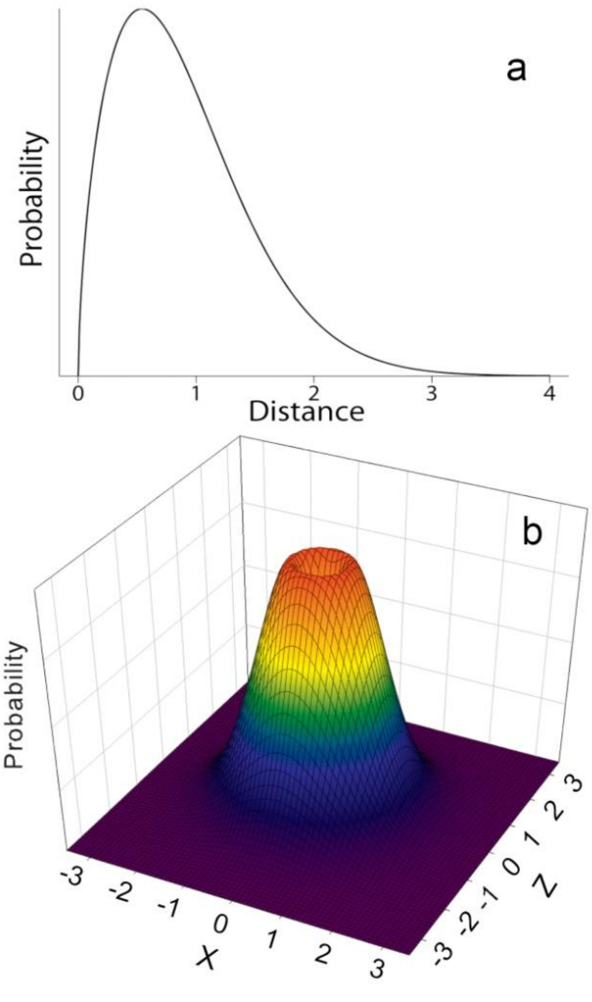

Figure 2: An example of a distance probability function or kernel in both 2 (a) and 3 dimensions (b). The function shown here is of the Weibull type.

Table 1: Overview of recent papers modelling movement and/or dispersal. Note the diversity in modelling techniques to simulate dispersal. The four papers represented in the chapters of this thesis are in the last four rows. (LDD is long distance dispersal).

				How was dispersal/movement modelled?	
Paper	**Subject**	**Type**	**Entity scale**	**Once in a lifetime event?**	**Dispersal modes**
(Mona et al 2014)	The combined effects of range expansion and habitat fragmentation	IBM	Individual level	Yes	N. neighbour with emigration rate + LDD with γ-kernel
(Kubisch et al 2014)	Modelling informed vs. random dispersal	IBM	Individual level	Yes	N. neighbour with emigration rate
(Travis et al 2013b)	Evolution of Predator Dispersal in Relation to Spatio- Temporal Prey Dynamics	IBM	Individual level	Yes	N. neighbour with emigration rate or several informed moves by predators
(Nagelkerke and Menken 2013)	Species coexistence in multiple habitat landscapes	Analytic	Species level	Yes	Colonization rate
(Henry et al 2013)	Eco-evolutionary dynamics of range shifts	IBM	Individual level	Yes	Negative exponential kernel
(Weiner and Xiao 2012)	Specialization and local diversity in model communities	IBM	Species level	Yes	Global dispersal
(Urban et al 2012b)	Competition and dispersal differences cause extinctions during climate change	Analytic	Species level	Yes	Leptokurtic kernel (Laplace distribution)
(Barraquand and Murrell 2012)	Predation selection on prey dispersal	IBM	Individual level	No	Gaussian kernel as juvenile + repetitions of dispersed juvenile distance as adults
(Bartoń et al 2012)	Risky movement increases the rate of range expansion	IBM	Individual level	No	Biased correlated random walk
(Boeye et al 2014)	Habitat structure and coexistence	IBM	Individual level	Yes	Gaussian kernel
(Boeye et al 2013)	Climate change selection on dispersal distance	IBM	Individual level	Yes	Gaussian kernel
(Boeye et al. under review)	Optimal dispersal kernels	IBM	Individual level	Yes	Function valued trait (flexible kernel)
(Boeye et al. in prep.)	Effects of current range expansion of life history of spider mite	IBM	Individual level	Yes	N. neighbour with emigration rate

1.7 Thesis outline and research questions

1.7.1 Thesis overview

Dispersal and the eco-evolutionary forces that shape selection on this trait are central to this thesis (see Figure 3 for overview). Our ultimate aim to expand our understanding of the complex network of abiotic influences, biotic interactions, and eco-evolutionary feedbacks in which the dispersal process is embedded. Each chapter offers a different angle on this complex issue and has its own approach to come to unique result. In chapter 2 we do not yet incorporate evolution but rather focus on the importance of spatial effects (i.e. landscape structure) on species interactions. One of our conclusions is that the strength of these spatial effects depends on the average dispersal distance. As Figure 3 shows, this chapter is less interconnected with the other chapters. In the general discussion (Chapter 6) we bridge this gap with a variant of the model where dispersal is allowed to evolve. Chapter 3 shift the focus towards the dispersal process itself. We introduce evolution of dispersal kernels in function of local density and develop a novel approach to optimize dispersal strategies. We find different optimal strategies in different spatial demographic scenarios. For instance, during a range expansion individuals are expected to disperse longer distances. This result is also found in chapter 4 where we couple this increase in dispersal to an increased capability of the population to deal with habitat fragmentation. Finally, in chapter 5 we apply our knowledge of range expansions to an empirical system. We realise that not just dispersal traits are under selection during range expansion but also a number of life-history traits that affect fecundity and longevity. These life-history traits undergo strong selection to become locally adapted during the expansion in order to synchronise the multiple generations per growth season with the season length which decreases with latitude. We compare the empirical results with those from a highly parameterized simulation and find interesting, non-trivial patterns. In Chapter 6 we present an integrated discussion on these chapters.

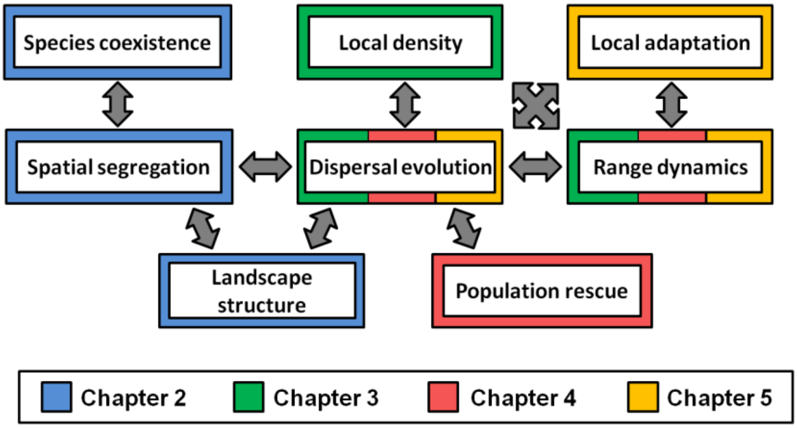

Figure 3: The interconnection of themes handled in this thesis. The colour codes show the focus of the chapters.

1.7.2 Overview and research questions per chapter

Chapter 2 aims to clarify the complex effects of habitat structure on the coexistence between two competing, specialist species. What are the most important landscape characteristics in such a system? Does fragmentation always destabilize coexistence? What are the different effects of random and structured landscape configurations? We systematically implement a wide range of habitat structures to answer these questions and measure whether or not species can coexist in the given configuration. When coexistence is possible we look into the specifics of the two species relation. How strong is intra vs. interspecific competition? Are the species overlapping spatially or restricted to separate ranges? Is one species dominant? Finally, we briefly investigate the effects of different average dispersal distances.

Chapter 3 reports on a study of optimal dispersal kernels under a range of costs and benefits to dispersal with a focus on the spatial distribution of densities. We extend current theory on optimal dispersal rates to actual dispersal kernels. A method was developed that allows genotypes to evolve under a local density that is constant over generations and set to a value of interest. This stable selection allows evolution to mould the kernel into its optimal shape. According to which distance function (e.g. Gaussian, negative exponential…) should individuals disperse to maximize their fitness? Do different functions apply under different condition or is there one function to rule them all? We test these questions for three scenarios, a range expansion, a meta-population with synchronous dynamics and a meta-population with asynchronous dynamics.

Chapter 4 is a study on range shifting dynamics. In this chapter we evaluate the effects of rapid dispersal evolution under different rates of climate change on the capabilities of a population to deal with habitat fragmentation after a period of range shifting. Could the known selection for higher dispersal distances under range shifting allow evolutionary rescue of the population?

Chapter 5 brings together empirical work and theory on range expansions. We try to gain deeper understanding of the effects of a recent range expansion on life-history traits of the spider mite *Tetranychus urticae*. Important traits of interest were the tendency to disperse; developmental time, and fecundity. Mites were sampled over a latitudinal range along the coastline from Belgium up to northern Denmark. We created a simulation that has the same spatial dimensions as the territory in which the expansion occurred. This model was parameterized with empirical data on mite life-history traits and a latitudinal temperature gradient to recreate and compare a stable range and an expanding range scenario.

2

Habitat structure mediates spatial segregation and therefore coexistence.

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This chapter was published in *Landscape Ecology* (2014) Vol. 29

2.1 Abstract

Understanding the mechanisms driving diversity in nature is an important and ongoing challenge in our changing world. To efficiently conserve biodiversity it is crucial to explain why and how species coexist. Over the last decades models explaining species coexistence have increased in complexity but usually don't incorporate a detailed spatial context. However, spatial structure has been shown to affect species coexistence and habitat deterioration is one of the biggest threats to biodiversity. We therefore explore a spatially explicit two species model and assess the effects of habitat structure on species coexistence using a wide diversity of fractal landscapes. Each species is specialized in a particular habitat type. We find that landscape structure has a major influence on the stability of a two species system and may be sufficient to explain the coexistence of two species. Well connected and highly structured habitat configurations allow spatial segregation of both species and this decreases local interspecific competition; in our model this is the most important process stabilizing coexistence.

2.2 **Introduction**

For more than half a century the question of what processes allow coexistence of competing species has been central in ecology. Early work by Lotka (1932) and Volterra (1926) provided the foundations of this field by demonstrating that two species can only coexist if intraspecific competition is stronger than interspecific competition. Coexistence among competing species is, however, a common phenomenon (Gravel et al 2011). This discrepancy between theory and reality can be explained by the simplifying assumptions in the basic Lotka-Volterra equations, such as an environment that is spatially homogeneous and temporally stable, with interactions occurring globally. Already in 1933 Nicholson stated that the environment has an important influence on the '*balance*' between species after competition. More recently, the importance of spatial complexity for species co-existence is slowly becoming fully appreciated (Chesson 2000; Snyder and Chesson 2004). Particularly, when resources are heterogeneously distributed, a "spatial storage effect" can take place, concentrating intraspecific competition relative to interspecific competition (Amarasekare 2003), resulting in a reduced spatial overlap of metapopulations (Murrell et al 2002a; Snyder and Chesson 2003; Hanski 2007). The inclusion of a spatial component and local interactions will in consequence alter predictions based on non-spatial models (Pacala and Tilman 1994; Neuhauser and Pacala 1999) and is therefore essential to understand metacommunity dynamics (Holyoak et al 2005) and biodiversity patterns in general (Jeltsch et al 2013). Although models explaining species coexistence have increased in complexity over the last decades, they usually don't incorporate detailed spatial properties and are thus not designed to explore the spatial parameter space allowing coexistence.

Spatial habitat structure is in its simplest form determined by two parameters, habitat availability and its level of clumping (i.e. the opposite of the level of fragmentation). It is known lowering either of these parameters can decrease the stability of species co-existence through the reduction of metapopulation sizes and the alteration of species interactions (Ewers and Didham 2006). Quite counter intuitively, the effects of habitat fragmentation per se (when ignoring the effects of habitat loss) on biodiversity are often positive (See Hanski 1995 and Fahrig 2003 for a review as well as Yaacobi et al. 2007, Bonin et al. 2011) and partially attributed to the fact that weaker competitors can find refuge in empty habitat fragments (Levin 1974) and/or that equally competitive species become spatially segregated (Hanski 2007). In order to test the impact of spatial structure on how two species interact and coexist, we developed a model simulating two competing habitat specialist along a variety of fractal landscapes consisting of two types of suitable habitat. A two specialist species system represents one of the simplest forms of competition and, following niche-theory, allows potential coexistence (Chesson 2000). We manipulate the competitive balance in the system by varying the proportions and spatial structure of two suitable habitat types which are favoured by either specialist. Furthermore, we test different dispersiveness levels over several simulations since higher dispersal distances are expected to destabilize coexistence (Débarre and Lenormand 2011). We hypothesize that when habitat availability and habitat clumping are high, coexistence will be most stable, although species with a competitive disadvantage due to rarity of their preferred habitat type might benefit from fragmentation.

2.3 **The model**

A version of this section following the ODD (Overview, Design concepts, Details) protocol has been added to the appendix (page 124) (Grimm et al 2006; Grimm et al 2010).

2.3.1 The landscape

We generated fractal landscapes on a square lattice using the diamond-square algorithm (Miller 1986) with dimensions of 64 x 64 grid cells. In earlier work these theoretical landscapes usually only consist of unsuitable and suitable habitat (McInerny et al 2007). Like Wiegand et al. (1999) we increased complexity by splitting the suitable habitat into two types, edge and core habitat, with the former typically surrounding the latter (see core-edge configuration in Figure 4). Each species is specialised in one of those two suitable habitat types (i.e. higher reproductive output), but apart from this both species are identical. The spatial structure of habitat patches is determined by the parameters P, H and P_{core}. P controls the total proportion of available suitable habitat (edge + core) and H stands for the spatial autocorrelation, which determines the degree of clumping of the suitable habitat patches (i.e. the opposite of the level of fragmentation). The third parameter P_{core} denotes the proportion of suitable habitat that is of the core type, 1-P_{core} would thus result in the proportion of suitable habitat of the edge type. The diamond-square algorithm creates a continuous 3D landscape with varying altitude. We simplified the altitude in this landscape into three discrete classes where the lowest altitudes become unsuitable habitat, the intermediate altitudes become edge habitat and highest altitudes become core habitat. Therefore, core habitat is typically, but not always, surrounded by edge habitat. We investigated population dynamics in landscapes where P, H and P_{core} systematically varied between their minimal (0.2 for P, 0 for H and P_{core}) and maximal value (1). Parameter values where changed in equidistant steps of 0.1, except for P_{core} in the random configuration which was changed in steps of 0.025 between 0.4 and 0.6. This led up to ±1000 possible combinations of P, H and P_{core} which all were tested. Each parameter combination was replicated 20 times in independently generated landscapes. The three spatial parameters are independent of each other and can result in unintuitive landscape structures. For example, when both habitat clumping (H) and availability (P) are low but P_{core} is high, it is possible to have a highly fragmented landscape with lots of edges but little “edge” habitat; instead, “core” habitat will directly border to unsuitable habitat, thus forming the “edge” of a habitat patch. However, in the majority of spatial parameter combinations core habitat is surrounded by edge habitat resembling fragmented landscapes with patches under influence of edge effects. This could for instance represent a system where an insect herbivore is confronted with host plants sensitive to edge effects having clumped distributions in the centre of an area of suitable habitat, and more stress tolerant host plant species inhabiting edges; or plants confronted with buffered soils surrounded by more micro-climatologically variable soils. In the first example, insect herbivores might either specialize on the plant species in the core or edge of the habitat, in the second case, plants could specialize to a buffered core- or unstable edge habitat.

In order to test the impact of this specific habitat structure generated by the diamond-square algorithm, we also generated a more scattered landscape with core and edge habitat randomly distributed within the suitable habitat cells (see random configuration in Figure 4). In this case it no longer makes intuitive sense to refer to core and edge habitat, but we keep doing so for reasons of consistency.

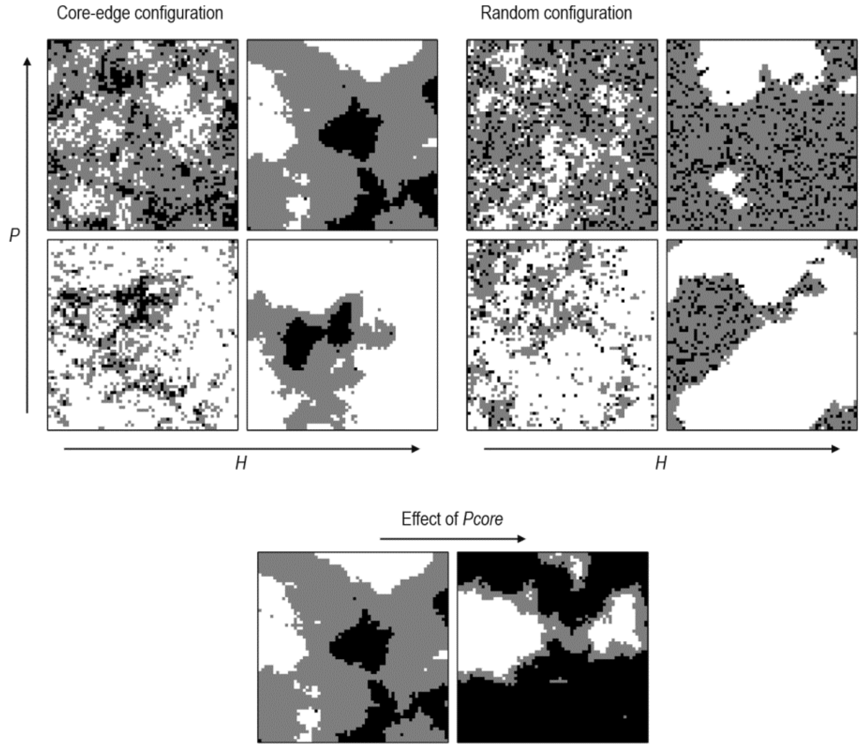

Figure 4: Illustration of the effects of the three landscape structure parameters *P, H* and P_{core} on the spatial configuration of the landscape. *P* is the proportion of suitable habitat (both core (coloured black) and edge habitat (coloured gray)) over unsuitable matrix (coloured white). *H* is the Hurst exponent and is a measure of spatial autocorrelation (the opposite of fragmentation. P_{core} is the proportion of core habitat over edge habitat. Both edge and core habitats are suitable to the model species.

2.3.2 The model species

We initialized the landscape with one thousand individuals of each of two specialist species. We only used two species to keep our model as simple as possible. No overlapping generations occur since adults die after reproduction. The reproductive output of individuals is sensitive to the type of suitable habitat they find themselves in. Also, the number of offspring produced is influenced by the total number of individuals (from both species) within a grid cell. The fact that individuals from both species contribute equally to the perceived local density makes intra-specific competition particularly strong since local density is the only driver of competition in our model. Offspring disperse a certain distance drawn from a predefined kernel (see below) and survive if they settle in a cell of suitable habitat. Reproduction was modelled as an asexual process. Within-population dynamics are based on well-understood density dependent demographic processes (Hassell and Comins 1976). The mean number of offspring μ which each individual will produce in its local habitat cell is calculated as follows:

$$\mu = \lambda(1 + aNt)^{-1}$$

with

$$a = (\lambda - 1)/N^*$$

Here, λ specifies the net reproductive rate which is different for the two species, N^* is the population equilibrium density for a single cell and is a constant set to 2, Nt is the summed local density of both species at time t; if Nt is higher than N^* the mean number of offspring (μ) will decrease below 1 due to competition and the local population will shrink. The actual number of offspring is drawn from a Poisson distribution with mean μ (Travis and Dytham 2002; Kubisch et al 2011). In our models individuals have a net reproductive rate (λ) of 1.5 if they find themselves in a cell of their non-preferred habitat type and 2.5 if the cell is of their preferred habitat type. These relatively low parameter values were chosen for reasons of speeding up computational power and because we found by sensitivity analyses that they did not qualitatively impact the model outcome.

2.3.3 Dispersal

In order to focus on the effect of competitive abilities generating coexistence, and not factors related to asymmetric dispersal, all individuals share the same dispersal kernel from which their individual dispersal distance is sampled. The shape of this kernel is defined by the parameter δ which determines the standard deviation of a two dimensional Gaussian distribution with mean zero (Bonte et al 2010). We use δ as a measure for dispersiveness since high δ values lead to wide kernels with approximately 32% of the population moving beyond distance δ (principal characteristic of a Gaussian distribution). We explore the effect of different δ values in several simulation runs; the standard value is 1 and results in an average dispersal distance of 1.3 grid cells (for more details see Boeye et al. 2013).

2.3.4 Quantifying population dynamics & coexistence

After 1000 generations we measure three population statistics. The first one is a measure of coexistence at the global scale, i.e. co-occurrence under equilibrium conditions at the landscape level. This value is calculated by dividing the number of individuals of the rarest species at the last time step by the number of individuals of the most abundant species and multiplying this number by 100. The global coexistence is at its maximum (100%) when on a global scale both species are equally abundant whereas a value of 0% indicates the total exclusion of one species. The second value is the percentage of inhabited grid cells occupied by individuals of both species (i.e. the local co-occurrence) and is a measure of the rate of interspecific competition at the final time step. By combining these two values we are capable of inferring whether, and to what extent, species coexist and interact on a local and global scale for each landscape structure. The third value represents the habitat fidelity; it is a measure of how true individuals of a species are to their preferred habitat type and is calculated by dividing the number of individuals in the preferred habitat type by the total number of individuals from that species. The habitat fidelity results are summarised in Appendix Figure 1.

2.3.5 Statistics

In order to partition the variance explained by landscape parameters P, H and P_{core} and their interactions we performed logistic regression on the population size of one species relative to the total population size based on 20 replicates within each parameter combination. The three variables were modelled as random effects to determine the percentage of explained variation.

2.3.6 Sensitivity analysis

The size of the landscape has a positive effect on the success of the weakest species in any type of habitat structure. It also increases the range of parameter combinations in which two species share a significant number of habitat cells. Increasing the length of simulations from 1000 to 2000 generations had no significant effect on the results, although some additional extinctions occurred in scenarios where one species was rare. However, we chose not to further increase the length of the simulation since the assumption of temporal stability then becomes increasingly unrealistic. Changing the reproductive output of both species had no qualitative effect on the results as long as the average reproductive output of both species in the two suitable habitat types was equal.

Table 2 Overview of all parameters and variables. Note that σ has a value of 1 in all simulations except those where the effect of dispersiveness was explicitly tested. The maximum value for Nt is not applicable since in theory there is none.

Parameters	Explanation	Value/range
$\lambda_{preferred}$	The growth rate in preferred habitat	2.5
$\lambda_{unpreferred}$	The growth rate in unpreferred habitat	1.5
σ	The standard deviation of the Gaussian dispersal kernel	0.5, 1 or 2
P	The total proportion of suitable habitat (core + edge type)	0.2 - 1
H	The Hurst exponent denoting habitat clumpedness	0 - 1
P_{core}	The proportion of core type habitat within the suitable habitat	0 - 1
N^*	The population equilibrium density (per grid cell)	2
Measured variables		
N_t	The summed local density of both species (per grid cell)	0-n/a
Global coexistence	How even both species abundances are on a global level, it is maximal when the two species abundances are equal and minimal when one species is extinct.	0-100%
Local co-occurrence	The proportion of occupied grid cells that are occupied by the two species	0-100%

2.4 **Results**

2.4.1 The impact of landscape structure: habitat availability (P), clumping (H) and distribution (P_{core}).

The outcome of competition is principally determined by the relative proportions of core and edge habitat (P_{core}), which alone explained 44% of the variation in species coexistence and another 39% in interactions with the total proportion of habitat P (15%), its clumpedness H (16%) and the three way interaction with these two (8%). When we focus on the sole effect of P_{core} we notice that global coexistence gets higher as P_{core} values approach 0.5 (Figure 7: a); this results from a gradual shift in dominance from the edge specialist to the core specialist as we increase P_{core}. When we do include the effects of P and H we notice that the parameter space of global coexistence becomes smaller and less predictable in landscapes where little habitat is available and clumping is low (P and H are low) compared to when both are high (Figure 8). Thus, although P_{core} is the main factor mediating global co-occurrence, P and H determine the exact outcome of competition (see Figure 5,Figure 6 and Figure 8) and local level co-occurrence (See Figure 5: b and Figure 6: b and an online animation through Link 1 in the appendix). Furthermore, the impact of both parameters is highly interactive and has a major effect on local community structure (See Appendix Figure 1). For instance, when both habitat availability and clumping are low, conditions are so poor that stable coexistence is only possible on a global level when both species don't interact locally due to spatial isolation. Only when more suitable habitat becomes available and when it is more clumped together stable local coexistence becomes possible (see Figure 5 and Figure 6).

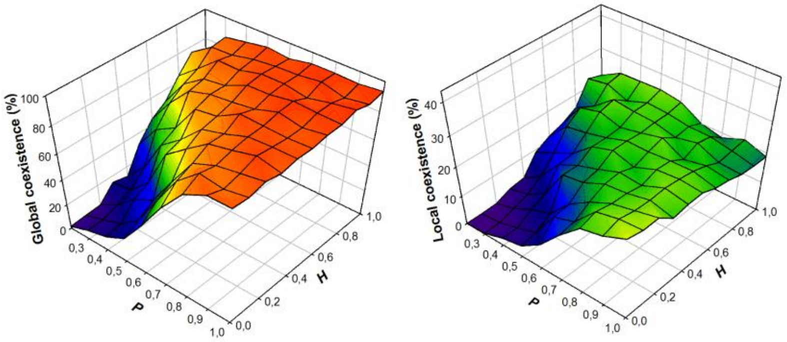

Figure 5: A representation of the outcome of competition after 1000 generations in the scenario with a core-edge habitat configuration. The extent of global co-occurrence for 99 combinations of P and H is represented in the graph to the left. In the right graph the percentage of local co-occurrence is depicted for the same parameter space. For both graphs the proportion of core habitat is 0,5. The prevalence of local co-occurrence strongly increases when P and H approach a value of 0,6 but remains rather constant

above this value (±25% local co-occurrence). This is due to spatial segregation of both species within one species aggregations. Note that in this scenario the H value has an influence on both the fragmentation of the suitable habitat itself and on the core habitat within.

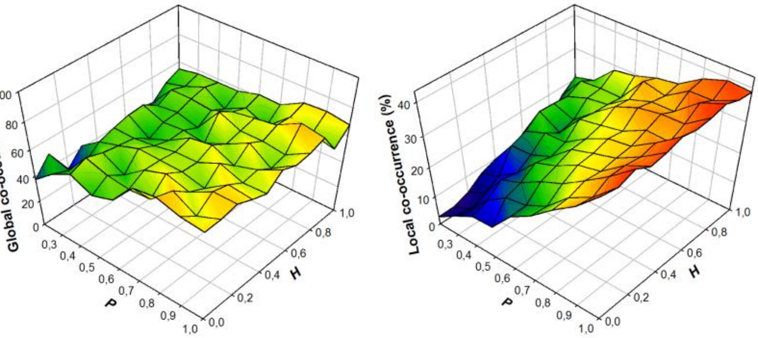

Figure 6: As Figure 5 but for the scenario with a random configuration of suitable habitat. The prevalence of local co-occurrence increases with P and to a lesser degree with H to reach values up to 40%. Note that in this scenario H only has an influence on the fragmentation of the suitable habitat and not on the distribution of the two habitat types within. This means that when P is 1 there is no effect of H.

When little habitat is available and clumping is low, the parameter space, in which coexistence is possible, shifts to low P_{core} values (Core-edge in Figure 8: a, Appendix Figure 1). This means that core specialists tend to benefit from these conditions relative to edge specialists since they can coexist when their preferred habitat type is scarce. In contrast, when habitat availability and clumping are high, the outcome of competition becomes very predictable in that both coexist according to the proportion, of their preferred habitat (Core-edge in Figure 8: i). The predictability of the outcome of competition can be explained by the fact that when more suitable habitat becomes available and when it is more clumped together, continuous areas of either the core or edge type become available and the two species tend to monopolize the areas where they have the competitive advantage. When habitat availability and clumping are sufficiently high the spatial distribution of species thus tends to equal the spatial distribution of both habitat types. Furthermore, this process of spatial segregation stabilizes coexistence, since interspecific competition is excluded from the centres of monopolized areas and only occurs near borders. Therefore, in the core-edge configuration, the proportion of local co-occurrence increases steadily when both habitat availability and clumping are low, but remains constant once the combined effects of habitat availability and clumping allow continuous areas of one habitat type (see Figure 5: a). This can only be explained by a process reducing interspecific competition, since total population size and thus global density increases with habitat availability (data not shown).

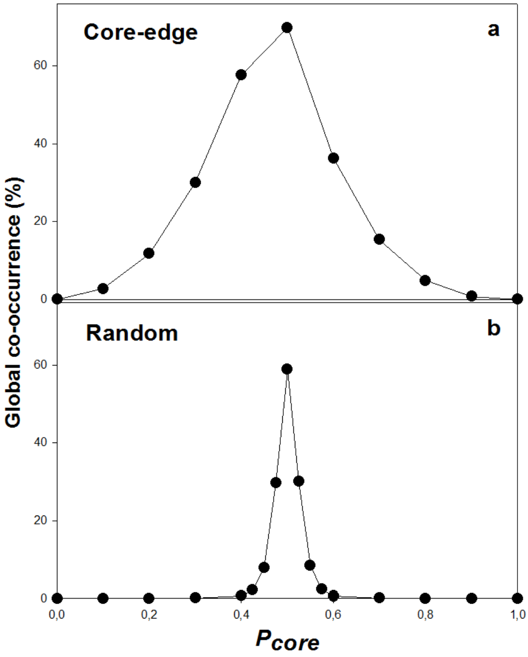

Figure 7: The separate effect of Pcore on the prevalence of global occurrence when other parameter dimensions are averaged out for both the core-edge and random habitat configuration. Of all spatial parameters Pcore has by far the strongest influence on the outcome of competition. The separate effects of P and H are negligible; however the interactions with Pcore can be highly significant (Figure 5,Figure 6 and Figure 8).

2.4.2 The effect of random habitat distribution within patches.

When both habitat types are distributed randomly within the suitable habitat, P_{core} becomes the only determinant of the global outcome of competition single-handedly explaining 92% of the variance. Moreover, the range of P_{core} values allowing global coexistence becomes much smaller (see Figure 7: b), there is thus a more rapid shift in dominance. While in the more spatially structured core-edge habitat configuration global and local coexistence is prevalent within P_{core} values of 0.1 - 0.8 (regardless of P and H values), this is now only the case in the narrow range of 0.4 - 0.6 (see Figure 7: a, b and an online animation through Link 1 in the appendix). If we repeat our statistical analysis in this narrow range of P_{core} values other parameters also become significant; P_{core} then only explains 29% of the variance individually and the interaction with P becomes equally important (31%). Weaker explaining variables of significance are P individually (8%), the interaction between P_{core} and H (9%) and the three way interaction between P_{core}, P and H (10%).

When both species coexist within a landscape where both habitat types are distributed randomly within the suitable habitat, the proportion of local co-occurrence can increase up to a maximum of 41%, relative to 28% in the core-edge habitat configuration when *P* = 1 (see online animation through Link 1 in the appendix). This means that interspecific competition is much more prevalent in the random landscape structure after 1000 generations. The impact of habitat availability and clumping on the persistence of both species was different compared to the more spatially structured core-edge habitat scenario: predictability of the exact level of global coexistence remains low for all combinations of *P* and *H* and the benefit core-specialist seem to have from low *P* and *H* conditions is absent in the core-edge configuration (Figure 8: a).

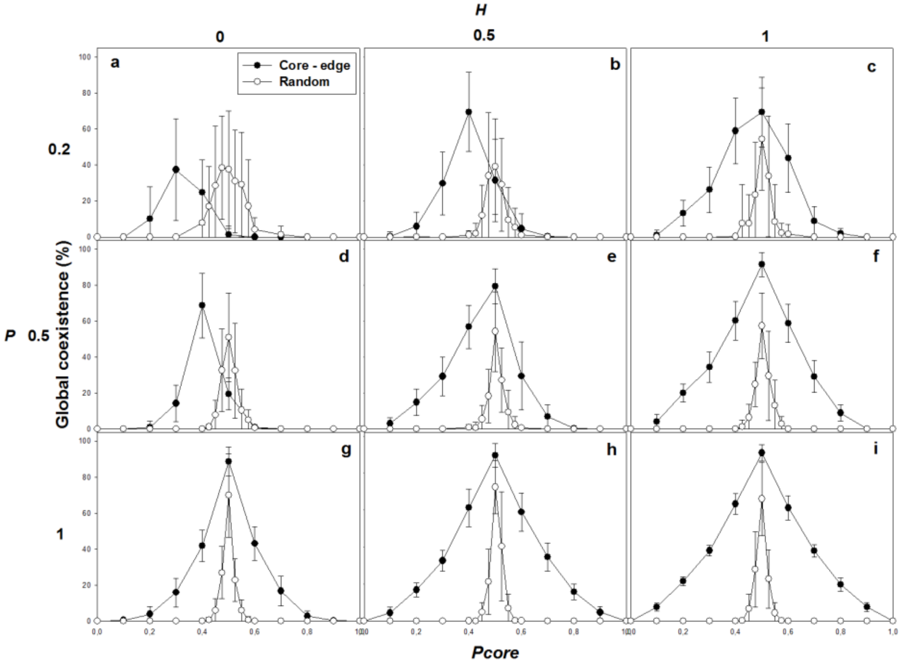

Figure 8: The global co-occurrence in relation to Pcore for different combinations of P and H, in the core-edge (full circles) and random habitat configuration (empty circles). The extent of global co-occurrence becomes larger and more predictable as P and H, allowing coexistence in a wider parameter space of Pcore. However, in the random habitat configuration the shift in dominance as Pcore increases always occurs very swift, resulting in a small parameter space where global co-occurrence is possible. The error bars denote the standard deviation based on 20 replicates.

2.4.3 The effect of dispersiveness

Dispersiveness has a negative effect on species coexistence. Higher dispersal distances increase the prevalence of interspecific competition and narrow the range of P_{core} values in which both species can coexist on a global (Figure 9: a, c) and local level (Figure 9: b, d). In a core-edge structure higher dispersal distances (δ=2) result in less local co-occurrence for either low or high values of P_{core}, however, for intermediate values of P_{core} the local co-occurrence increases (Figure 9: b). In a random configuration the results are less distinct yet qualitatively similar, although higher dispersal distances don't increase the maximal local co-occurrence (Figure 9: c, d).

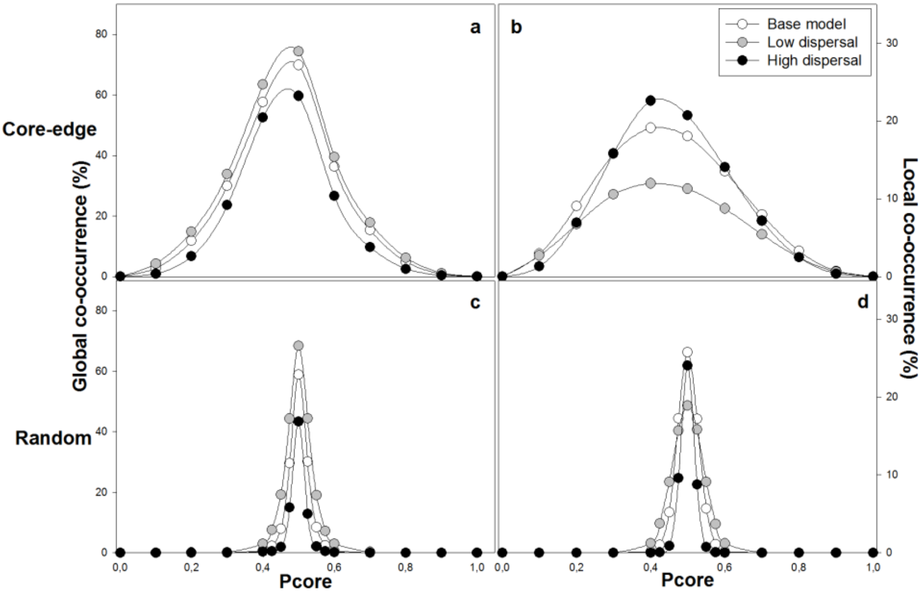

Figure 9: The effect of dispersiveness on the global (a, c) and local (b, d) coexistence over Pcore. Both values are averaged over all combinations of P and H. Dispersal distances are either low (δ= 0.5), normal (δ= 1) or high (δ= 2). Dispersal distances have a negative effect on the Pcore parameter space in which global coexistence occurs (a, c). The maximal local co-occurrence increases with dispersiveness in the core-edge configuration (b) but not in the random configuration (d).

2.5 **Discussion**

We aimed to gain insight into the influence of spatial structure on the interactions and coexistence of two species. Our findings can be summarized in four main points:

- Certain landscape configurations allow spatial segregation of both species resulting in a stabilization of coexistence through the avoidance of inter-specific competition.
- Shorter dispersal distances promote spatial segregation and consequently coexistence.
- The main determinant of the outcome of competition is the relative proportion of the two preferred habitat types (P_{core}). For example, if 75% of the suitable habitat is of the core type then the core specialist will dominate regardless of habitat configuration. However, on a lower level habitat availability and clumping will influence the exact outcome of competition.
- The effect of high fragmentation in combination with habitat loss was ambiguous. In most scenarios it decreased coexistence but under specific conditions it could coexistence was promoted.

2.5.1 The effects of both habitat availability and clumping over different habitat distributions (i.e. values of P_{core}).

Logically, the outcome of competition is primarily determined by the abundance of the two suitable habitat types (P_{core}); overall, species become dominant when their preferred habitat is most abundant. However, for a wide range of P_{core} values coexistence can be either stable or unstable depending on the amount of habitat availability (P), habitat clumping (H) and the exact spatial distribution of habitat types (i.e. in a core-edge or random fashion). In simulations with the core-edge configuration we find that in cases of a fully filled landscape (P and H =1) the proportions of both species are equal to the proportions of their preferred habitat type. Furthermore, when there is severe habitat loss and fragmentation, core specialists seem to profit compared to edge specialists. This is a rather unexpected result but was clarified by ad hoc tests in which we quantified the proportion of core habitat in all occupied grid cells after competition. This proportion is expected to be equal to the global proportion of core habitat (P_{core}) but was much higher under low P and H conditions (Boeye et al. unpub. results). Furthermore, when we look at the habitat fidelity of the edge specialist in these conditions this fidelity is lower in the core-edge configuration compared to the random configuration although in all other situations the opposite is true (Appendix Figure 1: a). This means that the core-edge configuration in low P and H conditions forces edge specialist to live in core habitat which gives them a competitive disadvantage towards the core specialist. They are forced there because under these circumstances the suitable habitat is very fragmented and many fragments are too small to maintain a local population. These small, uninhabitable fragments mainly consist of edge habitat; consequently in the larger habitat fragments, that do allow a local population to survive, the core habitat is overrepresented. In nature this would relate to a situation where edge specialists suffer more from fragmentation because the only fragments large enough to sustain a population, are high quality relicts where core specialists thrive. In addition to this, the dispersal mortality disadvantage that is inherently connected to the edge habitat lying on the outside of patches reaches its highest significance in these highly deteriorated landscapes. The importance of such edge habitat surrounding remnant vegetation for species conservation was emphasized in a recent review by Driscoll et al. (2013). When we distributed both habitat types randomly, core habitat was no longer overrepresented in large habitat fragments and the effect disappeared. Therefore, this difference is entirely driven by the configuration of the landscape (core-edge or random) rather than by the habitat composition, since P, H and P_{core} did not differ among the scenarios.

2.5.2 Reduced competition by spatial segregation

Competition typically results in the local exclusion of the weaker competitor and thus destabilizes local coexistence. The inherent spatial nature of competition implies an important role of the environmental structure. When this structure allows competitors to become spatially segregated, local interspecific competition will be avoided and coexistence stabilised (Hanski 2007; Snyder 2008). Such an intraspecific aggregation stabilises competitive interactions (Remer and Heard 1998; Amarasekare 2003) and increases species diversity at the landscape scale (Wassmuth et al. (2009)) . Nevertheless there has been debate about the importance of spatial segregation and under what conditions the process can stabilize coexistence (Murrell et al 2001; Chesson and Neuhauser 2002; Murrell et al 2002a; Rejmanek 2002). Our results allow us to compare a landscape configuration that does not allow stable spatial segregation, the random configuration, with one that can allow this, the core-edge configuration. These results indicate that there is a large range of spatial parameter values in which coexistence is only possible when the landscape is structured so that spatial segregation becomes possible; this is clearly visualized in Figure 7 and an online animation through Link 1 in the appendix. Furthermore we found that spatial segregation is only possible if both species can claim continuous areas of habitat that are large enough, relative to the dispersal distance, so that competitors can be excluded from the centre of these areas. This requires high habitat availability and clumping (i.e. high P and H) which allows high fidelity towards the preferred habitat type (Appendix Figure 1). Do note that in our model segregations results from local exclusions and short distance dispersal rather than aggregation behaviour. Moreover, once an area has been monopolised the local species will benefit from a numerical effect over invaders.

When habitat types are distributed randomly species no longer form stable intraspecific aggregations, since there are no more homogeneous areas of one habitat type, from which they can exclude each other.

2.5.3 The effect of dispersiveness

Reduced dispersal distances (δ = 0.5) decreased local co-occurrence and allowed populations to become spatially segregated thereby promoting global coexistence. Increasing dispersal distances (δ = 2) had the opposite effect because more dispersive individuals tend to end up further from their natal grid cell and therefore have a higher chance of competing with heterospecific individuals. In addition to enlarging the dispersal distance we also tested a scenario where dispersal resulted in a random repositioning of individuals on the landscape (results not shown). In this scenario global coexistence became much rarer in the core-edge configuration, with results comparable to those from the random configuration with the standard dispersal distance. In the random configuration the maximal local co-occurrence did not increase with dispersiveness. This is due to the fact that there is very little intraspecific aggregation in this habitat structure and the chance to co-occur with a heterospecific individual is thus not affected by the dispersal distance.

There is a large body of evidence demonstrating the importance of dispersal scale relative to the scale of landscape heterogeneity on the stability of coexistence, with the relationship between spatial segregation and dispersal distance not necessarily being linear (Débarre and Lenormand (2011)). Both Snyder and Chesson (2003) and Zhang et al. (2006) concluded from theoretical models that lower dispersal distances can enhance the effects of spatial variance thereby facilitating spatial segregation of species and eventually promoting coexistence. However, in general, the prevalence and outcome of interspecific competition reflects dispersal ability and patch composition as much as the intrinsic competitive abilities of species themselves (Bowers and Dooley (1991)). While previous theoretical work often envisaged dispersal-competition trade-offs (Slatkin 1974), our results are in accordance with recent findings and predictions on the effects of dispersal on species coexistence (Nurmi and Parvinen 2011). This effect is negative because higher dispersal distances destabilize coexistence, such that dispersive populations are less likely to become spatially segregated. This, subsequently, increases the global level of intraspecific competition.

2.5.4 Conclusions

We have demonstrated that habitat structure is an important driver of the outcome of a two species competition model. We found that the parameter space allowing coexistence is much wider when the landscape is distributed in a core-edge habitat configuration compared to when both habitat types are distributed randomly. This highlights the importance of spatial segregation by local competitive exclusion as a process stabilising coexistence. Although spatial segregation is not a novel phenomenon, we here elucidate the mechanism behind this process by linking coexistence explicitly to the landscape’s structure and dispersal.

2.6 Retrospective

Since the publication of this chapter our modelling expertise has grown. In addition, we have had the opportunity to discuss our work with fellow researchers who raised certain questions and uncovered potential issues. This allows us to look back and reflect on what improvements we would make if we were to repeat this study.

Concerning the implementation of dispersal we would not sample from a Gaussian kernel twice to find a dispersal distance in both x and y directions but rather sample the dispersal distance from a preferred kernel once and then sample a random direction in which to disperse. This method is standard in the field and allows for a much clearer understanding of the dispersal distance distribution and mean dispersal distance. A second issue with the dispersal implementation in this study is a grid artefact. Since all individuals are assumed to be in the centre of their respective grid cell and since dispersal distances are rounded to the nearest integer our individuals are biased to stay in their natal cell. This issue could be resolved by assigning random x and y coordinates within the grid cell to each individual prior to dispersal. This alternative method combines the benefits of, realistic, continuous space and a grid.

A second point that has recurred in several discussions is the issue of scale. We assume a very low carrying capacity of cells which implies that these cells have a limited spatial scale. The fact that we only model a 64 by 64 grid system makes the entire landscape rather small; so small in fact that one could argue whether it is appropriate to refer to it as a landscape. While we did perform a sensitivity analysis on both carrying capacity and the grid size, the parameter space we tested was restricted due to computational limitations. A much larger landscape would increase the global coexistence while we can assume that much higher carrying capacities would also increase the local coexistence.

2.7 Acknowledgments

This research was funded by FWO project G.0610.11 to DB and JB. DB is supported by the FWO Research Network EVENET and the BelSpo IAP project Speedy. AK is supported by a grant from the German science foundation (HO 2051/3-1). We thank Ghent University for access to the high performance computing infrastructure. This is publication ISEM-2013-032 of the Institute des Sciences de l'Evolution.

3

The evolution of density-dependent dispersal kernels

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This chapter is under review at *The American Naturalist*

3.1 **Abstract**

All organisms need to disperse, or to disperse their offspring, to maximize their inclusive fitness. While we currently have a good understanding of the selection pressures leading to emigration, we lack a clear understanding of the evolution of dispersal distance strategies, despite their fundamental importance for spatial population dynamics. Dispersal kernels represent the probability distribution of individual dispersal distances. Insights on the optimal shape of these kernels relative to the prevailing selection pressures and relevant environmental and demographic processes are therefore essential to increase the reliability of predictive methods in spatial ecology.

To fill this gap, we followed an optimality approach to theoretically infer how the relevant cost-benefit balances shape the optimal dispersal kernel as a function of local population density. We find that the shape of density-dependent dispersal kernels ranges from short distance dispersal to unimodal distance probability distribution functions.

Consequently, dispersal kernels cannot be described by a single function and need to be adjusted according to the prevailing spatial environmental conditions. Beside yielding novel insights into the evolution of dispersal distances our results provide a guide for kernel selection in predictive spatial ecology, which, to date, too often uses arbitrary criteria in this context.

3.2 **Introduction**

Dispersal --- the individual process that connects local populations in space --- is a well established field of research in ecology and evolution because of its profound impact on ecological and evolutionary dynamics (Clobert, Baguette, Benton 2012). Dispersal is for instance a key factor influencing species coexistence, diversity patterns and community assembly (Chave et al 2002; Nathan 2006; Carrara et al 2012). It is also the driving force behind biological invasions and range shifts (Kubisch et al 2014). A profound understanding of the ecological and evolutionary dynamics within a spatial context therefore requires well grounded insights into the causes and consequences of dispersal (Bowler and Benton 2005; Ronce 2007; Bonte et al 2012). However, not all research in this field includes space explicitly and few studies consider the selection pressures leading to different dispersal distances despite the fact that biodiversity dynamics can only be understood in the light of individual space use across various spatio-temporal scales (Jeltsch et al 2013).

Summarizing a dispersal strategy into a single mean dispersal distance neglects biologically relevant variation. This variation is generated by proximate, often stochastic, factors related to the environmental conditions (such as for instance weather and landscape; (Travis 2001)) as well as by ultimate factors related to bet-hedging and kin-competition (Bowler and Benton 2005). Therefore, a better approach is to consider the distribution of dispersal distances, which is typically summarized by a probability density distribution, the dispersal kernel (Kot and Schaffer 1986; Nathan and Muller-Landau 2000; Hovestadt et al 2012). To date, empirically derived point patterns or densities at different distances from a source have been fitted to a variety of functions, ranging from power, negative exponential to mixed Weibull functions (Cousens et al 2008a). As the identity of the fitted statistical function will determine the fatness of the tail and the subsequent frequency of long-distance dispersal events (LDD), it is clear that a proper kernel formulation is essential to appropriately summarise the dispersal strategy. The selected kernel function will affect predictions of species' spread, for instance in the context of invasion dynamics (Kot et al 1996) and range expansion under climate change (Travis et al 2013a).

Only recently, some theoretical (reviewed in Hovestadt et al (2012)) and empirical studies (Bitume et al 2013; Fronhofer et al 2015) have focused on the evolution of dispersal kernels rather than dispersal rates. Such approaches scale up individual dispersal responses towards a population-level statistic (the kernel). While dispersal distance clearly is a context-dependent trait (influenced by e.g. water currents, wind flows, landscape cues), the kernel itself can have a genetic basis (Bitume et al 2011) and is modelled in this sense. Because of obvious reasons of simplicity, theoretical studies focusing on dispersal distances assume an a priori determined function for the dispersal kernel, be it Gaussian or negative exponential (e.g. Murrell et al (2002); Bonte et al (2010); North et al (2011)).

Therefore, the fundamental question of the shape of the evolutionarily stable distribution of dispersal distances remains to be answered in all its complexity. Hovestadt et al (2001) demonstrated that auto-correlated landscapes lead to the evolution of fat-tailed dispersal kernels (LDD), while Bonte et al (2010) showed the evolution of such patterns in a large variation of landscapes differing in habitat availability and spatial correlation. Using a different approach, Rousset and Gandon (2002) explored the influence of a variety of dispersal cost functions on the evolution of dispersal kernels. The cost function appeared to be a crucial component shaping the dispersal kernel since it describes an accumulation of dispersal costs limiting dispersal (Bonte et al 2012). Overall, dispersal costs increase with dispersal distance, for instance in plants by seed size-germination trade-offs and in animals by higher predation and energy risk during further displacements.

Detailed knowledge and theoretical predictions about the shape of the dispersal kernel are essential, as considering only overall selection on dispersal distance does not yield any information on higher moments of the kernel, such as skew or kurtosis (tail weight), and does not take into account the possibility of multimodal distributions. Often, natural selection acts on skew and kurtosis of the kernel and might not influence the mean: in a recent study Fronhofer et al (2014) showed empirically and theoretically that spatially correlated extinctions select for longer dispersal distances (higher tail weight) but against emigration overall. As a consequence, one cannot assume that selection on one moment of the kernel, for example the mean, is a good approximation for effects on other moments. This becomes very clear in Fronhofer et al (2015), who show that while maternal investment in dispersal does not influence the mean of the dispersal kernel, the distribution shows more long distance dispersal and becomes bimodal. These changes in turn have important consequences for ecological dynamics, such as increased population persistence, for example.

While recent theoretical work demonstrated the additional importance of parent-offspring conflicts (Starrfelt and Kokko 2010) and maternal investment (Fronhofer et al 2015), it is clear that local competition is a central force influencing the evolution of dispersal. Both dispersal rates (e.g. Hamilton and May (1977); Metz and Gyllenberg (2001); Poethke and Hovestadt (2002); Matthysen (2005); De Meester and Bonte (2010); Baguette et al (2011)) and distances have been shown to be conditional on local density (Wender et al 2005; Bitume et al 2013; Martorell and Martínez-López 2014). With the exception of Poethke et al (2011), who followed an individual-based modelling approach focused on informed settlement decisions, we lack insight on how dispersal distances and by extension dispersal kernels are conditional on local population density. Clearly, this hampers further theoretical and empirical progress.

We here fill this gap and demonstrate theoretically how the shape of dispersal kernels should change according to local population density (i.e. competition) and dispersal costs for passively dispersing organisms.

While the principal aim of our study is to develop a coherent theoretical framework on the evolution of density-dependent dispersal kernels, we additionally make use of our theoretical results to synthesize which types of traditionally used dispersal kernel functions fit best to the optimal dispersal kernels we derive. This overview can serve as a guide for kernel selection.

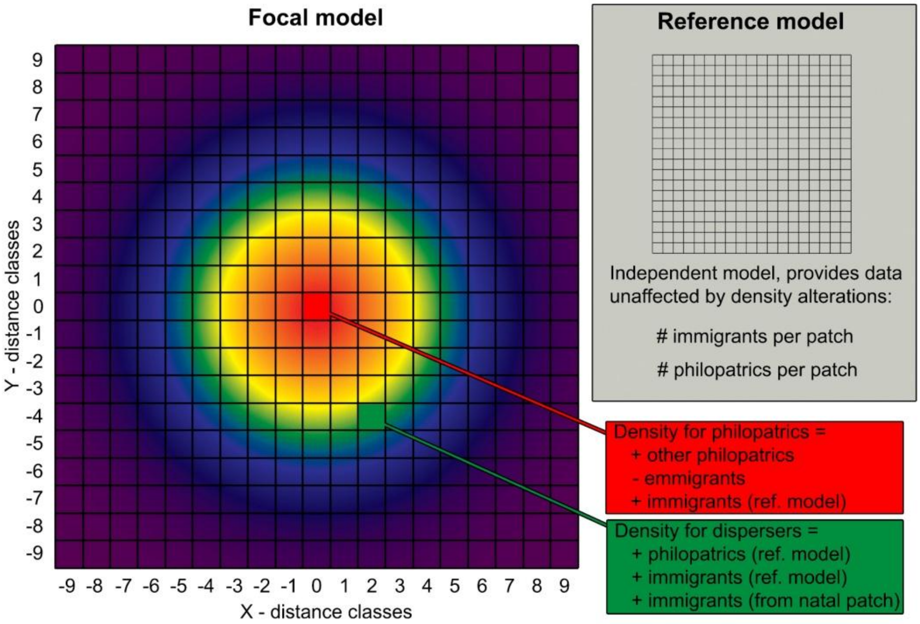

Figure 10: Overview of the methodology. The colour gradient in the focal model graph shows the density of individuals originating from the central patch after the dispersal phase (red = high, blue = low). After dispersal individuals will reproduce according to the density they perceive (see red and green box). Offspring will be shuffled between patches to avoid artefacts and the population density will be altered to the desired value by randomly deleting or adding individuals. This procedure is repeated for all patches in the focal model. The reference model has the same dispersal mortality and carrying capacity but unlike the focal model, there are no alterations of local density. This model is at equilibrium and numbers of philopatrics and immigrants per patch are sampled from it. While the 19x19 grid is wrapped into a torus there is no overlap possible between dispersers from the same patch since each individual can only disperse 9 distance classes in any direction.

3.3 Methods

3.3.1 General model structure

We model a semelparous organism with discrete generations, living in a spatially structured population (e.g annual plants and corals: Pringle et al (2014)). We consider the spatially explicit landscape to be comprised of 19x19 patches. These are connected by dispersal and individuals disperse according to their individually specific dispersal kernel.

3.3.2 The kernel as a function valued trait

We model these individual dispersal kernels as function-valued traits (Dieckmann et al 2006), since we are interested in how the optimal shape of the dispersal kernel changes as a function of population density. This approach allows us to avoid any potential bias of the outcome by making a priori assumptions on a specific functional relationship. Function-valued traits have been used previously by Hovestadt et al (2001); Starrfelt and Kokko (2010); Fronhofer et al (2014); Fronhofer et al (2015) who analyzed the evolution of dispersal kernels in different contexts. The underlying idea is to discretize a continuous function, such as the dispersal kernel in our case, into a finite number of (distance) classes. We here used ten such classes, which were equivalent to dispersing 0, 1, 2, ..., 9 distance units (i.e. patches). For each distance class the individual carries an allele, which represents the probability to disperse to that specific distance and which can be optimized independently.

3.3.3 Population dynamics

Local population dynamics were regulated using the Hassel discrete-time model of density-dependent growth (Hassell 1975), we assumed parthenogenetic reproduction in non-overlapping generations. Newborn individuals survive until adulthood with a density-dependent probability $s_{i,t}$.

$$s_{i,t} = \frac{1}{(1 + aN_{i,t})^{b}}$$

$$\text{with } a = \frac{\lambda^{\frac{1}{b}} - 1}{K}$$

Equation 1

Where K is the carrying capacity, a is a measure of susceptibility to crowding and λ is the growth rate (K=50 and λ=2 unless stated otherwise); b defines the type of competition which changes from a contest to a scramble type as b increases (b = 1 unless stated otherwise).

Since we assume asexual reproduction, offspring inherit all their alleles from a single parent. Every single allele has a 0.5% probability to mutate when passed from parent to offspring. This is a relatively high mutation rate but since we want to optimize kernels as fast as possible rather than recreate realistic rates of evolution this forms no problem. Mutation sizes were sampled from a Gaussian distribution with average 0 and a standard deviation ($SD_{mut)}$ decreasing exponentially over time from 2.1 to 0.1 according to the function:

$$SD_{mut} = 0.1 + e^{\frac{-5t}{t_{max}}}$$

Equation 2

Where t and t_{max} are the current and last simulated generation, respectively. This mutation procedure allows a more efficient search of the adaptive landscape such that optimal values can be found more rapidly (Poethke et al 2010; Fronhofer et al 2014). Allele values are allowed to decrease below zero, although all values below zero have the same phenotypic effect, i.e. no dispersal to that particular distance. In the initial population, the ten dispersal alleles are drawn from a uniform distribution between 0 and 1.

3.3.4 Dispersal

Surviving juveniles disperse in a random direction from their natal patch and travel a distance, which is drawn from their respective dispersal kernels. Therefore, for each individual all kernel values (i.e. the probabilities for each distance class) are standardized to sum up to 1 (negative values become 0). The distance is then drawn from the resulting probability density distribution and the individuals travel to a patch at that distance, while the direction is chosen at random. In order to minimize computational load and allow optimization of the kernel to the furthest distance class (i.e. 9) we implemented a landscape with periodic boundary conditions.

Dispersal is associated with several costs, including energy or opportunity costs or a mortality risk (Bonte et al 2012). To account for that we assume a per step mortality (m_s) which results in an exponential dispersal mortality function $M = 1 - e^{-m_s d}$, where M is the realized mortality and d the dispersal distance (Bonte et al 2012); for a systematic analysis of cost functions see Rousset and Gandon (2002). We varied m_s by using all values from the interval [0,0.005,0.01,0.05,0.1,0.2,0.5,0.7]

3.3.5 Optimizing dispersal kernels

There are many difficulties to optimizing kernels to particular densities. We fixed pre-dispersal densities to a value of interest and changed this value between different simulations to obtain the optimal strategy for a range of densities. This approach has, however, the problem that it changes the costs and benefits of dispersal. With costs we here explicitly mean the risk of immigrating into high density patches, whereas arriving in populations with lower density is a huge benefit. If all populations are fixed to the same density, there would be no cost (except for mortality) or benefit (except for kin-competition) to dispersal. Therefore, we carefully created a specific experimental design allowing us to fix population densities without affecting the fitness gains or losses due to dispersal. After a large number of generations this steady selection regime will cause a stable, optimal dispersal strategy to evolve.

The core idea is to separate the model into two parts, one in which we manipulate population densities and where we optimize the dispersal kernels, i.e. the 'focal simulation', and a second unaltered model --- the 'reference simulation' --- which is used as a source for unbiased, realistic demographic values, which we then use in the focal model to inform population dynamics (see Figure 10). This procedure restores the missing eco-evolutionary feedback. We hereby use the following procedure:

1. We start by running a reference simulation with given dispersal kernels, in which population densities are not fixed. We do not allow for dispersal evolution in these simulations. Instead we record for 100 generations the numbers of immigrants and population densities after dispersal, but before reproduction. This gives us information on the distribution of the numbers of philopatrics (i.e. non-dispersing individuals) and immigrants per patch.

2. Subsequently, we run a simulation in the focal landscape for 3,000 generations. After dispersal, all individuals get a number of offspring, this number is calculated for philopatrics and (surviving) dispersers separately according to Equation 1. For the philopatrics, $N_{i,t}$ is given by their density in patch *i* at time *t* plus the number of immigrants sampled from the reference simulation. While for the dispersers, the density in their patch of destination is the number of philopatrics in that patch (sampled from the reference simulation) plus the numbers of immigrants in that patch (sampled from the reference simulation) plus the number of dispersers originating from the same natal patch (see Figure 10). Note that the reference simulation only provides an integer number of both immigrants and philopatrics per patch which is passed on to the function calculating the number of offspring; no actual individuals with traits are transferred.

3. To keep population densities at their respective fixed values in the focal landscape, we then either decrease density by randomly deleting individuals or increase it by randomly introducing cloned individuals from the whole metapopulation. It is evident that this procedure severely affects local kin structure. Thus we decided to exclude kin-competition altogether from our model by shuffling individuals between populations multiple times throughout their life-cycle (for further details see Poethke et al (2007); Kubisch et al (2013)).

4. Of course, the kernels initially used in the reference simulation in step 1 are non-optimal and this will affect the distribution of population densities and immigrant numbers this simulation delivers to the focal simulation, which in turn will result in non-optimal kernels. To account for that, we place the steps 1-3 in a loop and pass the optimal kernels evolving in the focal simulation on to the reference model in subsequent iterations until the dispersal kernels do not change any further. This allows us to obtain optimal dispersal strategies/kernels for all given densities without destroying the eco-evolutionary feedback between population dynamics and dispersal.

The scenario we use here assumes a metapopulation at equilibrium and asynchronous dispersal between patches (they release dispersers one patch at a time). Evidently, the costs and benefits of dispersal may change, for example if population densities are spatially autocorrelated. For a detailed analysis of alternative scenarios, including a methodological description, we refer to the appendix. Note that our results are qualitatively robust against such changes. The standard scenario we use here is referred to as the 'equilibrium asynchronous' scenario in the appendix.

3.3.6 Validation of the approach and sensitivity analysis

We validated our modelling approach by comparing an appropriately simplified version of our model with analytical results by Poethke and Hovestadt (2002) for density-dependent emigration (assuming nearest-neighbour dispersal, see Appendix Figure 2). We could show that our modelling approach is valid as we could recapture the analytical results of Poethke and Hovestadt (2002). We further conducted a sensitivity analysis by varying the values of per capita growth rate λ and the strength of competition β. We found that the presented results are robust against these changes (Appendix Figure 5).

3.3.7 Analysis of the optimal density-dependent dispersal kernels

To assess which probability density functions fitted the optimized kernels best we performed a nonlinear least squares regression analysis (R package for statistical computing version 2.15.2; function `nls') for a series of known functions (Gaussian, linear increase, log-normal, negative exponential, Wald, Weibull) on each kernel. The results of this analysis can be found in Appendix Figure 5. We also performed a more generic analysis of kernel shapes by determining whether they were consistently decreasing, increasing or unimodal. A summary of these results can be found in Figure 12.

3.4 Results

Our model produces optimal kernels for a given (forced) local density and a certain dispersal mortality function. By keeping the dispersal mortality constant we can create a 3D plot showing how the change in local density affects the kernel shape (Figure 11). From this figure we can derive that the shape of the optimal dispersal kernel is indeed density-dependent. With increasing density it changes from an exponentially decreasing to a much more skewed, unimodal shape. Clearly, this results in an increase of the average dispersal distance with local population density. The shape of the optimal density-dependent emigration function obtained by Poethke and Hovestadt (2002) (Appendix Figure 2) is identical to the probability of remaining philopatric (dispersal to distance class zero) in Figure 11. Note that the function's shape is inverted as the probability to emigrate = 1 - the probability of philopatry. This clearly shows how our results add a dimension, namely dispersal distance, to current theory on optimal density-dependent emigration rates. For a detailed analysis of different kernel metrics see Appendix Figure 6.

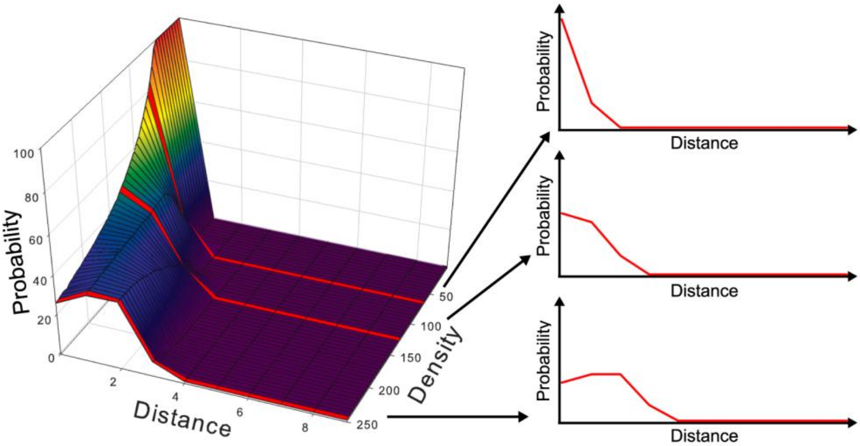

Figure 11: Optimal density-dependent kernels for (dispersal mortality m_s = 0.05). The three outtakes summarize the change of the kernel shape from a steeply decreasing (negative exponential) over a more Gaussian shaped kernel to an increasingly skewed unimodal shape. The height of the curve represents the probability to disperse to a given distance.

Figure 12 generalizes these results and provides a summary of the shape of density-dependent kernels depending on a range of dispersal costs (in Figure 11 the per step dispersal mortality was fixed to $m_s = 0.05$). As a rule, dispersal distances increase with local population densities and kernel shapes shift from no dispersal below a certain threshold to monotonously decreasing and finally unimodal shapes. Generally, increasing dispersal costs counteract this trend. In the extreme case of no dispersal costs monotonically increasing kernels (distance probability density function) can be found. This increase in probability to disperse a certain distance will result in an even density distribution of dispersers over the landscape as the surface area associated with each distance class increases exponentially. A detailed analysis of which functions fit best to the kernel shapes in Figure 12 and two alternative parameter settings (higher growth rate and stronger competition) can be found in Appendix Figure 5 (equilibrium, asynchronous scenario). In general, the results show in Figure 12 are robust to such changes.

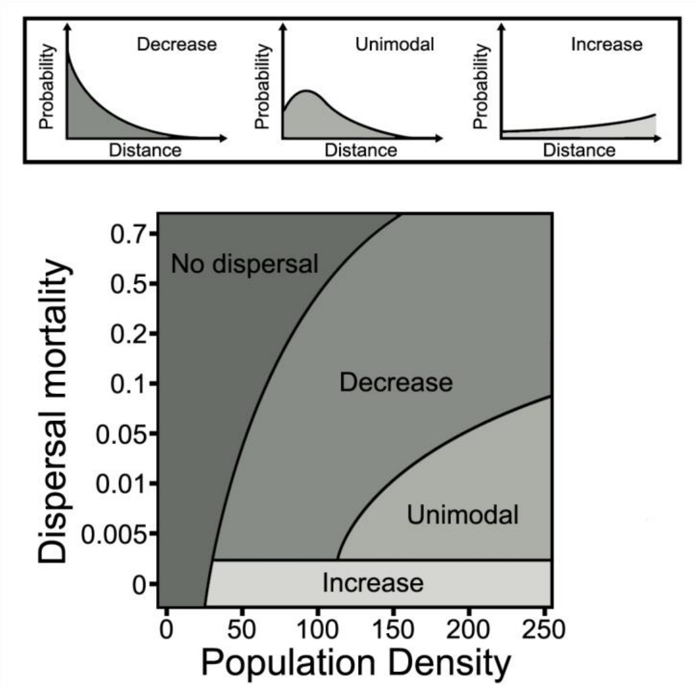

Figure 12: A summary describing the optimal density-dependent kernel shapes qualitatively in dependence of the explored range of dispersal mortalities. The `no dispersal' category comprises kernels with less than 3% dispersal. Note that the dispersal mortalities on the y-axis do not decrease linearly. For an overview of which probability function fits best to each kernel shape represented here see Appendix Figure 5.

3.5 Discussion

Information on local population density is one of the key factors shaping the dispersal behaviour of individuals (Poethke and Hovestadt 2002). With this study we theoretically investigate optimal density-dependent dispersal kernels --- a topic largely untouched in the literature but of major importance for spatial ecology. Although a wide variety of kernel shapes has been used in both applied and fundamental research, a kernel's optimal shape relative to the prevailing environmental context has rarely been considered (but see e.g. Hovestadt et al (2001); Starrfelt and Kokko (2010); Fronhofer et al (2014); Fronhofer et al (2015)). Our study reveals that, if individuals are able to adjust their dispersal kernel in an adaptive way, a number of known kernel shapes can evolve in response to variation in local population density and dispersal costs. Kernel shapes range from a negative exponential distribution for low densities to unimodal and even monotonously increasing shapes in high-density environments (Figure 12 and an online animation through Link 1 in the appendix), and from increasing Weibull to steeply declining functions with increased dispersal mortality. In accordance with the analytical model presented by Poethke and Hovestadt (2002) we predict no dispersal below a certain threshold density value.

As empirically demonstrated, individuals from the population adaptively adjust their dispersal distances according to the local density, and in response to others, to maximize fitness (Bonte et al in Press). Therefore, the kernel is the ultimate target of optimization, either through selection (Fronhofer et al 2014), epigenetics (Bitume et al 2014) or plasticity (Wender et al 2005; Bitume et al 2013), but selection will act upon the morphological, behavioural and physiological features that influence individual dispersal (Hovestadt et al 2012). So, while it is well recognized that realized kernels are strongly context dependent (Nathan 2006), mean, variance and higher moments (e.g. kurtosis, skew) of the dispersal distance distribution need to be optimized by the controlling actor, which either be the mother when dispersal is natal such as in the case of seeds, vertebrates and invertebrates with planktonic larvae or the individual itself in cases where dispersal is active (Bonte et al 2012). A functional analysis of seed dispersal in *Arabidopsis thaliana* (Wender et al 2005) indeed shows that maternal environmental factors impact specific morphological plant attributes that in turn affect kernel properties rather than mean distance only.

To avoid model artefacts, kin-competition had to be excluded. Since kin-competition is well known to promote dispersal (Poethke et al 2007; Kubisch et al 2013) we can thus expect that our results underestimate the average dispersal distances. Moreover, Bitume et al (2013) have shown that high genetic relatedness in spider mites results in more skewed and fat-tailed dispersal kernels. In addition to the exclusion of kin-competition (see appendix for more details) there are some model simplifications, which were necessary to conduct this study. We do, for example, only use one specific cost function form (for a systematic analysis of cost functions see Rousset and Gandon (2002). Also, we assume a homogeneous world with all patches being equal in quality. Hovestadt et al (2001) investigated the evolution of dispersal distances in heterogeneous environments and found fat-tailed dispersal kernels in auto-correlated landscapes. North et al (2011) showed that the amount of available habitat as well as its spatio-temporal arrangement shape dispersal distance evolution in complex ways. They did, however, not allow for changes in the dispersal kernel's shape. Further we assume that dispersal distance is controlled by the maternal genotype rather than that of the individual itself. Therefore, our model is applicable to species in which natal dispersal is under maternal control. Such anticipatory maternal strategies are expected to evolve when fitness balances are predictable at relevant spatio-temporal scales. Such strategies are usually associated with sessile organisms (Burgess and Marshall 2014) but may be more widespread in other animals as well (De Meester and Bonte 2010; Bitume et al 2014). Without maternal control kernels, we expect the evolution towards less fat-tailed kernels (Starrfelt and Kokko 2010).

The density-dependency in our evolved kernels is in perfect accordance with empirical findings of Bitume et al (2013). In an experimental mite mesocosm, higher population densities lead indeed to the evolution of longer dispersal distances and decreases in the level of kurtosis and skew. Unfortunately, solid empirical tests of dispersal kernel evolution are difficult to design or to evaluate in more natural environments. In plants, a large amount of research has been spent on understanding mechanisms, which result in long distance dispersal (Nathan 2006; Schurr et al 2009). Moreover, the majority of studies investigating kernel evolution in plants and other passively dispersed taxa deals with vector based dispersal (Nathan et al 2008; Fronhofer et al 2013). However, only a limited number of studies have looked into the response of dispersal distance to environmental cues. These studies confirmed long distance dispersal as a consequence of: nutrient deficit (Imbert and Ronce 2001), density (Donohue 1999), density in combination with water stress (Brändel 2007; Martorell and Martínez-López 2014) or low nutrient availability (Mandák and Pyšek 1999). Strong inverse power kernels were recorded for the bog fritillary in an isolated metapopulation points. These kernels showed strong temporal variation, with fatter tails emerging in years of high female densities (Schtickzelle et al 2012). As predicted by our model, substantial dispersal costs among the remaining patches and female densities explained this spatiotemporal variation in dispersal kernels.

Our theoretical framework is thus able to explain how changes in the kernel shape are related to changes in density and connectivity. This insight provides an avenue for comparative, inverse approaches to infer relevant larger-scale spatiotemporal processes from quantitative snapshots of dispersal kernels. When collected for comparative analyses in time or space, it should be theoretically possible to use kernel shape statistics as indicators for spatiotemporal processes such as changes in range expansion dynamics (i.e, inferring range spread dynamics from point patterns) or changes in connectivity (sensu organismal, not geographical) relative to reference situations. Kernel quantifications to assess changes in connectivity in response to restoration efforts, or among different metapopulations as in Schtickzelle et al (2006), will be especially worthwhile when data collection can be handled efficiently, such as for instance in cases where dispersal trait distributions (wing or plume load for instance) can be inferred by limited sampling. An implicit validation of this potential application should clearly be a next step following this theoretical development.

Our findings point at additional important implications for range shift modelling. To date, predictions of range shifts in response to for instance climate change are predominantly made by the inclusion of simple, constant spread rates. While in some cases, simple diffusion models can predict spread rates (Meier et al 2014; Giometto et al 2014), alternative Lagrangian, mechanistic models are being constructed and implemented (Bocedi et al 2014). Using reference data of mean dispersal distances, our framework can guide modellers to apply various types of kernels depending on the nature of the system, connectivity and population dynamics. Such an approach is especially valuable for species in which more mechanistic or semi-mechanistic spread models are lacking (see for instance Travis et al (2011)). Under the assumption of optimality, i.e. fast adaptive dynamics through selection or plasticity, modelling approaches using dynamic kernels will lead to the development of computationally simple though more realistic and predictive spread models (Travis et al 2013a). Theoretically expected shifts in the kernel properties can for instance be integrated into integrodifference approaches of spread dynamics (Neubert and Caswell 2000).

3.5.1 Conclusions

Our modelling framework allows us to pin point the optimal dispersal kernel given the relevant environmental conditions, here local density, dispersal costs and the spatial demographic context. We demonstrate different optimal kernel shapes as a function of these conditions, with a shift from short distance dispersal to decreasing and unimodal functions with increasing density and decreasing costs. We argue that this synthesis provides the basis for an informed choice of dispersal kernels for modelling and statistical analysis which is to date most of the time arbitrary with respect to the choice of dispersal kernels. This study advances our general understanding of the mechanisms that shape dispersal kernels and yields testable hypotheses for future empirical research.

3.6 **Acknowledgments**

JB is funded by FWO project G.0610.11. DB was supported by the FWO Eve-Net research network and IAP Belspo project P7/04 (Speedy). E.A.F. thanks the Eawag for funding. RS was supported by the KU Leuven Center of Excellence program PF/2010/07. This is ISEM publication Nr. 2015-XXX. We thank Ghent University for access to the high performance computing infrastructure.

4

More rapid climate change promotes evolutionary rescue through selection for increased dispersal distance.

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This chapter was published in *Evolutionary Applications* (2013) Vol. 6

4.1 **Abstract**

Species can either adapt to new conditions induced by climate change or shift their range in an attempt to track optimal environmental conditions. During current range shifts, species are simultaneously confronted with a second major anthropogenic disturbance, landscape fragmentation. Using individual-based models with a shifting climate window we examine the effect of different rates of climate change on the evolution of dispersal distances through changes in the genetically determined dispersal kernel. Our results demonstrate that the rate of climate change is positively correlated to the evolved dispersal distances although too fast climate change causes the population to crash. When faced with realistic rates of climate change, greater dispersal distances evolve than those required for the population to keep track of the climate, thereby maximising population size. Importantly, the greater dispersal distances that evolve when climate change is more rapid, induce evolutionary rescue by facilitating the population in crossing large gaps in the landscape. This could ensure population persistence in case of range shifting in fragmented landscapes. Furthermore, we highlight problems in using invasion speed as a proxy for potential range shifting abilities under climate change.

4.2 Introduction

There is a consensus that global temperatures have been drastically increasing over the last decades and that this trend will not be halted in the forthcoming decades (IPCC 2007). How fast this global warming will take place is difficult to predict due to uncertainties in upcoming human impact, which may either speed up or slow down the process (Pereira et al 2010). In addition, there is evidence that certain regions on this planet are more sensitive to climate change than others (Simmons and Thomas 2004; Loarie et al 2009). Similarly, the rate of climate change will be perceived differently by different species due to interspecific differences in thermal sensitivity, dispersal and generation time (Berg et al 2010) generating a wide variety in responses (Chen et al 2011). The current rate of climate change, in combination with other global environmental impacts forces organisms to either adapt, migrate or go extinct (Visser 2008). While there is ample evidence that species from a wide range of taxonomic groups are moving polewards and to higher elevations (Parmesan 2006; Thomas 2010; Chen et al 2011), a large proportion of species are still expected to become extinct (Thomas et al 2004; Pereira et al 2010). The combined action of habitat fragmentation and climate change rates has indeed been demonstrated to be a deadly cocktail for the persistence of species (Warren et al 2001; Travis 2003).

A wide range of models have been developed to predict future species ranges in order to understand the biological effect of, and responses to climate change. Correlative approaches that determine climate envelopes are widely used (Hampe 2004), but there are several limitations in the approach, amongst others neglecting dispersal as a fundamental process in range shifting. Analytical models such as reaction-diffusion (Shigesada and Kawasaki 1997), integro-difference (Neubert and Caswell 2000) or (semi-) mechanistic models (Katul et al 2005) all do incorporate the dispersal process in one way or another but typically only consider populations in spatiotemporally stable environments. While there have been some attempts to parameterize simple analytical models to infer range expansion (Bullock et al 2008), there has recently been an increased appreciation of individual-based models to generate more generic insights into the mechanisms by which global change might impact the capacity of a population to spread and persist (Brooker et al 2007; Phillips et al 2008; Mustin et al 2009; Kubisch et al 2010; Fronhofer et al 2011). These models account for the presence of spatially shifting climate windows and, in some cases, focus solely on ecological dynamics (Brooker et al 2007; Mustin et al 2009) while in others eco-evolutionary responses are explored (Phillips et al 2008; Kubisch et al 2010; Fronhofer et al 2011). However, none of these studies have looked into the impact of the rate of climate change when dispersal is allowed to evolve. Dispersal has been repeatedly shown to evolve under influence of landscape changes (e.g., (Bonte and Lens 2007; Cheptou et al 2008; Hanski and Mononen 2011)), and such evolutionary changes may induce evolutionary rescue. This rescue process is defined as ‘the idea that evolution might occur sufficiently fast to arrest population decline and allow population recovery before extinction ensues’ (Gonzalez et al 2013). Moreover, the use of dispersal distance in a spatially explicit context instead of a dispersal propensity in combination with different rates of climate change is expected to yield novel and more realistic insights of eco-evolutionary mechanisms related to range shifting under climate change.

The significance of evolution as an important driving process of range expansions is currently recognized in both empirical (Thomas et al 2001; Phillips et al 2006; Phillips et al 2008; Léotard et al 2009) and theoretical work (Garcia-Ramos and Rodriguez 2002; Travis and Dytham 2002). The evolution of dispersal rate has received considerable interest and generated insights on range shifts and range border formation. In theoretical work by (Dytham 2009) dispersal rates have for instance been shown to increase towards range margins with increased environmental and demographic stochasticity, but to decrease if habitat gradually becomes less available. Results from a simulation model developed by Phillips (2011) suggest that recent range shifts could even promote the formation of stable range edges because more dispersive individuals experience environmental gradients more intensively. However, a different model suggests that when dispersal costs at range margins become too high, selection against dispersal may eventually induce range contraction (Kubisch et al 2010).

Most studies do not consider the evolution of dispersal distance, although high dispersal rates are known to evolve at range borders and to induce evolutionary rescue in theoretical studies (Travis et al 2009; Bonte et al 2010; Fronhofer et al 2011). While we do not doubt that models inferring dispersal rate by implementing either nearest neighbour or global dispersal provide fundamental insights on dispersal evolution, we emphasise that in reality dispersal kernels as well as emigration rate will be under selection, which will exert pressure especially on those traits determining dispersal distance (e.g. Bonte et al. 2009; Bartoń et al. 2012). For instance, in plants all seeds disperse to some degree, but selection on traits such as seed weight, plant height or specific dispersal structures (from fruits to wings; see Bonte et al. 2012) will eventually determine how long seeds can remain airborne, and as such how far they can be potentially spread (Cousens et al 2008a). Given the importance of dispersal distance in range expansion (Simmons and Thomas 2004; Phillips et al 2008) or spatial populations dynamics (Leibold et al 2004; Cousens et al 2008a), it is surprising that the evolution of dispersal kernels has only received marginal attention (Ronce 2007).

Evolution at range borders results from two complementary processes, i.e. natural selection within populations and the spatial sorting of genotypes near expanding range margins (Shine et al 2011). Spatial sorting increases the frequency of dispersive genotypes near the expanding range edges based on the standing variation in populations rather than by mutations in the edge populations. This is because dispersive genotypes tend to be overrepresented near the expanding front and are thus more likely to mate with each other (the Olympic village effect) (Phillips et al 2008). The magnitude of both natural selection and spatial sorting will be influenced by the rate of climate change because variation herein will determine the availability of unoccupied but suitable habitat beyond the current range border and mortality of low-dispersive individuals near the trailing edge of the range (Phillips et al 2008;

Dytham 2009). Regardless of the exact rate of climate change we expect the population density to increase from the expanding front onwards. (Dytham 2009) showed that such gradients in population dynamic parameters can influence local selection pressures and result in a gradient in dispersiveness.

Given the expected variation in how different species perceive the rate of climate change, it is reasonable to assume that different species will show different ecological, but also evolutionary responses towards climate change speed. A fast climate change is expected to be worse than a slow one because it reduces the time available for species to adapt to the new environment or to shift their range to cooler regions (Visser 2008). By developing a generic individual-based model, we here provide insights on how dispersal distance evolves in relation to the rate of climate change in an asexual plant species. We are interested in establishing whether the dispersal distance that evolves at an expanding front is the lowest that enables the population to track the changing climate. We also explore the degree to which these evolutionary changes allow populations to spread across gaps in the landscape and as such induce evolutionary rescue under the combined action of climate change and habitat fragmentation. While it can be expected that gaps are more readily crossed when climate change proceeds slowly because of an increased time window of opportunity and larger population sizes, we provide evidence of the opposite; somewhat counter-intuitively, we show that slightly faster climate change can facilitate spread across fragmented landscapes due to evolution of increased dispersal distances. Furthermore, we emphasise that population spread projections developed from spatially stable landscapes, such as implemented in analytical wave-speed models (Neubert and Caswell 2000; Katul et al 2005; Jongejans et al 2008) may not be accurate predictions of range expansion ability under climate change.

4.3 Methods

We developed a spatially explicit, individual-based model to investigate the evolution of dispersal kernels during range shifts. Simulations were run in discrete time and took place on a cellular lattice (y=100, x=1000) (see Appendix Figure 9 for schematic representation). We used absorbing (i.e. lethal) boundaries since they are most appropriate for modelling passive dispersal (Burton and Travis 2008). We also tested a landscape without borders (torus), but patterns remained qualitatively similar (Appendix Figure 10).

4.3.1 Population dynamics

We approximated the ecology of an annual plant species; within one generation adults produced a density dependent number of seeds just before they die. These seeds inherit an allele from their parent which determines how wide their dispersal kernels are. Seeds will disperse a certain distance according to this kernel and survive to become adults if they settle in a suitable habitat that is exposed to the right environmental conditions (i.e. within the climate window). To keep things as simple as possible we modelled reproduction as an asexual process. Within population dynamics were based on well understood density dependent demographic processes (Hassell and Comins 1976). Each individual in a cell with local density N at time t gives birth to a number of offspring drawn at random from a Poisson distribution with mean μ calculated from the following expression:

$$\mu = \lambda(1+ aNt)-1$$

Here, λ specifies the net reproductive rate, a is a measure of patch quality and is defined as:

$$a = (\lambda-1)/N*$$

Where $N*$ is the population equilibrium density; if the local density Nt is lower or higher than this value the average number of offspring will increase or decrease respectively due to competition. The actual number of offspring Λ is drawn from a Poisson distribution with mean μ; as such demographic stochasticity is introduced into the model (Travis and Dytham 2002; Poethke and Hovestadt 2002; Travis et al 2009). In our models we used the parameter values λ=2 and $N*$=2, decreasing these values resulted in unviable populations whereas increasing one of them improved population resilience. However, general patterns in our results remained unaltered (Boeye et al., unpub. data). We only allow plants to produce a few seeds, doing so we improve computational power and as such mimic low establishment success of seeds (Jakobsson and Eriksson 2000). There are no additional costs to dispersal in the base model except for the fact that the chance to end up outside the landscape or climate window inevitably increases with the dispersed distance, but we additionally modelled dispersal dependent costs to constrain dispersal distances in a biologically meaningful sense (see sensitivity analysis). Survival and reproduction are only possible within suitable habitat inside the climate window. This window moves in the x direction at a speed varying from 0.05 to 6 grid cells / time step. By varying this rate it is possible to simulate different rates of climate change. We used climate windows of 40 grid cells wide but also tested smaller (20 grid cells) and larger (80 grid cells) windows (see Appendix Figure 10).

Table 3: Average and longest dispersal distance of 10000 seeds with a certain 'dispersal distance' δ^* i.e. the standard deviation of a Gaussian kernel.

δ^*	Average distance	Longest distance
0,5	0,6	2,2
1	1,3	5,0
2	2,5	9,2
3	3,8	15,6
4	5,0	17,5
5	6,3	21,9
6	7,5	25,5
7	8,9	30,1
8	10,0	36,4
9	11,3	43,5
10	12,5	47,4

4.3.2 Evolution of dispersal

Each individual inherits a single allele from its parent which determines the shape of the individual's dispersal kernel defined as the parameter δ. More specifically the allele value (δ) determines the standard deviation of a Gaussian distribution with mean zero. Dispersal is then modelled by sampling displacement distances in two dimensions from this distribution (see Bonte et al. 2010). Since the allele value describes a probability distribution rather than an exact value the heritability of effective dispersal distance is less than one, which is in line with empirical work (e.g. Bonte & Lens 2007; Cheptou et al. 2008; Bitume et al. 2011). We use δ as a measure for dispersiveness since individuals with high δ values have wide kernels with approximately 32% of the population moving beyond distance δ (principal characteristic of a Gaussian distribution). Individuals with a kernel with high δ consequently have a higher probability to disperse a long distance (See Table 3). For ease of reading we will refer to this kernel parameter as dispersal distance. Since we assume for simplicity uninformed, passive (wind) dispersal, long distance dispersers from the tail of the kernel have a relatively high chance to disperse out of the population's suitable range, but this probability depends largely on the size of the climate window. When the model is initialized each individual's allele value is set as a random value from the uniform distribution between 0 and 10. This leads to high standing genetic variation and allows spatial sorting to act. We also ran simulations after 500 generations of dynamics in a stable range, combined with changes in mutation rate thereby decreasing the level of standing genetic variation to derive the sensitivity of our conclusion regarding evolutionary rescue (See Table 4). Mutations on the allele occur with a probability of 1% in the base model and are randomly drawn from a uniform distribution (-1,1). As a reference to the evolutionary scenario we determined invasion speed of populations with a fixed dispersal distance in landscapes without climate change (see later), we kept the kernel parameter fixed and did not allow any mutations, thereby precluding evolution.

4.3.3 Maximal tolerance of climate change and invasion speed

If we allow evolution of the dispersal distance we expect that for each viable rate of climate change an evolutionary stable dispersal distance should arise over time. We compare the rate of climate change under which a certain dispersal distance allele (δ) has evolved to the fastest rate of climate change that population could track if the same dispersal distance allele (δ*) was fixed and equal in all its individuals. We call the latter rate the maximal "tolerance" of climate change and it is assessed as the maximal rate of climate change that a population with a genetically fixed dispersal distance allele (δ*) can keep up with over the whole length of the landscape during 30 runs without going extinct once. Next, we compare this rate to the speed at which the same population can invade empty habitat. It makes intuitively sense that a population which can invade empty habitat at a certain speed could shift its range equally fast when it is forced to by a climate window; therefore both rates are expected to be similar. The invasion speed is defined as the average speed of the invasion front (furthest individual), calculated over 30 runs. Note that when we use a fixed dispersal distance parameter it is not the dispersal distance itself that is fixed but the dispersal kernel shape (see earlier), we always denote fixed dispersal distance values with a "*".

4.3.4 The influence of the rate of climate change on gap crossing capacity

To test the degree to which the speed of the moving envelope (rate of climate change) affects the probabilities that a shifting population crosses unsuitable habitat, we introduced a gap into our virtual landscape. Therefore, we considered an area of habitat from position x= 900 onwards as unsuitable habitat in the baseline model (see Appendix Figure 9). The width of this gap was fixed but varied between different scenarios (See Table 4). We ran the simulation 50 times for each combination of climate window speed and gap size. During these replications we measured how often the population succeeds in crossing the gap.

To assess how population size changes and the dispersal distance (δ) evolves during such a simulation we chose one specific set of parameter values and studied it in more detail. We moved the climate window at two grids cells / time step and used a gap width of 7 grid cells. We repeated this simulation 100 times and calculated average population size and dispersal allele value (δ) for each time step. This simulation slightly differed from the base model since we did not move the climate window during the first 500 time steps, allowing us to check how this affects the results. After 980 time steps the climate window reached the gap.

4.4 **Results**

4.4.1 The rate of climate change a species can track is lower than the rate at which it can invade

The rate at which a population can expand in a landscape without a climate window (invasion speed) is linearly correlated to the implemented dispersal distance parameter δ^*. At lower δ^* values there is also a linear relationship with the maximum climate window rate a population can tolerate without going extinct. However, at high dispersal distances ($\delta^*>6$) this relationship does not hold; indeed higher δ^* does not allow persistence in scenarios of faster climate changes and perhaps counter intuitively, the maximum rate of climate change that a species with very high δ^* can tolerate may be lower than that which a species with lower δ^* can tolerate (Figure 13 a). There is thus a divergence between invasion speed as determined in a spatiotemporally stable (empty) landscape and the maximal rate of climate change that a population with the same δ^* can keep track of. The extent of this divergence grows with an increase in the dispersal distance parameter δ^*.

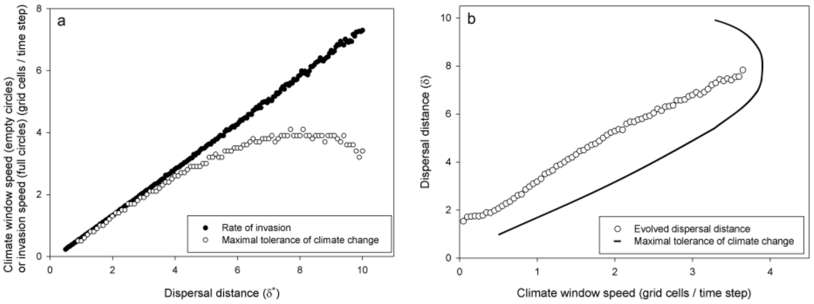

Figure 13: a) The rate at which a population with a fixed dispersal distance parameter (δ^*) can invade an empty spatially stable landscape (full circles) and the maximal climate window speed a population with the same dispersal kernel can track (empty circles). b) Impact of climate window speed on evolved dispersal distance δ (open circles). The solid line depicts the maximal tolerance of climate change as depicted in figure a.

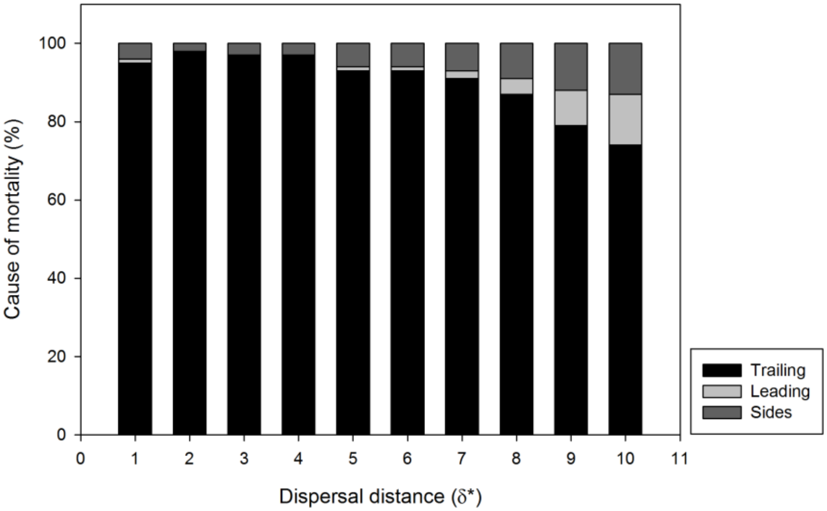

Figure 14: The proportional causes of mortality in a number of simulations with parameter values derived from the results in Figure 13a. Mortality is a result of ending up outside the suitable climate window. When dispersal distances are high, a relatively larger number of individuals land in front or to the sides of the climate window (as a seed) and die.

4.4.2 Evolved dispersal distance increases with the rate of climate change and is higher than necessary

Increasing rates of climate change induce evolution towards higher dispersal distances δ (Figure 13b). Comparison of the average evolved dispersal distance δ with the lowest dispersal distance δ^* that allows a population to track the shifting window without going extinct (full line from Figure 13b), indicates that evolved dispersal distances are always higher than is absolutely necessary for tracking a shifting climate window. For each rate of climate change there is selection for the genotypes that optimally balances dispersal mortality and the capacity to track the climate window, resulting in a maximization of the population size (Appendix Figure 11). When the speed of climate change exceeds 3.7 grid cells / time step, the combination of high mortality by the trailing edge of the climate window and high mortality of long distance dispersers pushes the population to the limit of what is theoretically possible in our model. This is why there is no crossing of the full line with the open symbols in Figure 13b. Evolution can thus only allow individuals to keep track of climate change until a critical climate change rate. Under higher rates of climate change, dispersal distance δ evolves to such values that mortality due to ending up outside the climate window becomes too high. Increased costs of dispersal, here implemented by inducing higher rates of mortality due to ending up outside the suitable range, thus constrain the capacities to keep track of a shifting climate envelope. When the climate window moves slowly short dispersal distances evolve and the trailing edge accounts for almost 100% of deaths while at higher rates of climate change, and the subsequent evolved high dispersal distances, mortality due to crossing the leading or side edges becomes more substantial (Figure 14). We present an online animation of the spatial distribution of individuals within the climate window for different rates of climate change and species' dispersal distance (see Link 3 in appendix). These dynamics are also influenced by the size of the landscape, with reduced costs of ending up aside the landscape in wider or in continuous landscapes modelled as a torus. This implies that evolution towards higher dispersal distances will be easier in populations that occupy a large distribution range or face lower dispersal costs, thereby allowing individuals to keep track of faster moving climate windows (Appendix Figure 10). Populations that have smaller ranges due to for instance local adaptation towards specific climatic conditions will be subject to an even stronger selection for higher dispersal distances but are less feasible to persist since they are more likely to disperse into an unsuitable environment. Simulations with evolved dispersal distances always resulted in larger population sizes than equivalent simulations where instead we used the lowest fixed dispersal distance parameter δ^* that allowed tracking of the climate window (Figure 15).

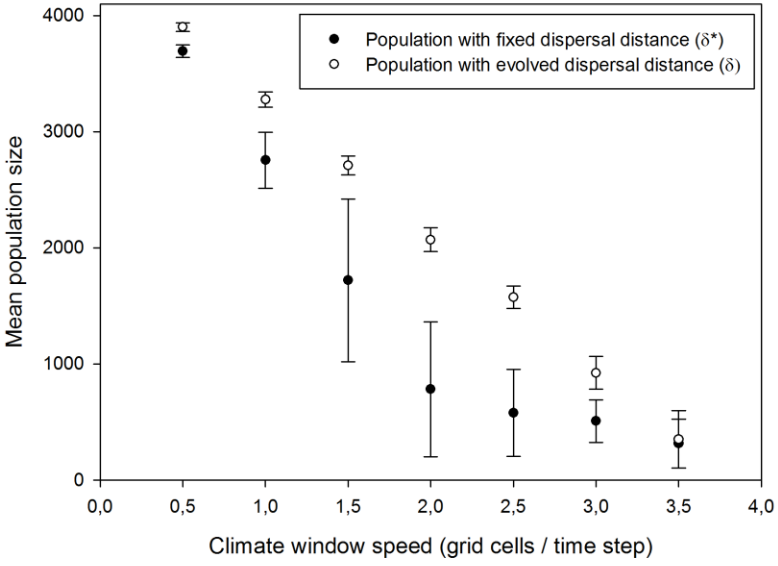

Figure 15: The difference in average population size between populations having the lowest fixed dispersal distance parameter (δ*) that allows tracking the climate window and evolved dispersal distance (δ) for several climate window speeds. The error bars denote the standard deviation based on 10 replicas.

Table 4: The average success rates of 100 populations which had to track a moving climate window and cross a gap of unsuitable habitat in different scenarios. Note that in all (viable) scenarios the success rate initially increases as the climate window moves faster (i.e. evolutionary rescue).

	Rate of climate change	0,5	1	2	3	4	5
Gapsize = 5	Mutation rate 0.01 (i.e. standard scenario)	1.00	1.00	1.00	1.00	0.07	0.00
	Mutation rate 0.001	0.91	1.00	1.00	1.00	0.14	0.00
	Mutation rate 0.0001	0.90	1.00	1.00	1.00	0.05	0.00
	Mutation rate 0	0.80	1.00	1.00	1.00	0.11	0.00
	Climate window 80 grid cells wide	1.00	1.00	1.00	1.00	1.00	0.35
	500 gen. equilibrium + mutation rate 0.01	0.97	1.00	0.98	0.02	0.00	0.00
	500 gen. equilibrium + mutation rate 0.001	0.88	1.00	0.11	0.00	0.00	0.00
	500 gen. equilibrium + mutation rate 0.0001	0.63	0.96	0.00	0.00	0.00	0.00
	δ x 0.005 dispersal mortality	0.93	1.00	1.00	0.89	0.00	0.00
	δ x 0.01 dispersal mortality	0.88	1.00	1.00	0.00	0.00	0.00
	δ x 0.02 dispersal mortality	0.64	0.99	0.48	0.00	0.00	0.00
Gapsize = 10	Mutation rate 0.01 (i.e. standard scenario)	0.01	0.24	0.91	0.91	0.01	0.00
	Mutation rate 0.001	0.00	0.09	0.96	0.84	0.03	0.00
	Mutation rate 0.0001	0.00	0.13	0.92	0.88	0.03	0.00
	Mutation rate 0	0.00	0.18	0.94	0.90	0.03	0.00
	Climate window 80 grid cells wide	0.25	0.72	1.00	1.00	1.00	0.31
	500 gen. equilibrium + mutation rate 0.01	0.03	0.22	0.93	0.06	0.00	0.00
	500 gen. equilibrium + mutation rate 0.001	0.00	0.15	0.08	0.00	0.00	0.00
	500 gen. equilibrium + mutation rate 0.0001	0.00	0.02	0.00	0.00	0.00	0.00
	δ x 0.005 dispersal mortality	0.01	0.15	0.70	0.36	0.00	0.00
	δ x 0.01 dispersal mortality	0.02	0.07	0.46	0.00	0.00	0.00
	δ x 0.02 dispersal mortality	0.00	0.03	0.02	0.00	0.00	0.00
Gapsize = 15	Mutation rate 0.01 (i.e. standard scenario)	0.00	0.00	0.11	0.26	0.00	0.00
	Mutation rate 0.001	0.00	0.00	0.12	0.22	0.00	0.00
	Mutation rate 0.0001	0.00	0.00	0.15	0.20	0.00	0.00
	Mutation rate 0	0.00	0.00	0.08	0.24	0.00	0.00
	Climate window 80 grid cells wide	0.00	0.01	0.85	1.00	1.00	0.21
	500 gen. equilibrium + mutation rate 0.01	0.00	0.00	0.03	0.00	0.00	0.00
	500 gen. equilibrium + mutation rate 0.001	0.00	0.00	0.00	0.00	0.00	0.00
	500 gen. equilibrium + mutation rate 0.0001	0.00	0.00	0.00	0.00	0.00	0.00
	δ x 0.005 dispersal mortality	0.00	0.00	0.05	0.02	0.00	0.00
	δ x 0.01 dispersal mortality	0.00	0.00	0.02	0.00	0.00	0.00
	δ x 0.02 dispersal mortality	0.00	0.00	0.00	0.00	0.00	0.00

4.4.3 High variability in dispersiveness is maintained in a moving climate window.

After 500 time steps (generations) without climate change average dispersal distance allele values are strongly reduced (see Figure 16), however, kin-competition withholds the dispersal distance from evolving to zero. At this stage only a few long distance dispersal genotypes (δ>3) remain (Figure 17). After the onset of climate change, these genotypes become more abundant relative to those that are less dispersive and new, even more dispersive, mutants arise. This pattern holds when decreasing mutation rates up to 10e-6. However, the maximal rate of climate change a population can track increases with the mutation rate (See Table 4). Soon after the initialisation of climate change a large difference in average dispersal distance allele values between leading and trailing edge subpopulations arises, this difference gradually diminishes over time but continues to exist. In both the subpopulations near the leading and trailing edge average dispersal distance allele values reach equilibrium after 200 time steps of climate change (t=700). Even after the distribution of genotypes has stabilized a remarkably large standing genetic variation in dispersal distance alleles remains, ranging from the least dispersive genotype that can tolerate a climate window moving at 2 grid cells / time step (δ =±2.7 see Figure 13a and Figure 17 at t=700) to much more dispersive genotypes.

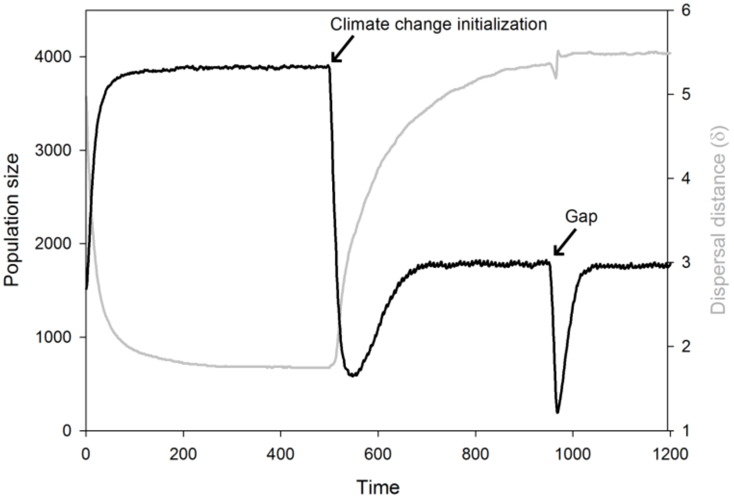

Figure 16: The average population size (black line) and average dispersal distance (δ) (grey line) over time. During the initial 500 time steps without climate change the average dispersal distance decreases and reaches equilibrium. As soon as the climate window starts to shift, the dispersal distance increases rapidly. There is a small drop in average dispersal distance when the climate window is reached. The population size crashes initially but eventually recovers and stabilizes at less than half the population's size without climate change. When a gap in the landscape is reached the population almost goes extinct but eventually recovers.

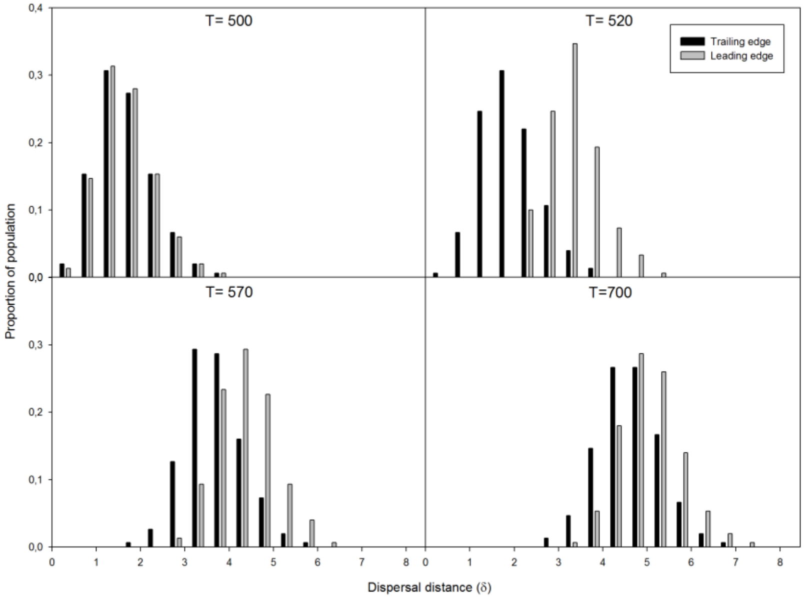

Figure 17: The average frequency of dispersal distance genotypes near (distance < 5 grid cells) the leading (gray) and trailing edge (black) of the climate window at four different moments in time (T) calculated over 1000 simulation runs. In this model the climate window only started moving after 500 generations (T=500), the upper left figure thus gives us the equilibrium distribution of genotypes before climate change. There is a strong selection favouring more dispersive genotypes when the climate window starts to shift (T=520, 570). Which eventually results in a stable frequency distribution of genotypes after 200 generations of climate change (T=700). For this specific model we used a climate window moving at 2 grid cells / time step.

4.4.4 Faster climate change increases gap crossing capacities of a population

The speed of the shifting climate window has a pronounced impact on the gap size that can be crossed (Figure 18). In absence of any climate change or at lowest climate change speed the gap size that can be successfully crossed is around 6 units, gaps of twice that size can be successfully crossed at a climate window speed between 2-3.7 grid cells / time steps. At high climate window speeds (>3.7 grid cells per time step) the success rate drops drastically and eventually populations become extinct before they reach the gap. The exact outcome of this model was sensitive to a number of parameters and conditions but the qualitative pattern of temporarily increased persistence always remained prevalent (See Table 4).

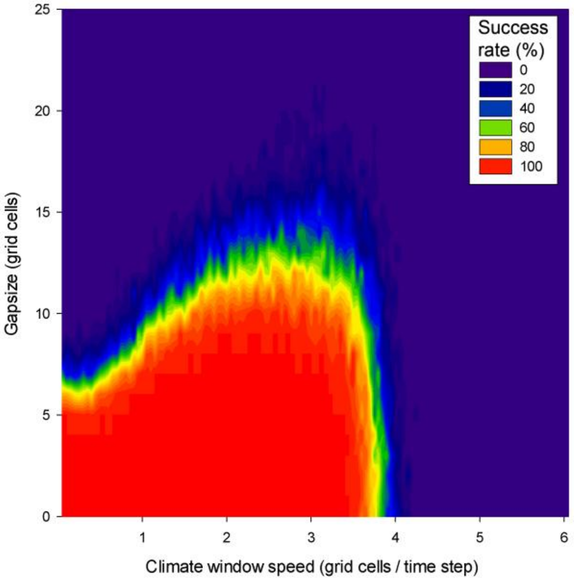

Figure 18: Success rate of gap crossing in populations with evolving dispersal distance (δ) according to the speed of climate change (X-axis) and gap size (Y-axis). Faster moving climate windows induced selection for more dispersive genotypes and increased the probability of the population to cross the gap.

4.5 Discussion

By means of generic modelling we show that: (i) increased rates of climate change select for larger dispersal distances; (ii) evolved dispersal distances are higher than strictly necessary to keep track of the climate window and maximize population size; (iii) the maximal rate of climate change that a population can successfully track is lower than the rate at which a population expands in empty landscapes, not affected by a shifting climate window (invasion speed); (iv) the evolution of dispersal distance induces a rescue mechanism when gaps of unsuitable habitat need to be crossed during range expansion under climate change.

Dispersal kernels evolve towards larger displacement distances by both natural selection and spatial sorting when the rate of climate change increases. In accordance with previous studies on emigration rate (Travis and Dytham 2002; Travis et al 2009; Burton et al 2010), spatial sorting processes are most important at the onset of climate change, while natural selection on dispersal distance becomes the main mechanism at the leading edge. Interestingly, evolved dispersal distances are always higher than necessary for range expansion through invasion in a landscape without shifting climate windows. Populations characterized by a specific kernel will subsequently show larger range expansion in unoccupied landscapes when climate windows do not limit them. Classical invasions (Shigesada and Kawasaki 1997) do not impose the same limitations on population expansion as a climate window, i.e., increased mortality due to overshooting the climate window dimensions and to a lesser extent mortality at the trailing edge (Cousens et al 2008a). Modelled invasion rates (Neubert and Caswell 2000; Katul et al 2005) should therefore be applied with some caution to estimate the maximal rate of climate change a species can tolerate. Methods developed to predict the rate of expansion in empty habitat do not account for limitations in spatial dynamics under climate change and could thus overestimate the rate of climate change a species can track. In our model the only difference between an invasion and a range shift with a moving climate window is the presence of two extra boundaries in a shifting climate window, thereby limiting the population’s spread. In accordance with Pease et al. (1989) we showed that a larger distance between the leading and the trailing edge of the climate window allowed the populations to keep track of a faster moving climate window. A larger climate window decreased dispersal mortality and thus allowed the evolution towards higher dispersal distances. The opposite was true for a smaller climate window. In reality this effect is likely to be experienced by populations that have narrow distribution ranges due to local adaptations to climate heterogeneity or the preference of a rare type of habitat. In these populations, highly dispersive individuals would have low survival chances because they incur a high risk of ending up in unsuitable habitat, at least in the case of passive dispersal. We implemented absorbing border conditions on the non-shifting edges of the climate window. Such absorbing boundaries strengthen the selection against long distance dispersal (Burton and Travis 2008). Assuming no edge effects by wrapping boundaries using a torus did not, however, change the results in a qualitative way given the proportional marginal mortality effects at these edges relative to mortality at the trailing or leading edge.

Because of spatial sorting, even despite the absence of assortative mating and subsequent natural selection, a large difference in average dispersal distance (δ) between individuals near the trailing and leading edges occurs after 10 to 20 generations. From this point onwards natural selection slowly starts excluding low fitness genotypes that are either not dispersive enough to consistently keep up with the window and highly dispersive genotypes that are too likely to disperse outside the window. This leads to a decreasing difference in dispersal distance between individuals from the trailing and leading edge, thereby generating stabilising selection towards an optimal dispersal strategy and a maximisation of the total population size (Appendix Figure 11). Spatial gradients in selection pressures inside the climate window generate a large standing genetic variation during range expansion, ranging from the least dispersive individuals that could track the window to much more dispersive individuals. This explains why the average dispersal distance allele value was higher than necessary to keep track of a certain rate of climate change. Near the leading edge, dispersive individuals with wide kernels have an advantage since they are more likely to colonize the empty habitat that constantly becomes available at this location (Travis et al 2010b; Phillips 2011). However, when approaching the trailing edge, population densities gradually grow and increase competition, thereby benefiting lineages consisting of shorter dispersal distance genotypes. Because wide dispersal kernels incur a cost of ending up beyond the window (Figure 14) the eventual evolutionarily stable dispersal distance (δ) will depend on the dimensions of the landscape. From earlier work, it is known that mortality due to low colonization success in unsuitable habitat at the edge of a population’s distribution is a mechanism of range border formation (Holt and Keitt 2000). According to the landscapes dimensions, a threshold point of climate change speed has been observed beyond which populations become too small to remain viable during the process of tracking the climate window.

Evolutionary rescue is the process where the rise in frequency of a few well adapted genotypes can counter the decline of an overall maladapted population during a period of environmental change (see Ferrière et al. (2004) for theory), and typically results in a U-shaped function of population size over time (Holt and Gomulkiewicz 2004). The potential importance of this process in conservation biology has been topic of several theoretical (Heino and Hanski 2001; Travis et al 2010b) and empirical studies (Bell and Gonzalez 2011). In our study, somewhat higher rates of climate change increase the capacity of a population to cross gaps in the landscape during climate driven range expansion for a wide range of parameter space (Table 4). As such, slightly faster climate change may induce evolutionary rescue for species experiencing locally fragmented habitat (Fischer and Lindenmayer 2007).

A first evolutionary rescue event takes place at the onset of climate change. Under these conditions, only dispersive genotypes survive (and thrive) and low population sizes are overcome (Figure 16). The second rescue event, gap crossing, is enhanced at higher rates of climate change and again a typical U-shape in population size is observed with only highly dispersive individuals making it across the gap (Figure 16). Population history subsequently strongly affects this second rescue event (Phillips 2011). Of course, these rescue mechanisms will only be relevant in species and/or populations showing sufficient standing variation in dispersal traits (Pease et al 1989) through for instance diverging selection pressures in heterogeneous landscapes (Bonte et al 2010). However, while not a focus of this study, local adaptations in heterogeneous landscapes could in turn impede range shifts trough a high genetic load caused by maladapted immigrants (Polechová et al 2009; Atkins and Travis 2010; Duputié et al 2012). In theory, we might make the initially counterintuitive suggestion that those species that have long life cycles may benefit most from the dispersal enhancing selection pressure that facilitates gap crossing since they experience time and thus the rate of climate change faster (the generation effect). Similar rescue mechanisms may be equally more relevant for species living in biomes characterized by fast climate change such as savannah compared to biomes that are subjected to relative slow climate change such as tropical coniferous forest (Loarie et al 2009); at least if range expansion and evolution do occur in more continuous suitable landscape.

Traits determining dispersal distance are shown to have a genetic basis and subject to multiple costs (Bonte et al 2012). While the evolvable maximal dispersal distance is expected to be constrained due to morphological, physiological and life history trade-offs (Travis et al 2012), our simulations demonstrate that evolution towards increased dispersal distances may rescue species up to specific limits that are determined by dispersal costs, the level of standing genetic variation and the landscape context (here size of the gap and climate window). The loss of genetic variation during a phase of genetic equilibrium without a shifting climate window additionally decreases evolutionary rescue probabilities and increases the sensitivity towards low mutation rates (Table 4). The exact rates of climate change which could induce evolutionary rescue are therefore likely to differ strongly among species. So, while there is currently a consensus that too fast climate change will be detrimental for many species (e.g. Visser 2008; Berg et al. 2010), our modelling approach shows that under an increased rate of climate change that does not generate direct extinction, evolutionary dynamics in dispersal are likely to induce rescue mechanisms especially in landscapes that suffer from rather limited habitat fragmentation. While it will be extremely challenging to predict which species may be rescued by evolutionary dynamics, our results at least should make it possible to identify species that will face problems in keeping track with increasing rates of climate change, i.e. species experiencing distance related dispersal costs, having small distribution ranges, limited genetic variation in traits determining dispersal distance and/or experiencing large barriers in the landscape or too high rates of climate change relative to their dispersal distance.

Populations facing climate change need to adapt to the new environment or track the climate window in order to avoid extinction (Visser 2008). Here we demonstrate the importance of combined responses, changes in the dispersal kernel as an adaptation. We show that fast climate change can induce selection for wider dispersal kernels, as such ensuring population persistence and even evolutionary rescue in case of range shifting in fragmented areas. Interestingly, our model demonstrated a discrepancy between the rate of climate change a population can tolerate and the rate at which the same population can invade empty habitat. This warns us to be careful when estimating the maximal rate of climate change a species can tolerate based on the invasion speed of that species. While the impact of climate change rate on range expansion and dispersal evolution is clear from a theoretical point of view, processes are expected to be much more complicated in reality due to trade-offs in life history traits (Burton et al 2010), multiple species interactions (Urban et al 2012a) and several (novel) costs involved during the dispersal process (Travis et al 2012; Bonte et al 2012). Model approaches such as applied here, are however, a first and important step to understand the huge variation in range shifting patterns relative to life history traits such as dispersiveness, reproductive ability and ecological generality (Angert et al 2011).

4.6 Retrospective

There are certain issues with the dispersal procedure which we already discussed in the retrospective from chapter two on page 32.

4.7 Acknowledgments

This research was funded by FWO projects G.0057.09 to DB and JB, and G.0610.11 to DB, JB and RS. JMJT, DB and RS are supported by the FWO Research Network EVENET.

5

Integrating empirical and theoretical approaches to understand life history evolution during range expansion along a latitudinal gradient.

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Chapter 5: Integrating empirical and theoretical approaches to understand life history evolution during range expansion along a latitudinal gradient.

5.1 **Abstract**

Range shifting by species is a phenomenon off all times. In the context of climate change and species invasions, however, it is increasingly gaining attention because the rate at which it occurs in the Anthropocene induces fast shifts in biological assemblages. During range expansion, species are expected to experience multiple selection pressures. Especially for the many poleward expansions, a straightforward interpretation of the observed evolutionary dynamics is hampered because of the joint action of evolutionary processes related to spatial sorting and local adaptation along a latitudinal gradient.

In a common-garden environment, we studied evolutionary divergence in life-history traits related to the recent northward range expansion of the two-spotted spider mite, *Tetranychus urticae* Koch (Acari, Tetranychidae). We then contrasted the evolved trait divergence with expected patterns from a simulation model in which predictions from spatial sorting could be separated from predictions from local adaptation.

We demonstrate how, in both empirical and modelling results, spatial sorting and local adaption jointly affected life-history evolution in T. urticae. In particular dispersal and developmental speed showed contrasting patterns. Dispersal was clearly shaped through genetic sorting along the invasion front, showing a clear increase towards northern latitudes. Developmental speed, on the other hand, showed typical adaptations towards colder temperatures and shorter breeding seasons at higher latitudes (i.e. a saw-tooth pattern).

Divergence in life-history traits in a species shifting its range poleward under climate change is consequently jointly determined by contemporary evolutionary dynamics resulting from sorting processes and fast local adaptation to the environmental gradient.

5.2 Introduction

Species ranges have always been dynamic, they shrink and expand in response to changing conditions and, accordingly, numerous species are currently shifting their ranges due to contemporary climate change (Parmesan 2006). Moreover, a growing number of species are currently expanding their range after being introduced in a new environment by humans (*i.e*. invasive alien species) [*e.g.* (Richardson and Rejmánek 2011)]. During such range expansions, species undergo multiple selective pressures (Phillips et al 2010). Especially in the many cases where the shift is along a latitudinal gradient, a complex interplay of selective forces arises (Shine et al 2011).

On the one hand, species expanding their range along a latitudinal gradient inherently experience a selection pressure due to changed local abiotic conditions (*i.e*. pressure for local adaptation). Especially shorter breeding seasons and lower temperatures are expected to affect species life histories. Indeed, range expansion often infers entering unknown, potentially harsh environments. Several studies using the Colorado potato beetle therefore stressed the role of diapause behaviour and related physiological changes during range expansion (Piiroinen et al 2011; Lehmann et al 2014). The length of the breeding season is another important factor. Season length limits the possible number of generations within a season (*i.e.* voltinism), and when the season is sufficiently long, an extra generation is generally favoured (Roff 1980). This can be accomplished through a sharp decrease in development time (*i.e*. a more rapid development of all generations, resulting in time available for an extra generation within the growing season, and, logically, in a lower age at maturity for all generations) (Roff 1980). Accordingly, when season length gradually decreases, each generation has to develop faster and faster, until the point where the time available becomes too limited. At such a point, an additional generation is sacrificed, leaving more time to develop for the remaining generations and thus a sudden slowing down of development speed. The pattern arising from such systematic sharp changes in a trait value is called a saw-tooth pattern (Roff 1980). Since development time is suggested to share an underlying mechanism with growth rate (Kivelä et al 2011), high latitude populations not only tend to compensate for the shorter breeding seasons through these changes in development time, but also through the evolution of genetically faster growth rates [*i.e.* counter gradient variation, (Conover and Schultz 1995)]. When this increased growth rate perfectly compensates for the shortened development time, individuals at high latitudes will have a similar adult size as individuals from lower latitudes (Blanckenhorn and Demont 2004). Alternatively, when growth rate over or under compensates for the rapid development, a Bergmann cline (larger adult size) or, respectively, converse Bergmann cline (smaller adult size) arises (Blanckenhorn and Demont 2004). These clines might moreover show saw-tooth patterns, since changes in voltinism can affect growth rate and body size just as well as development time.

On the other hand, a range expansion equally entails a selection pressure typical for the expansion process *per se* [*i.e.* spatial sorting, see (Shine et al 2011)]. Since the most dispersive phenotypes inevitably accumulate at the expansion front, assortative mating takes place (Phillips et al 2010). This results in increased dispersal abilities at the front, as has already been illustrated for a growing amount of invertebrate [*e.g.* (Mitikka and Hanski 2010; Hill et al 2011) and vertebrate [*e.g.* (Phillips et al 2006)] species. It is thus acknowledged that dispersal evolution both affects (Kubisch et al 2014) and is affected by range expansion [reviewed in Hill et al (2011)]. Furthermore, because of the locally low densities, individuals in the vanguard of an expanding range experience *r*- rather than *K*-selection, translating into a higher investment in reproductive traits (Phillips 2009; Phillips et al 2010). This could be an investment to reproduce more, as well as an investment to reproduce faster (*i.e.* faster individual growth rates to reach reproductive size earlier).

The evolutionary potential of traits such as development speed, dispersal and reproductive rate greatly depends on the available genetic variation and possible trade-offs. The importance of genetic and energetic constraints in limiting adaptive evolution in natural populations is, however, not well understood. Some authors expect a negative relationship between dispersal and fitness-related traits such as survival or development time (Stevens et al 2012). Direct trade-offs between dispersal and reproduction have also already been predicted and shown in several wing-dimorphic insect species (Zera and Denno 1997). Moreover, Hughes et al. (2003) more specifically found a trade-off between thorax mass (as a proxy for dispersal) and the number of eggs (as a proxy for reproduction rate) between core and edge populations of an expanding butterfly species [but see (Saastamoinen 2007)]. Dispersal and reproductive rate are, however, complex traits that are difficult to measure directly. Therefore, Phillips et al. (2010) consider it unlikely that all traits determining dispersal trade-off with all traits determining reproductive rate. Both dispersal and reproductive rate should instead be able to increase at the expansion front (Phillips et al 2010). Nonetheless, the evolution of both traits could still be hampered through trade-offs with other traits; especially those that are important at high population density (*e.g.* competitive ability) (Phillips et al 2010). Indeed, a model of Burton et al. (2010) showed how individuals at the front invest more in dispersal and reproduction, while those in the core of the range invest more in competitive ability.

Though increasing efforts are being made to investigate this matter, we are only just starting to gain knowledge on trait evolution during range expansion. Empirical studies with butterflies [*e.g.* (Hill et al 1999) and toads [*e.g.* (Phillips et al 2006)] have played a crucial role in developing our current understanding, but generally, most research to date is theoretical [e.g. (Travis and Dytham 2002; Burton et al 2010; Alex Perkins et al 2013)]. Furthermore, research so far is limited to a small set of species and traits and does seldom frame evolutionary changes within a full life-history perspective. Therefore, there is an urgent need for more empirical research on a broader set of organisms and a broader set of dispersal related and other vital, possibly coevolving, traits. Recent work of Therry et al. (2014a), for example, showed how range expansion can also affect the larval stage and adult immune function of a damselfly and, undoubtedly, many more effects of range expansion remain to be found.

Moreover, practically no efforts have been made so far to incorporate latitudinal effects. Most theoretical and empirical research on trait evolution during range expansion focuses on the effect of the range expansion process *per se*, while neglecting the effect of the changed local abiotic conditions in the newly populated environment. This can be problematic, as spatial sorting and local adaptation can generate similar latitudinal patterns, like for example in dispersal (Travis and Dytham 2002). Erroneous conclusions could thus be made regarding the cause of observed life-history patterns. To date, Therry et al. (2014b) is the only study we know of that tried to distinguish between both these effects. They showed how the increased dispersal ability in the damselfly *Coenagrion scitulum* at the range edge was not caused by the local temperatures, but probably by spatial sorting. They also witnessed a poorer body condition at range expansion fronts, which could have been the result of both local abiotic conditions and higher energetic costs associated with increased dispersal. This illustrates the difficulty of distinguishing between the effects of local adaptation and spatial sorting. Consequently, we currently have no idea on the relative importance of both forces in shaping traits during range expansion.

In an attempt to cope with these shortcomings, we assessed quantitative genetic variation in an array of life-history traits and contrasted the evolved trait divergence with expected patterns from a model in which predictions from spatial sorting could be separated from predictions from local adaptation. Along a latitudinal gradient from range core to edge, we sampled populations of the spider mite *Tetranychus urticae* Koch (Acari, Tetranychidae), which has recently expanded its range in Europe from South (Mediterranean) to North (Denmark) (see Carbonnelle et al (2007)). In a common garden environment, we quantified the genetic variation of the biologically most relevant life-history traits (fecundity, longevity, sex ratio, egg and juvenile survival, development time, adult size), to get a full life-history perspective on trait evolution during range expansion. Because of their relevance in the context of range expansion (cfr. supra), we also included diapause behaviour, and dispersal latency and propensity. In parallel, we built a custom individual-based simulation model consisting of three contrasting scenarios differing in spatial sorting and genetic adaptation: one for a stable range along a latitudinal temperature gradient, one with range expansion along this gradient and one with range expansion in a homogeneous landscape. Afterwards, we contrasted our empirical findings with the theoretical predictions based on our model to test which of the different model scenarios best explained our data.

5.3 Materials and Methods

5.3.1 Life history variation along the sampled gradient

Study species

T. urticae is an agricultural pest species with a worldwide distribution. It reproduces through arrhenotokous parthenogenesis, whereby unfertilized eggs develop into males and fertilized eggs into females. The species has the ability to disperse by means of aerial currents. In Europe, the mite species has expanded from Mediterranean to Northern European regions (Denmark) over the last decades [see (Carbonnelle et al 2007)].

Fieldwork

We collected spider mites during the summers of 2011 and 2012. Based on satellite images (Figure 20), we first selected several collection sites along a 1000km latitudinal gradient from north-western Belgium to northern Denmark. In order to minimise variation due to host plant adaptation and human pressure and to maximise latitudinal variation relative to variation in how land-inward sites are located, all these sites were situated in (semi-) natural area along the coast. Then, all selected sites were visited and mites were sampled when present. In 2011, spider mites were found and sampled in twenty different sites (i.e. in the majority of the selected sites) (Table 5). In 2012, we optimized the sampling design and spider mites were only sampled in twelve out of these twenty sites, thereby omitting populations that were very close to each other (Table 5).

Mites were collected through the harvesting of infested leaves, mostly of European honeysuckle (*Lonicera periclymenum*), European spindle (*Euonymus europaeus*) and common hop (*Humulus lupulus*). These leaves were then stored between towel paper in an unclosed plastic bag for the rest of the trip. Once in the lab, between fifty and several hundred mites per population were put on whole bean plants (*Phaseolus vulgaris*, variety Prélude) and maintained at room temperature with a light-regime of 16:8 LD for minimal one generation prior to synchronisation (cfr. infra), to minimize maternal effects (including host plant mediated effects). All experiments (with the exception of diapause assessment) were performed with mites from these common garden stock populations (one population for each collection site).

Synchronisation

Before the start of an experiment (with the exception of diapause assessment), a synchronisation of the mites was each time performed to obtain a large pool of same aged mated adult females. For this purpose, several adult females from the stock populations were put on a bean leaf (one to several leaves for each of the stock populations) and allowed to lay eggs for 24 hours in a climate room at 27°C, with a light regime of 16 hours light/ 8 hours dark. These same-aged cohorts of eggs were then allowed to develop, and the resulting synchronised adult females were used for the experiments described below All experiments were thus performed with at least third generation mites (at least one generation in the stock population, plus one generation of synchronisation). For practical reasons, some experiments were performed with mites gathered in the field in 2011 (diapause, fecundity, longevity, egg survival, juvenile survival, development time), while others were performed with mites from 2012 (dispersal, sex ratio, adult size).

Data collection: dispersal propensity and latency

Dispersal propensity and latency of mites from 2012 were measured with a method largely based on Li and Margolies (1993, 1994) in a climate room at 27°C. The propensity to disperse by air was assessed by counting the percentage of female mites showing the aerial take-off posture (i.e. upraised first pair of legs and cephalothorax, to increase drag). Dispersal latency was then assessed by counting the minutes between the start of the three hour observation and the moment the focal female showed the aerial take-off posture. Only one-day-old, freshly mated females were considered, since they are the main dispersing stage. (See Li and Margolies (1993, 1994) for more details). The experiment was repeated for high, medium and low densities. These densities were obtained by synchronising (*cfr. supra*) on a piece of leaf of, respectively, 4cm^2, 7.5cm^2 or 12cm^2. This gave a measure of the density experienced by the mother at the time of egg laying (*i.e.* ‘density mother’). The density experienced by the focal mites themselves was also taken into account by quantifying the density of female offspring on each piece of leaf (*i.e.* ‘density daughter’). Because of the obvious strong correlation between both density measures, only the measure explaining the most variation in the dispersal data was later kept for the statistical analysis.

Data collection: diapause

Between nineteen and twenty five (Danish and German populations) and six and eleven (Dutch and Belgian populations) days after sampling a population in the field (in 2011), data on diapause incidence of the population were collected. At this point, the mites were still temporarily stored on bean leaves in a regular room with no specific light regime. Mites had spontaneously started to go into diapause, allowing us to assess the proportion of diapausing female mites for each population.

Data collection: classical life-history traits

Fecundity and longevity

Fecundity and longevity of mites from 2011 were assessed by putting a one-day adult female on a small piece of bean leaf and counting the number of days and the number of eggs per day until she died. Data on both daily and lifetime fecundity were thus obtained. For each population, three same-sized pieces of bean leaf were put on wet cotton in each of four Petri dishes, resulting in twelve replicates per population. All Petri dishes were stored in a climate room at 27°C, with a light regime of 16 hours light/8 hours dark.

Egg and juvenile survival and development time

Egg survival, juvenile survival and development time of the mites from 2011 were assessed by putting three four-day adult female mites on a piece of bean leaf and following up the development of their offspring. Four-day adult females were used because, on average, female *T. urticae* have their maximum daily fecundity when they are four to five days old (own observation). The females were allowed to lay eggs for 24 hours in a climate room at 20°C, with a light regime of 16 hours light/8 hours dark, after which they were removed and their eggs were left to develop. We here used a temperature of 20°C because this allowed a steady development, hence a higher probability of detecting differences in development time. (The temperature of 27°C, used in all other setups, was chosen to allow a relatively fast development and therefore a relatively fast progress of the experiments). For each population, three same-sized pieces of bean leaf were put on wet cotton in each of four Petri dishes, resulting in twelve replicates per population. All Petri dishes were checked daily at approximately the same hour of the day to examine i) for each egg if it had hatched ii) the developmental stage of each juvenile iii) the sex of each freshly moulted adult. Afterwards, egg survival was calculated as the number of hatched eggs divided by the total number of eggs, juvenile survival as the number of adults divided by the number of larvae, and development time as the number of days between the day an egg was laid and the moult into an adult spider mite (*i.e.* age at maturity).

Sex ratio

Offspring sex ratio was assessed in all populations from 2012 by putting a one-day adult, freshly mated female on a small piece of bean leaf, allowing her to lay eggs during seven days. We chose seven days because the majority of eggs is laid within this period (Krainacker and Carey 1989). More specifically, sex ratio was calculated as the number of male offspring divided by the total number of offspring. For each population, three same-sized pieces of bean leaf were put on wet cotton in each of five Petri dishes, resulting in fifteen replicates per population. All Petri dishes were stored in a climate room at 27°C, with a light regime of 16 hours light/8 hours dark.

Adult size

For each population of 2012, between twenty seven and thirty, two-day adult females were immobilised through snap freezing at -80°C and later photographed one by one with a digital camera (Nikon Coolpix 4500) mounted on a stereomicroscope. To be able to calibrate the photographs, each female was positioned on a small measuring plate (accurate to 50µm). Using ImageJ 1.47v (Wayne Rasband, National Institutes of Health, USA), all photographs were afterwards analysed and the surface area (mm^2) of the mites (legs and capitulum excluded) was calculated (Schneider et al 2012).

Statistics

Prior to univariate analyses, we performed a multivariate distance ANOVA to test for variation in multivariate life history parameter space using the vegan and permute packages of R version 3.1.0 (The R Foundation for Statistical Computing, 2014). Relationships between Gower's distances of all life-history traits were assessed with the Adonis function. Because such distance-based methods cannot handle random effects and specific distributions, we used overall population averages.

All univariate analyses were then performed in SAS 9.4 (SAS Institute Inc. 2013), using the MIXED procedure for mixed linear models (daily fecundity, adult size) or the GLIMMIX procedure for generalized linear mixed models (all other analyses). Latitude and host plant (i.e. the plants species from which mites were gathered in the field) were always used as the independent variables, and for dispersal propensity and latency, 'density mother' and the interaction with latitude was also added. For the analysis of diapause, the time lag between the collection of mites in the field and the observation of the behaviour in the lab was furthermore added as a covariate. According to the dependent variable, a normal (daily fecundity, adult size), Bernoulli/binomial (diapause, dispersal, egg and juvenile survival, sex ratio) or Poisson (development time, longevity, lifetime fecundity, latency) error structure was modelled with the proper link function. For diapause and the classical life-history traits (except for adult size), Petri dish identity (nested within population) was modelled as a random effect. For egg and juvenile survival and development time, leaf identity (nested within Petri dish) was furthermore modelled as a second random factor. This was done to control for dependency among the leaves on each Petri dish and among the mites on each piece of leaf. By modelling residual variation as an additional random factor (in the glimmix procedure), we corrected for potential overdispersion (Verbeke and Molenberghs 2000). The denominator degrees of freedom for the tests of fixed effects were computed according to a general Satterthwaite approximation. All non-significant contributions (p>0.05) were omitted by a backwards selection procedure and validated by model selection. Finally, post-hoc Tukey tests were used to obtain the pair-wise differences among densities (dispersal propensity).

5.3.2 Inferring mechanisms by contrasting the empirical data with a parameterised individual based model

The model

We designed an individual-based model, inspired by that of Bancroft & Margolies (1999), resembling the coastal area from Belgium up to Denmark. In contrast to most other range shift models, our simulations had a fine temporal scale that allowed the incorporation of subtle, yet important effects such as a gradient in the length of the growing season. The model was parameterised with only those life-history data on *Tetranychus urticae* (Sabelis 1981) that were expected to be prone to selection. It allowed us to compare three scenarios differing in spatial sorting and local adaptation: two scenarios of life-history evolution during range expansion, one with and one without a latitudinal gradient in temperature, with a stable range scenario (*i.e.* with all patches occupied from the start) on the same latitudinal gradient.

Model settings: temporal and spatial temperature gradients

Sabelis (1981) showed that the temperature experienced by a mite affects its development time (appendix section 7.4.1), its juvenile and adult mortality rate (appendix section 7.4.3), and its fecundity (appendix section 7.4.4). To simulate appropriate local temperatures throughout the year, two trigonometric functions were created to match the actual average daily temperatures in locations in the extreme south and north of our gradient.

(The used weather stations were, respectively, Brussels, Belgium and Gothenburg, Sweden). For locations in between these two extremes, an intermediate function was calculated, assuming that the two functions converged linearly. This resulted in a unique temperature regime (seasonality) for each latitude. To account for extreme weather conditions in winter, we assumed an additional winter mortality which was imposed once each winter by killing 50% of all individuals in the south and 80% of all individuals in the north (with a linear increase in winter mortality between these two). To avoid mortality under these harsh conditions, adult spider mites were allowed to enter diapause. An inactive state in which they aged slower and experienced no temperature mortality. This came with a fecundity cost; individuals in diapause cannot produce eggs.

Model settings: spatial dimensions and dispersal

The spatial dimensions of our model resemble a 1000 by 50km strip of land along the coastline from Belgium to Denmark. The landscape is divided into 100x5 patches measuring 10 by 10km each. Individuals can disperse into neighboring cells with a 10% probability of succes (i.e. 90% dispersal mortality). Only adult individuals can disperse and their probability to do so is embedded in their genome as an emigration rate. We compare this value to the dispersal propensity which was measured empiricaly. We did not include density dependent dispersal because the empirical results showed no such effect (see later).

Model settings: population dynamics

The mean predicted number of eggs produced by a mite in a particular time step (day) was calculated by dividing the predicted lifetime fecundity by the predicted longevity of the mite (appendix section 7.4.2). Both these parameters were updated daily according to the local temperature. The actual predicted number of produced eggs was sampled from a normal distribution with the calculated mean (*cfr. supra*) and a standard deviation of 1.48, based on real data for *T. urticae* (De Roissart et al. under review). Since we only considered females in this model, we assumed asexual reproduction and halved the number off eggs produced according to Sabelis et al. (1981) to take into account the absence of males.

Each time step, all non-diapausing individuals faced a temperature-dependent mortality which increased rapidly as local temperatures reached either too low (10°C) or too high (35°C) values (appendix section 7.4.3). Adults additionally suffered from an age-dependent mortality (appendix section 7.4.2). When the local average temperature in a patch dropped below 10°C, all eggs, all subadults and all non-diapausing adults in that patch died. Adult mites enter diapause in autumn and exit this state in spring based on two temperatures embedded in their genome.

At the end of each time step, all patches local population sizes were assessed. If overcrowding occurred, individuals were randomly deleted from the patch until the number of individuals matched the carrying capacity (200). This procedure improves computational performance by keeping populations at a manageable size. As a consequence the population sizes in our model are low given the large spatial scale. We compensate for these low values by assuming a relatively low dispersal mortality (90%) when dispersing into an adjecent 10 by 10km patch. We realise this is a compromise where we lose realism but to our knowledge it is impossible to combine realistic density dependence (on the single-leaf or plant level) with the large spatial scale required to investigate range expansion dynamics.

Model Settings: trade-offs and evolutionary dynamics

Several trade-offs were implemented in the model. All trade-off related traits (four in total) were embedded in the genome and underwent a mutation probability of 1% at the birth of an individual. A mutation's effectsize was sampled from a uniform distribution between -10 and 10%. The first two trade-off related traits were the temperatures at which mites decided to go into diapause in autumn and reactivate in spring. Reactivation at a low temperature in spring came with the competitive benefit of producing eggs more early in the season, but with the cost of an increased temperature mortality risk. Postponing diapause in autumn allowed continued egglaying but again with the same risk. The third trade-off related trait was based on general knowledge (Nunney 1996) and common sense. No true life-history trade-offs have so far been found in *T. urticae*. Yet, such a trade-off was truly essential in our model, as mites would otherwise evolve to become 'Darwinian demons' with very short development times and a high number of offspring (Law 1979). Inspired by Yadav & Sharma (2014), we allowed mites to invest in a faster development at the expense of their fecundity and *vice versa*. Despite not yet being found in *T. urticae*, such a trade-off is very likely to exist. The development time in this mite species is just so short, that small changes in it would easily go unnoticed unless mites are monitored constantly. This important trade-off was summarized in a single value varying between 0 and 100 % where a value of 0% meant maximal investment in developmental speed at a maximal cost in fecundity while a value of 100% resulted in the opposite. Logically, a 'trade-off balance' value of 50% resulted in no shift in investment to either trait. Since we can only assume the existence of this trade off we conducted a sensitivity analysis on the relative impacts of the trade-off on both fecundity and development time (Appendix section 7.4.5 and Appendix Table 1). For this analysis we compared all possible scenarios with maximal effects of 50, 20, or 10% on either trait resulting in 9 different scenarios in total. The scenarios with a trade-off setting of a maximal effect of 20% on developmental speed *vs.*

50% on fecundity resulted in a good fit between empirical and modelling data and were analysed in more detail (see later).

Analysis of the saw-tooth pattern

Under certain trade-off settings, a clear latitudinal saw-tooth pattern in the trade-off balance between development time and fecundity emerged (see appendix section 7.4.6); for literature on this pattern see: Masaki (1967); Roff (1983); Iwasa et al (1994). From this simulated latitudinal pattern in the trade-off balance we could calculate the latitudinal pattern in developmental time (see Figure 19 for schematic explanation). To match our empirical results we calculated what the local development time for mites from all latitudes would be if they were to be reared at an optimal temperature. After fitting a smoothing spline to this pattern in developmental time, we could calculate the average wavelength and amplitude of the saw-tooth pattern. The wavelength was calculated by taking the mean distance (in latitude) between subsequent maxima and subsequent minima of the response variable. The amplitude was calculated as the mean difference between subsequent maxima and minima of the response variable.

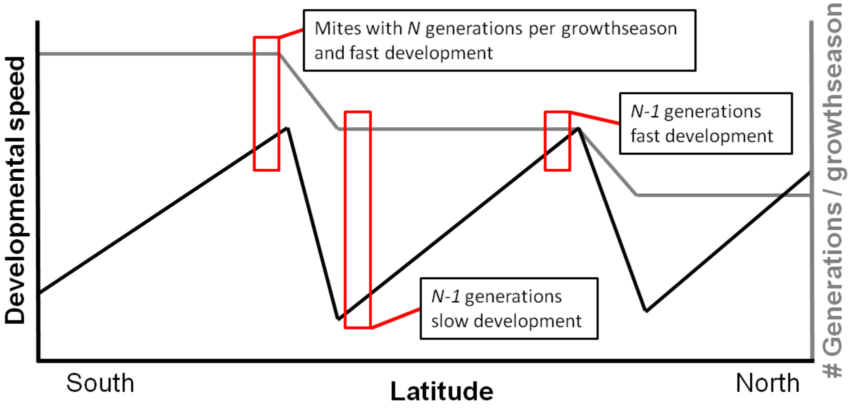

Figure 19: Schematic representation of the saw-tooth pattern in developmental speed and how it is affected by voltinism (i.e. the number of generations per breeding season). The breeding season length decreases gradually from South to North. As a consequence the voltinism decreases step-wise with increasing latitude. In between these downward steps, the voltinism is constant and the latitudinal decrease in season length is mitigated by an increase in the developmental speed. The downward steps in voltinism coincide with a rapid decrease in developmental speed. This latitudinal pattern of local adaptations evolves as each lineage synchronizes its voltinism to the local season length and maximizes its fecundity which trades-off with development speed.

Comparison of empirical and simulation results

We followed a pattern-oriented, approximate Bayesian computation (ABC) approach [cfr. (Csilléry et al 2010; Baiser et al 2013; Wiegand and Moloney 2014)] to detect the most likely scenario (*i.e*. selection pressure) that gave rise to the observed life-history trait divergence. For each of the different model scenarios (either a stable range with latitudinal climatic variation, an expanding range in a climatic homogenous environment or a range expansion scenario along the climatic gradient), we extracted the same statistical patterns (regression slope coefficients and the saw-tooth parameters) as for the observed data. The simulation envelopes were subsequently reconstructed based on 100 independent runs. The goodness-of-fit for each model scenario was derived by randomly sampling one value out of the simulated envelopes in all three scenarios, after which the deviance from the observed value was calculated. The competing model with the lowest deviance was considered to have the best goodness of fit. The probability for each scenario to have the best goodness-of-fit was achieved by repeating this procedure 10000 times for each pattern statistic.

5.4 Results

5.4.1 Life history evolution along the sampled gradient

Multivariate analysis of life-history evolution

The multivariate distance ANOVA showed considerable variation in life history strategies among the different sampled populations. This pattern held for those populations sampled in both 2011 and 2012, for which data on all parameters (those examined in 2011 and those examined in 2012) were available ($F_{1,8}$=2.2285; p=0.051), but also for those parameter for which data on all populations were available (*i.e.* the parameters investigated using data from 2011, when all populations were sampled) ($F_{1,16}$=3.6568; p=0.009).

Furthermore, five significant and two borderline significant trait correlations among populations were found (Appendix Table 2), of which only one remained significant after applying a Bonferroni correction for multiple testing (positive correlation between longevity and lifetime fecundity).

Dispersal

Dispersal propensity and latency were both significantly affected by latitude. Dispersal propensity increased with latitude ($F_{1,2235}$=33.93; p<0.0001) (Figure 21a), while latency showed the exact opposite trend ($F_{1,470}$=4.33; p=0.0379) (Figure 21b). Furthermore, the effect of latitude on dispersal did not differ between different densities ($F_{2,2230}$=0.03; p=0.9702). Instead, dispersal propensity was, on average, always higher for a low (0.2822 ± 0.0191SE) than for a medium (0.1706 ± 0.0130SE) (t=4.95; p<0.0001) or high (0.1921 ± 0.0137SE) (t=-3.91; p=0.0003) density of mothers (F2,2235=13.38; p<0.0001) (Figure 21c). There was no effect of host plant species (F3,2232=1.85; p=0.1356).

Diapause

The diapause incidence of the mites was significantly affected by the host plant on which the mites were collected ($F_{3,50.13}$=9.86; p<0.0001). Mites originating from *L. periclymenum* (0.3315 ± 0.0950 SE) had a (marginally) significantly higher diapause incidence than those originating from *H. lupulus* (0.0019 ± 0.0018 SE) ($t_{46.57}$=-4.75; p<0.0001), *S. nigra* (0.0024 ± 0.0026 SE) ($t_{75.32}$=4.20; p=0.0006) or *E. europaeus* (0.0523 ± 0.0293 SE) ($t_{25.04}$=2.59; p=0.0585). The difference in diapause incidence between mites collected on *E. europaeus* and *H. lupulus* ($t_{64.35}$=-3.36; p=0.0079) or *S. nigra* ($t_{126.1}$=2.83; p=0.0331) was also significant. No effects of latitude were found ($F_{1,1645}$=0.01; p=0.9202) (see appendix figure 19).

Fecundity and longevity

Lifetime fecundity ($F_{1,98.31}$=17.82; p<0.0001) (Figure 22a) and longevity ($F_{1,87.57}$=13.33; p=0.0004) (Figure 22b) both decreased significantly with an increasing latitude. For daily fecundity, however, no effects of latitude were found ($F_{1,68}$=0.69; p=0.4103). Instead, daily fecundity was affected by the host plant species ($F_{3,69}$=5.59; p=0.0017). Mites collected on *L. periclymenum* (3.8231 ± 0.3171SE) laid significantly fewer eggs than mites collected on *H. lupulus* (5.6887 ± 0.4930SE) (t_{69}=3.18; p=0.0115), *S. nigra* (5.8043 ± 0.6037SE) (t_{69}=-2.91; p=0.0248) or *E. europaeus* (5.1914 ± 0.3486SE) (t_{69}=-2.90; p=0.0249).

Egg survival, juvenile survival and development time

With an increasing latitude, the relative amount of hatched eggs increased significantly ($F_{1,103.1}$=6.76; p=0.0107) (Figure 22c), but the proportion of juvenile mites reaching the adult life stage showed no latitudinal pattern ($F_{1,1315}$=0.19; p=0.6663). Furthermore, towards higher latitudes, female ($F_{1,67.13}$=11.50; p=0.0012) and male ($F_{1,64.01}$=19.16; p<0.0001) spider mites had a significantly shorter development time (i.e. a faster development) (Figure 22d). There was no effect of host plant species for females ($F_{3,57.79}$=1.86; p=0.1462), nor males ($F_{3,60.61}$=2.20; p=0.0971).

Sex ratio

From more southern to more northern latitudes, the sex ratio of the sampled populations increased significantly ($F_{1,61.97}$=6.73; p=0.0118) (Figure 22e). The populations thus become increasingly male-biased with increasing latitude. There was no effect of host plant ($F_{3,50.9}$=2.10; p=0.1124).

Adult size

The adult size of the female spider mites was significantly affected by the host plant species from which they were collected ($F_{3,343}$=3.64; p=0.0130). Mites originating from *L. periclymenum* (78240 ± 659.46SE) were significantly larger than those from *S. nigra* (72067 ± 1948.86SE) (t_{343}=3.00; p=0.0153). No effects of latitude were found ($F_{1,342}$=1.19; p=0.2761) (see appendix figure 20).

5.4.2 Inferring mechanisms by contrasting the empirical data with a parameterised individual model

The stable range scenario was a good predictor for the observed pattern in developmental time, although it overestimated the amplitude of the saw-tooth pattern. Considering dispersal, however, it performed considerably worse than the expansion scenarios (Figure 24 and Table 6). In both range expansion scenarios, all the observed empirical patterns were situated within the range of the simulated outcomes (Figure 23, Figure 25). The scenario with range expansion in a homogeneous landscape showed the best goodness of fit for the dispersal values observed in the field, but the empirical saw-tooth variables were underestimated by the model (Figure 25 and Table 6). The scenario with range expansion along an environmental gradient gave the best overall fit to the empirical data (Figure 23 and Table 6).

A short discussion of the patterns emerging from the model is provided in appendix section 7.4.6.

Table 5: Overview of the field collection sites in Belgium (BEL), The Netherlands (NTL), Germany (GER) and Denmark (DEN). The denoted plant species is the species on which the mites were sampled in the field.

code	collection site	city - country	coordinates (WGS 84)	plant species
SKA	Flagbakkevej	Skagen - DEN	57.721200, 10.531983	*Lonicera periclymenum*
SVI	Sletteåvej	Fjerritslev - DEN	57.151567, 9.334400	*Lonicera periclymenum*
TVE	Hindingvej	Thisted - DEN	57.041050, 8.618333	*Lonicera periclymenum*
BLA	V. Hennebysvej	Henne - DEN	55.7402, 8.22300	*Lonicera periclymenum*
HED	Picnic-place on 11/24	Gredstedbro - DEN	55.390800, 8.739383	*Lonicera periclymenum*
HAV	Stagebjergvej	Rømø - DEN	55.10048, 8.53086	*Lonicera periclymenum*
SPO	Kieferneck	St. Peter-Ording - GER	54.31412, 8.610985	*Lonicera periclymenum*
ARE	Arenscherweg	Cuxhaven - GER	53.84701, 8.63284	*Lonicera periclymenum*, *Humulus lupulus*
LAU	Schildhoek	Lauwersoog - NTL	53.40563, 6.21705	*Euonymus europaeus*
BAZ	Elzenlaan	Bergen aan Zee, NTL	52.662694, 4.637417	*Lonicera periclymenum*
CAS	Hoofdweg	Heemskerk, NTL	52.528500, 4.648694	*Euonymus europaeus*, *Lonicera periclymenum*
AER	Juliana van Stolberglaan	Aerdenhout, NTL	52.368000, 4.591861	*Euonymus europaeus*
WAS	Wassenaarseslag	Wassenaar, NTL	52.161333, 4.358972	*Euonymus europaeus*, *Lonicera periclymenum*
OVO	Duinlaan	Oostvoorne, NTL	51.914528, 4.083667	*Euonymus europaeus*
OOD	Meester Snijderweg	Stellendam, NTL	51.831333, 4.015361	*Humulus lupulus*
KVS	Bosweg	Burgh-Haamstede, NTL	51.682722, 3.719556	*Sambucus nigra*, *Humulus lupulus*, *Lamium album*,…
ORB	Koningin Emmaweg	Vrouwenpolder, NTL	51.583111, 3.583333	*Humulus lupulus*
ZOU	Graaf Leon Lippensdreef	Knokke-Heist, BEL	51.350944, 3.336000	*Sambucus nigra*
DHN	Wenduinsesteenweg	De Haan, BEL	51.282250, 3.053778	*Euonymus europaeus*
ODK	Duinparklaan	Koksijde, BEL	51.124639, 2.683306	*Humulus lupulus*

Table 6: The results from a goodness-of-fit analysis between three competing scenarios with a maximal trade-off effect of 20% on developmental time and 50% on fecundity. These scenarios were selected from a larger sensitivity analysis shown in appendix table 1. For each of five variables, we randomly sampled one out of the hundred simulated results from the three scenarios to see which of these three random samples had the lowest deviation from the empirical value (this was repeated 10000 times). The percentages below show how often each model scenario provides the best fit to a particular empirical value. The range expansion models clearly are better predictors for dispersal (slope). The models incorporating a gradient, in contrast, clearly resulted in the best fit for development (slope) and development (wavelength). Overall, the model incorporating both factors gave the best fit. The expansion with no gradient scenario has an unexpectedly good fit for the amplitude of the saw tooth scenario in development. A closer look shows that this scenario consequently underestimates the amplitude (Figure 25). The two gradient scenarios overestimate the amplitude more often but since overestimations are not limited by the zero boundary like underestimations these values could be further off resulting in the relatively good fit to the no gradient scenario.

	Range expansion, no gradient	**Stable range, gradient**	**Range expansion, gradient**
Dispersal (slope)	62.39	4.89	32.72
Fecundity (slope)	29.33	27.13	43.54
Development (slope)	7.34	70.26	22.40
Development (wavelength)	12.69	55.56	30.67
Development (amplitude)	34.36	16.47	49.17

Figure 20: A map showing all the field collection sites in Belgium, The Netherlands, Germany and Denmark.

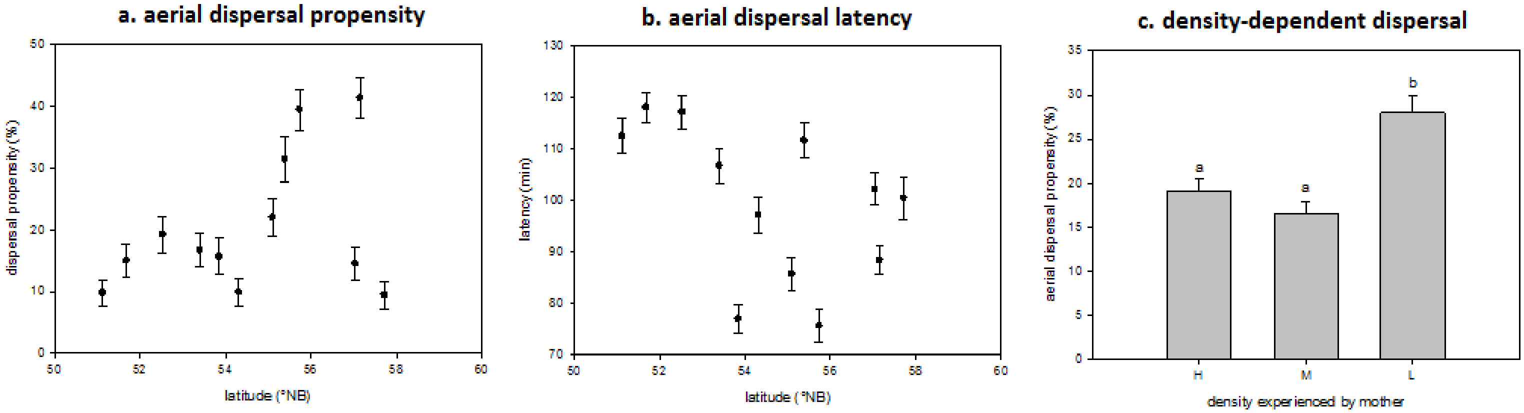

Figure 21: The mean value for dispersal propensity (a) and dispersal latency (b) is given for each sampled population. In the rightmost graph (c), mean values for dispersal propensity are given for each of three densities (H: high density, M: medium density, L: low density). Standard errors are represented by bars. Different letters above the error bars in figure c indicate significantly different outcomes according to the used statistical test.

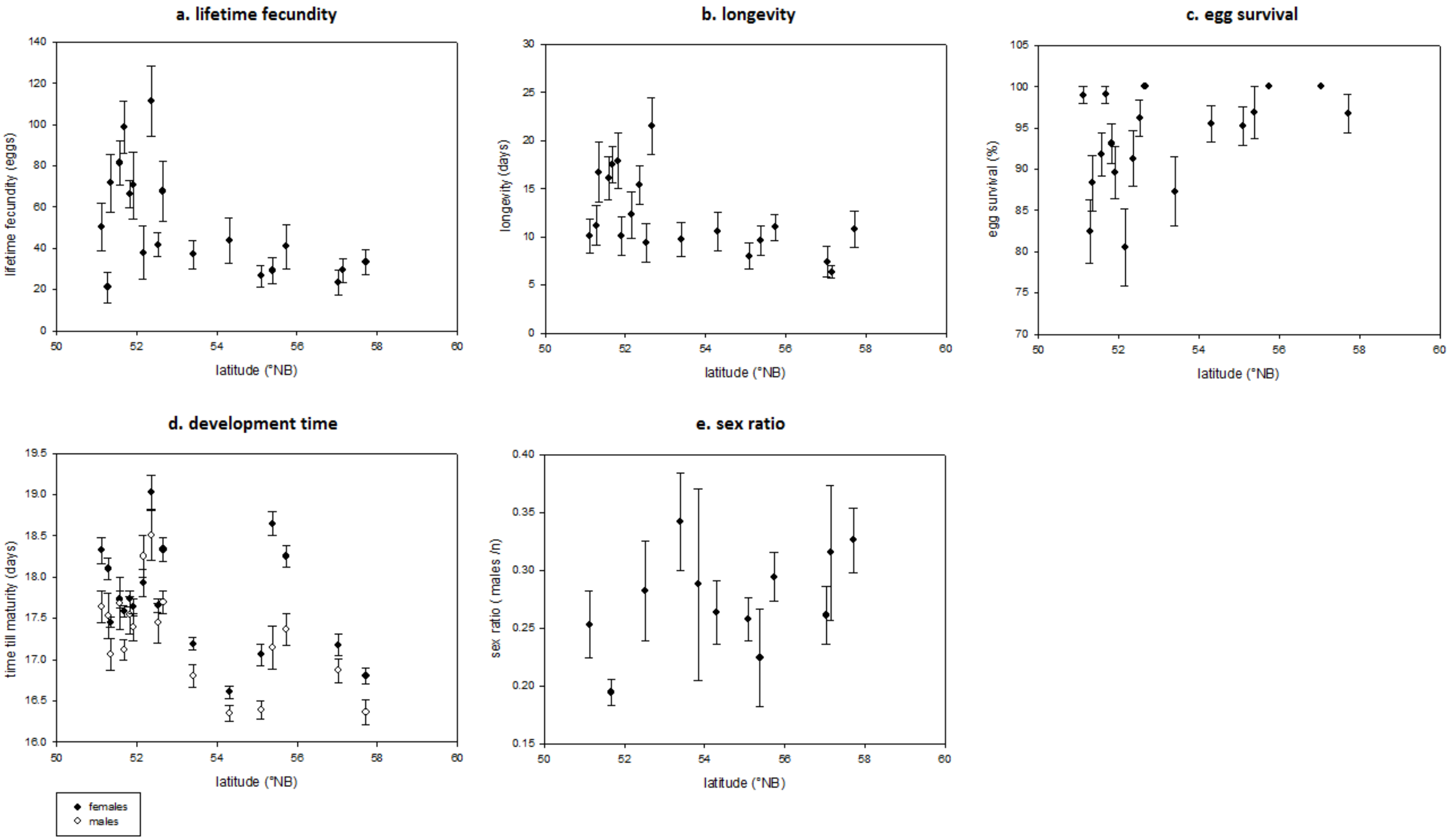

Figure 22: The mean value (averaged over the replicas) for lifetime fecundity (a), longevity (b), egg survival (c), development time (d) and sex ratio (e) is given for each sampled population. Standard errors are represented by bars. In figure d, development time is shown separately for females (closed circles) and males (open circles).

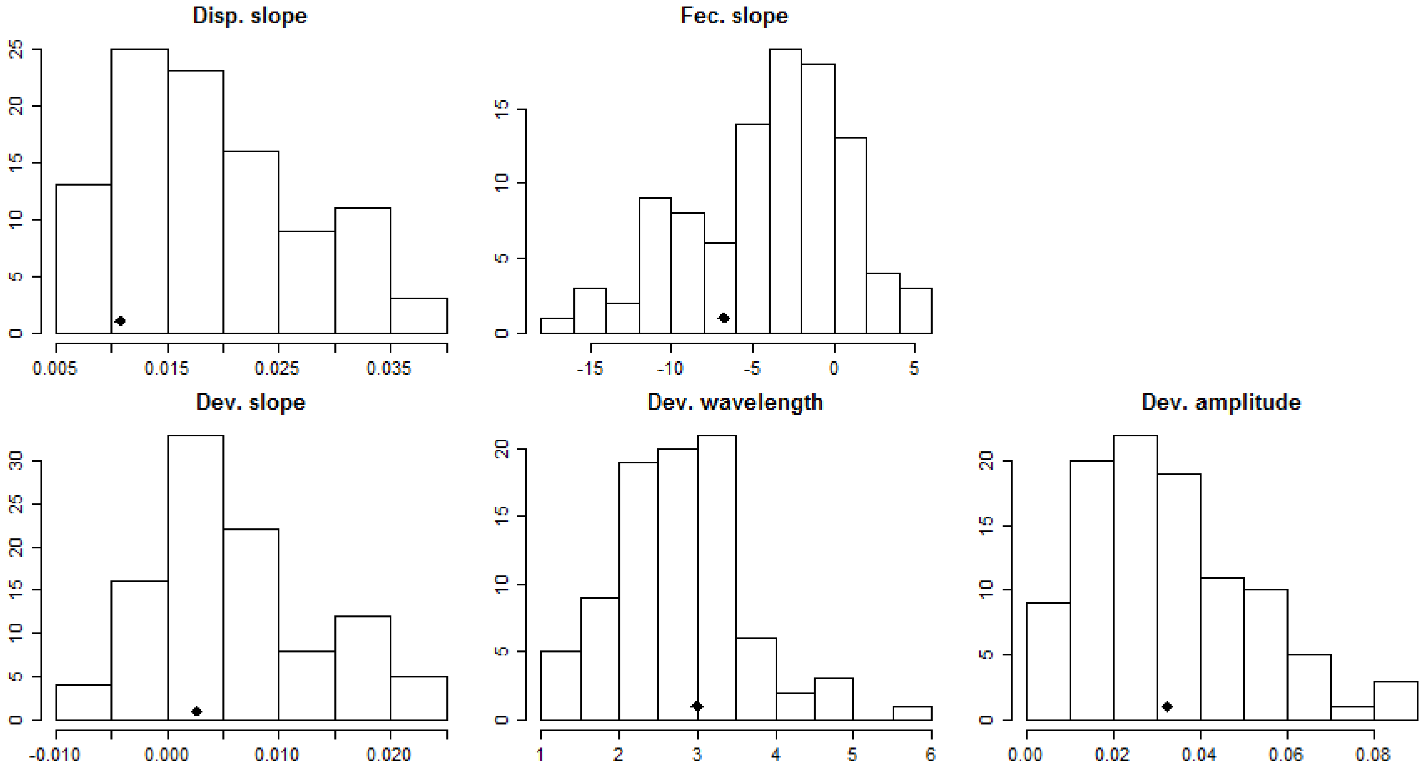

Figure 23: The distribution of 100 simulated results for 5 variables in the expansion on a latitudinal gradient scenario. The black diamonds represent the empirical value. Slopes are calculated from a linear regression over the latitudinal gradient, while wavelength and amplitude are calculated on the saw-tooth pattern in development. This scenario resulted in the best overall fit (Table 6).

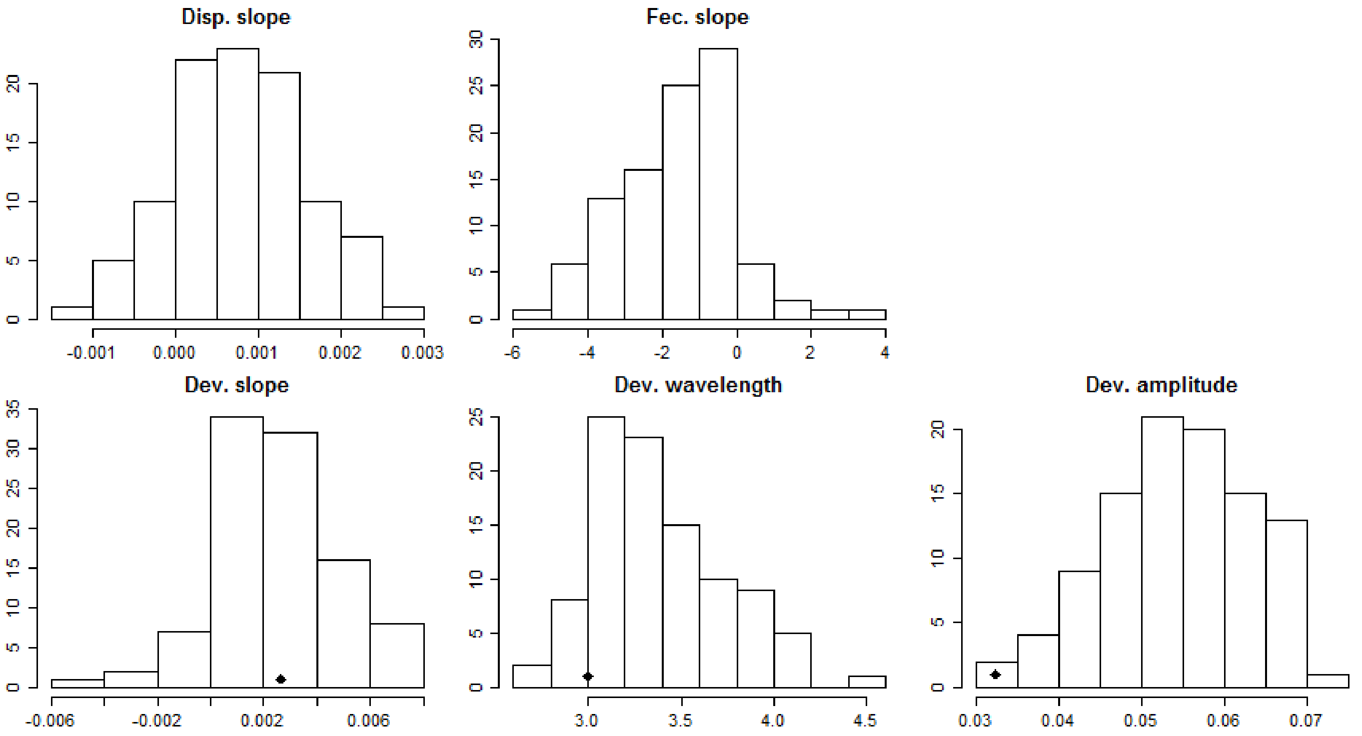

Figure 24: The distribution of 100 simulated results for 5 variables in the stable range on a latitudinal gradient scenario. The black diamonds represent the empirical value (absence means that the value is outside the distribution of simulated results). Slopes are calculated from a linear regression over the latitudinal gradient, while wavelength and amplitude are calculated on the saw-tooth pattern in developmental time. Note that the x-axes have a different scale on each of the figures. This scenario poorly predicted the empirically observed dispersal rates and overestimated the amplitude of the saw-tooth pattern in development time. However, it formed the best predictor for the slope and wavelength of the saw-tooth pattern in development time observed in the field.

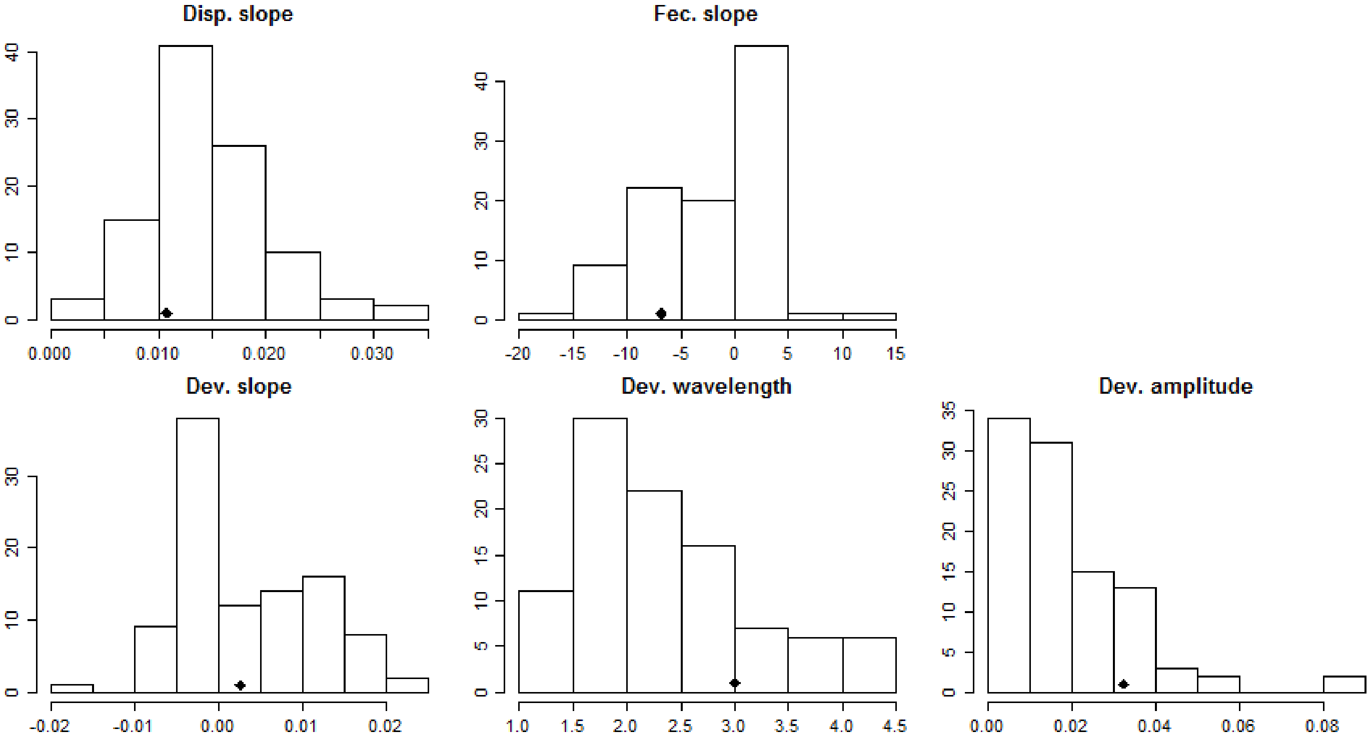

Figure 25: The distribution of 100 simulated results for 5 variables in the range expansion without a latitudinal gradient scenario. The black diamonds represent the empirical value. Slopes are calculated from a linear regression over the latitudinal gradient, while wavelength and amplitude are calculated on the saw-tooth pattern in development time. This scenario was the best predictor for the dispersal values observed in the field. In contrast, the empirical saw-tooth variables were underestimated by this scenario.

5.5 Discussion

Range shifting by species is a phenomenon off all times, but in the context of climate change and species invasions, it is increasingly gaining attention because the rate at which it occurs in the Anthropocene induces fast shifts in biological assemblages. As dispersal is an obvious central trait in these processes, it is acknowledged that dispersal evolution affects (Kubisch et al 2014) and is affected by range expansion [reviewed in Hill et al. (2011)]. Typically, dispersal-related traits are pronounced at the range front, with potential trade-offs with fecundity [*e.g.* (Hill et al 1999; Hughes et al 2003; Saastamoinen 2007)]. Furthermore, as range expansion often infers entering unknown, potentially harsh environments, several studies using the Colorado potato beetle stressed the role of diapause behaviour and related physiological changes during range expansion (Piiroinen et al 2011; Lehmann et al 2014). While the above does not provide a complete review of the literature, these studies typically focus on single traits and seldom frame evolutionary changes within a full life-history perspective. Moreover, life-history traits are often affected by several, sometimes opposing, selection pressures (Kubisch et al 2014), as is the case during range expansion along a latitudinal gradient. In an attempt to cope with these shortcomings, we assessed quantitative genetic variation in an array of life-history traits and contrasted the evolved trait divergence with expected patterns from a model in which predictions from spatial sorting could be separated from predictions from local adaptation. We thus tested which of three model scenarios (one for a stable range along an environmental gradient, one with range expansion along this environmental gradient and one with range expansion in a homogeneous landscape) best explained the patterns found in our empirical data.

We found considerable quantitative genetic trait variation in the sampled populations, with several of the examined traits showing strong latitudinal patterns. The observed increase in dispersal latency and propensity in edge populations matched best with the range expansion scenarios (*i.e* the scenario with range expansion along a gradient and the scenario with range expansion in a homogeneous landscape). In contrast, the scenarios with an environmental gradient (*i.e.* the stable range scenario and the scenario with range expansion along a gradient) gave the best fit for the data on the development traits. More specifically, the model output of the stable range scenario provided evidence for a saw-tooth pattern in development time. All these results are to a great extent in line with our *a priori* expectations. On the one hand, dispersal is the central trait affected by spatial sorting during range expansion, typically leading to an increased dispersal at the expansion front (Phillips et al 2010). On the other hand, changes in development time are most effective for maintaining an optimal reproductive outcome when a restricted growing season leads to changes in voltinism (Roff 1980). Overall, the model scenario that incorporated both range expansion and local adaptation gave the best fit (for each of the other two scenarios, some variable always gave a very poor fit), suggesting that local adaptation and spatial sorting jointly shaped genetic divergence in the field.

While fitting the model results on dispersal to the empirical data was rather straightforward, it was less so for the data on fecundity and development time. The model output concerning fecundity was very variable and none of the scenarios gave a markedly better fit to the empirical data compared to the others. Likewise, the saw-tooth pattern in development time didn't show a clear difference in fit between the competing scenarios. However, closer inspection showed that the expansion scenario without a latitudinal gradient generally underestimated the amplitude, while the stable range scenario generally overestimated the amplitude. This is interesting, since it might be an indication that *T. urticae* only recently reached the northernmost latitudes, therefore not yet showing 'full' adaptation to the local environment. Indeed, the expansion scenario without a gradient would then underestimate the amplitude, since some local adaptation did already occur, but the stable range scenario would overestimate it, since it assumes that the mites are fully locally adapted. Combined with the pattern in dispersal, our model-fitting thus confirms the recent character of the species' northwards range expansion (Carbonnelle et al 2007).

Only dispersal showed a clear, consistent trend in our model scenarios with range expansion, but the locally low-density environment at the range front could equally be expected to have affected some other traits through r-selection. Especially those traits that influence population growth rate (development time, fecundity, egg survival, juvenile survival) could be typical targets of such selection (Phillips 2009; Phillips et al 2010). Our empirical data on fecundity, however, showed a clear decrease, where an increase would have been expected if r-selection affected population growth rate through this trait (Cole 1954; Lewontin 1965). Furthermore, juvenile survival showed no clear latitudinal trend and the empirical patterns in development time (slope and saw-tooth variables) gave the best fit with the scenarios with an environmental gradient (*cfr. supra*). The overall trend of an accelerated development towards the higher latitudes and the accompanying increase in egg survival did, however, match with what would be expected under r-selection, as both traits positively affected the population growth rate. Just like development time, diapause (Danks 1987) and adult size (Blanckenhorn and Demont 2004) were expected to give the best fit with the stable range scenario. However, where development time showed a clear saw-tooth pattern (*cfr. supra*), our empirical data on both diapause and adult size were not affected by latitude (and thus the environmental gradient). The latter suggests compensatory growth to keep size constant despite strong changes in development time, hence the length of the growth period (Conover et al 2009).

Eco-evolutionary studies of range expansion show increasing interest in correlations between life-history traits on the individual level (Burton et al 2010; Duputié et al 2012). The presence of such correlations has quite often been reported on the population level [though some studies show opposing outcomes, *e.g.* (Hughes et al 2003) and (Saastamoinen 2007)]. It is thus striking that, given the number of traits under study, the only significant correlations found in this study were a positive correlation between lifetime fecundity and both daily fecundity and longevity and a negative correlation between juvenile survival and both dispersal and development time (of females), the former correlation being straightforward (the more eggs a mite produces per day and the longer it lives, the more eggs it can produce during its lifetime), and the latter potentially being mediated through the quality of the local environment during development (low food quality results in a hampered development and might hinder dispersal (De Roissart et al. under review). None of the traits previously found to correlate with dispersal [fecundity, *cfr.* (Hughes et al 2003; Saastamoinen 2007)] or development time [fecundity and longevity, *cfr.* (Yadav and Sharma 2014)] showed the expected correlation in our analyses. The trade-off between dispersal and fecundity found in Hughes et al. (2003), nor the opposing positive correlation between dispersal and fecundity found in the study of Saastamoinen (2007) were thus supported by our results. Our findings do, however, match with several studies where artificial selection on dispersal did not result in a correlated response in fecundity (Van Petegem et al.under review.; Li & Margolies 1994; Bitume et al. 2011). Interestingly, these studies were performed using *T. urticae* as a model species; like we did. This highlights the fact that inter-specific comparisons are difficult and potentially misleading, since different proxies for dispersal are typically used for different organisms. Possibly, some traits used as a proxy for dispersal will correlate with other vital traits, while other traits used as a proxy won’t [*cfr*. (Phillips et al 2010)]. Hughes et al (2003), for example, used a physical trait (thorax mass), while we studied a behavioural trait (aerial take-off behaviour). Finding an energetic trade-off between dispersal and fecundity thus indeed seems more plausible in the former than in the latter case.

Although latitude showed a significant effect on most traits, some trait variation might have been caused by our experimental breeding design. For example, some variation in diapause, but also in daily fecundity and adult size was explained by differences in the host plant species on which the population was found in the field. *T. urticae* is known to rapidly adapt to new host plant species [*e.g.* (Magalhães et al 2007)]. However, while Magalhães et al. (2007) measured adaptation to the new host after 15 generations, we measured life-history traits only a couple of generations after mites were transplanted to lab beans. This was sufficient to allow a control of maternal effects, but minimised the possibility of local adaptation to the lab conditions, both in terms of climate and host plant. Because the different host plants likely vary in their physical or chemical resemblance to the lab beans, this might have affected mite performance. Especially the performance and behaviour of mites collected on *L. periclymenum* deviated from those collected on other host plant species. This effect of host plant species might thus have blurred the signal of latitude for fecundity, adult size and, especially, diapause (which was measured immediately after sampling). Furthermore, we only measured traits at one specific, relatively high temperature (20°C or 27°C). Populations originating from higher latitudes might therefore have suffered more from the change in temperature from field to lab than southern populations. In such a changed environment, a higher proportion of males (the genetic equivalent of haploid recombinant genomes) might have been selected for, because it provides a faster response to selection and thus a more rapid adaptation to the new environment (Hartl 1971; Griffing 1982; Havron et al 1987). Sex ratio in *T. urticae* is usually female biased (3:1) (Krainacker and Carey

1989), but mothers can alter the sex ratio of their young (Young and Wrensch 1986). The high temperature in our setup might thus have triggered females to produce a more male-biased offspring, potentially resulting in the observed increase in sex ratio towards higher latitudes. To account for such a possible temperature effect, all life-history traits should be measured at a range of different temperatures (reflecting the range in the field). Measuring an array of traits for a range of temperatures for several different populations is, however, practically unfeasible. Instead, studies on temperature-effects typically only focus on one population and one to a few traits [e.g. (Margolies and Wrensch 1996)]. Finally, diapause is the single trait that possibly still showed some environmentally induced phenotypic differences, since mites showed the behaviour almost immediately after they were gathered from the field. Nevertheless, diapause is known to harbour a very strong genetic component [reviewed in (Tauber et al 1986)].

Several of the observed patterns could furthermore have resulted from genetic drift, following genetic bottlenecks or founder effects. Indeed, lifetime fecundity, longevity and egg survival, not only showed a decrease or increase with latitude, but also (and more so) a decreased diversity in the present phenotypes from approximately 53°NB onwards. Only a small subset of all the trait values present at lower latitudes remained at the higher latitudes. This could be an indication that the more northern populations were founded by a very small random subset of individuals or by exactly those individuals with specific trait values that allowed survival in these more northern environments. The fact that, for all three traits, the most extreme values and not just random values remain, might support the latter possibility (though extreme values could in principle also be randomly 'selected' for). Nonetheless, our common garden experiments showed very clear latitudinal trends in dispersal and development, which matched model predictions.

Where studies on range expansion are gradually shifting from a mere descriptive to a more mechanistic approach, most studies still fail to incorporate the broader context of a complex interplay between local adaptation and spatial sorting. Disentangling the effects of both these selective forces is, however, difficult to do purely empirically or purely theoretically. In a unique study, we therefore combined empirical data from common garden experiments with a simple though parameterised model, allowing us to disentangle the relative importance of local adaptation *versus* spatial sorting. Using *T. urticae* as a model species, this study is the first to demonstrate that local adaptation and spatial sorting jointly shape genetic divergence in ecologically relevant traits during range expansion along a latitudinal gradient. In our study species, dispersal was mainly shaped through spatial sorting, while local environmental conditions affected development time. Our results emphasize that simple, strategic models should be carefully interpreted when used to predict evolutionary changes, since they do not capture the genetic architecture of organisms. Alternatively, a critical interpretation and analysis of empirical data is also needed, because it is then not always clear which of the traits are shaped through the changed local environment and which by the expansion process *per se*.

5.6 Acknowledgments

We thank the Fund for Scientific Research - Flanders (FWO) for funding KHPVP and JB (project 6.0610.11). DB was supported by BelSpo IAP Project “Speedy”. Finally, we like to thank Joachim Teunen, Hans Matheve, Rik Puls and Jelle Van den Berghe for their help during the sampling of the mites in the field and Jasmijn Hillaert and Adinda Vanommeslaeghe for their short, but useful assistance during the data gathering in the lab. We thank Ghent University for access to the high performance computing infrastructure.

6

General discussion.

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6.1 Thesis overview

Dispersal and the eco-evolutionary forces which shape selection on this trait are central to this thesis. Each chapter offers a different insight on this complex issue and has its own approach to come to unique results (see Table 7 for overview). In chapter 2 dispersal affects species coexistence through its effect on spatial segregation, a phenomenon that decreases interspecific competition and is only possible in certain landscape configurations. Chapter 3 focuses entirely on dispersal itself and how different conditions affect the shape of dispersal kernels. We found that the distance probability function changes it shape according to local density and a number of environmental conditions. Chapter 4 looks into evolutionary rescue as a possible consequence of rapid dispersal evolution during range shifts. Intermediate rates of climate change had the greatest potential to promote rescue. Finally, chapter 5 deals with a real world system where we try to understand the consequences of local adaptation in combination with those of a recent range expansion on life-history traits. Through our simulation we were able to distinguish latitudinal life-history patterns typical to local adaptation from those typical for range expansion and found traces of both in the empirical data.

Table 7: Overview of the 4 research chapters with key results, causal effects and a comparison of model settings and scales.

	Chapter 2	Chapter 3	Chapter 4	Chapter 5
Causal effects	Landscape configuration + dispersal distance	Local density	Rate of climate change	Range expansion + local adaptation
Evolution	No	Dispersal (flexible kernel)	Dispersal (variance on Gaussian kernel)	Dispersal rate, development time-fecundity trade-off, diapause onset & termination
Empirical data	No	No	No	Yes
Single species	No	Yes	Yes	Yes
Range dynamics	No	Yes (expansion scenario)	Yes (range shift)	Yes (expansion scenarios)
Temporal resolution	1 Generation	1 Generation	1 Generation	1 Day
Main result	Habitat configurations promoting spatial segregation stabilize coexistence	Many different optimal kernel shapes depending on conditions	Intermediate rates of climate change can drive dispersal evolution and rescue populations	Traces of both range expansion and local adaptation found in empirical data

6.2 Range dynamics and eco-evolutionary feedbacks on dispersal

6.2.1 Should we always allow dispersal to evolve?

While chapter 2 assumes a fixed dispersal kernel the other chapters in this thesis highlight the importance of incorporating dispersal evolution. Moreover, a growing volume of both empirical (Phillips et al 2010; Brown et al 2014) and theoretical studies (Travis and Dytham 1999; Travis 2001; Murrell et al 2002b; Muller-Landau et al 2003; Kubisch et al 2014) stress the importance of dispersals evolvability. In a temporally stable system such as the model of chapter 2, incorporation of evolution would result in even more stable coexistence of two specialist competitors as long distance dispersal, away from suitable conditions and towards superior competitors would be selected against (Bowler and Benton 2005). In such a stable system the only drivers for more dispersal should be kin-competition and demographic stochasticity (due to scramble competition or predation). Moreover, we can expect more populations to persist in remote habitat patches when dispersal is allowed to evolve resulting in even more coexistence on a landscape level. A brief, visual test of this expectation can be found in Figure 26, where we allowed the evolution of dispersal in a 1 species model very similar to that of chapter 2. Here we see that selection indeed acts most strongly against dispersal in smaller and remote habitat clutches while the selective pressure of kin-competition is strong enough to increase dispersiveness in the centre of larger habitat clutches. In reality this selection against dispersal in isolated patches has resulted in many fascinating examples of poor dispersers on remote islands such as flightless birds and insects (Roff 1994) and plants with heavy seeds (Cody et al 1996). Even though we can expect dispersal evolution to increase the overall levels of coexistence in the model from chapter 2 the fixed kernel approach can be justified by the focus of the chapter on landscape configuration rather than dispersal evolution in specialist species and the sensitivity analysis on kernel shape. Moreover, when dealing with multiple species the intraspecific differences in dispersal due to dispersal evolution are expected to be on a smaller scale than the interspecific differences in the trait since dispersal is highly linked to species' phylogeny (Vellend et al 2014). Nonetheless it stands to reason that in many ecological models it is preferable to let the dispersal trait evolve to increase accuracy (Kubisch et al 2014). However, this requires an appropriate incorporation of the relevant costs and benefits to dispersal (Travis et al 2012; Bonte et al 2012) which are often unknown.

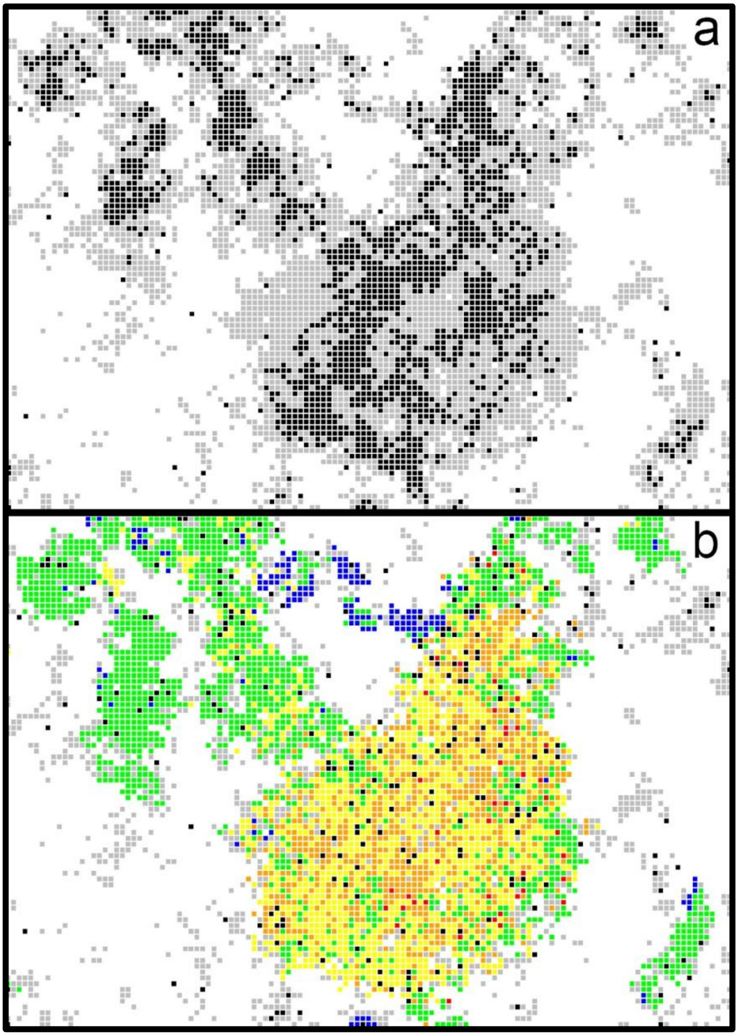


Figure 26: A visual confirmation that selection against dispersal is stronger in more fragmented/isolated parts of the landscape for the model from chapter 2. Figure *a* presents the landscape with white colouring for unsuitable matrix while black and gray are two suitable habitat types (see chapter 2); figure *b* shows the same landscape overlaid with the individuals whose dispersiveness allele has locally adapted after 10000 generations (i.e. equilibrium). The colour-code from high to low dispersiveness is red-orange-yellow-green-blue.

6.2.2 Dispersal evolution during range shifts

Since dispersal evolution plays a prominent role during range shifts and expansions within species it is hard to justify the absence of evolution on dispersal traits in a model on this subject (Phillips et al 2008). An example of the trouble biologist can get into when they ignore dispersal evolution can be found in the observation by Reid (1899) that current dispersal distances in trees are too low to explain their rapid expansion at the end of the last major glaciation which, according to pollen data from sediments, would range between 150 to 500 m/yr (Clark 1998; Cousens et al 2008b). This puzzling observation was coined as ‘Reid’s paradox’ by Clark (1998) who’s explanation for the mystery was the, hard-to-observe, fat tail of the dispersal kernel which represents rare, but very long distance dispersal events. A decade later (Phillips et al 2008) came up with an even stronger argument; dispersal kernels are not static and can evolve ‘fatter’ tails during expansions resulting in increased rates of spread. In chapter 4 we focussed on a consequence of this selection for higher dispersal distances during range shifts, an increased capability to deal with habitat fragmentation. In this chapter we also warn empiricists who measure dispersal capacities of species to keep in mind Reid’s paradox; the dispersal capacities of static populations may be a poor proxy of their capability to deal with range shifts as dispersal evolution may rapidly increase dispersiveness.

6.2.3 Evolutionary rescue

There are concerns that the current rate of environmental change is exceeding the capacity of many populations to adapt. Limiting the loss of biodiversity requires science that integrates both ecological and evolutionary responses of populations and communities to rapid environmental change, and can identify the conditions that allow the recovery of declining populations (Gonzalez et al 2013). Current theory and empirical work emphasize the importance of genetic variation and therefore population size (Bell and Gonzalez 2011; Bell 2013; Vander Wal et al 2013). However, even when species have a large standing genetic variation on a large spatial scale, local adaptation on a smaller scale may result in an overestimation of the populations evolvability and the potential loss of variance during a period of change (Schiffers et al 2013). Therefore, plasticity may be even more important than genetic diversity as it allows populations to respond quicker than through actual natural selection on genetic traits (Chevin et al 2013; Gienapp et al 2013). The evolutionary rescue in our model from chapter 4 relies on standing genetic variation and new mutations rather than plasticity. However, the particular example of dispersal may allow some optimism for species conservation as spatial sorting processes are expected to increase the rate of evolution (Shine et al 2011). Although the volume of theory on evolutionary rescue is rapidly expanding the greatest challenge remains to transfer this expertise to the field (Gomulkiewicz and Shaw 2013).

6.2.4 Kin-competition and the loss of genetic variance during range shifts

While the optimal kernels from chapter 3 already show a quite spectacular selection for long dispersal distances during a range expansion we can expect the effect to be even stronger in nature since kin-competition was switched off in this model. This effect has been theorized to be a major driver of dispersal evolution during range expansions due to high relatedness near the range front after consecutive founder events (Kubisch et al 2013). We performed an analysis on the decline in genetic variance during range shifts which confirms that genetic variance will decline rapidly after repeated founder events near the range front, thereby enhancing kin-competition (Boeye et al. in prep)(Figure 27). Nonetheless, we have learned from chapter 4 that when dispersal is allowed to evolve some genetic variation may be maintained due to different selection pressures within a climate window (Figure 17). In our analysis of the genetic variance the overall decline in genetic variance depends on the duration of the range shift and its spatial extent. Only once the trailing edge of the range surpasses the latitude of the pre-shift leading range border are all lineages that did not disperse along with the range shift lost. This condition may not be met in reality for a large number of species that span a wide latitudinal range. In those species, we expect a decreasing genetic variance towards the poleward range border during and after range shifting. A factor that may jeopardize the validity of this prediction is local adaptation to a latitudinal gradient within the species range (Atkins and Travis 2010). If individuals are locally adapted to such a gradient the latitudinal range in which they can thrive may be a lot slimmer than the latitudinal range of the whole species. In this case the trailing edge of the effective range of a locally adapted population will cross the original leading edge much quicker resulting in a faster loss of genetic variance and an overall lower chance to track the shifting climate successfully. In chapter 5 we found cues of local adaptation to the latitudinal gradient in season length. Although the mite system from this chapter resembles a range expansion rather than shift we can still expect local adaptation to have an effect on the range dynamics. A quick comparison of the progress made by the expanding range border between an expansion with or without a latitudinal gradient shows that the latter occurs much faster and at a more constant rate (see Figure 28). It is not surprising that a maladaptation of an important trait such as voltinism may slow down expanding range fronts especially since we expect the genetic variance to be low near range fronts (McInerny et al 2009). In the mite system maladapted voltinism will result in high temperature mortality in autumn on both juveniles and eggs. Perfectly adapted lineages would have individuals maturing just before the onset of winter when they would go into dormancy at relatively high temperatures since laying eggs at this part of the season is futile. Moreover, in our model, the variance on the voltinism trait decreases towards the north as under ever worsening conditions the number of strategies that will work decreases, e.g. in the south it may be possible to have 6 fast or 5 slow generations at the same latitude while in the north only one strategy works per latitude. The fact that at a certain point along the gradient the only viable strategy shifts from a rapid development to fulfil N generations to a very slow development to fulfil N-1 generations makes the voltinism example particularly interesting. If we imagine a fitness landscape then at the points where the only viable strategy shifts there is a low point between two fitness peaks which cannot be crossed too easily. This problem was recently coined as ‘the lost generation hypothesis’ by Van Dyck et al (2015) who observed the occurrence of a ‘suicide generation’ in a butterfly with poor developmental timing due to climate change. Certain local populations tried to complete three generations in a growing season while only two were possible and went extinct as a consequence. During a range expansion in our mite system it will take time and possibly lineages with a slower developmental strategy invading from the centre of the range to overcome this hurdle and further progress the range front. This time delay may explain the periods of slower expansion speed on the black line in Figure 28 and could allow a higher genetic variance near the range front. An alternative way to overcome this difficulty is a rapid expansion during a single growth season where lineages with a developmental speed that allows them to complete N generations at a certain latitude reach a more northern latitude where the same developmental speed allows them to complete N-1 generations. If this mechanism is at play we expect to see temporally isolated, vanguard populations who manage to survive winter in northern latitudes while the main population’s range front recedes further southward during winter. After several generations of local adaptation the gap between both ranges would disappear. In exploratory simulation runs we found latitudinal regions, deep within the expanding species range of presumed maladaptation where population densities consistently crashed at the end of winter for a large number of years. A more detailed analysis of this phenomenon could be a subject of future work.

This example shows how local adaptation can have an important effect on expanding range dynamics. Given the large spatial variance in (a)biotic environmental conditions and the progression and regression of range borders over time it not too hard to imagine how vanguard populations can become established in areas where they perform better because of some pre-adaptation. Our voltinism example shows how such a pre-adaptation doesn’t necessarily mean that conditions have to be identical to those in the original range. Moreover, when populations are adapted on a small spatial scale they may decrease the chance to successfully track a shifting climate window (Atkins and Travis 2010) or slow down a range expansion, thereby preserving a larger part of the genetic diversity.

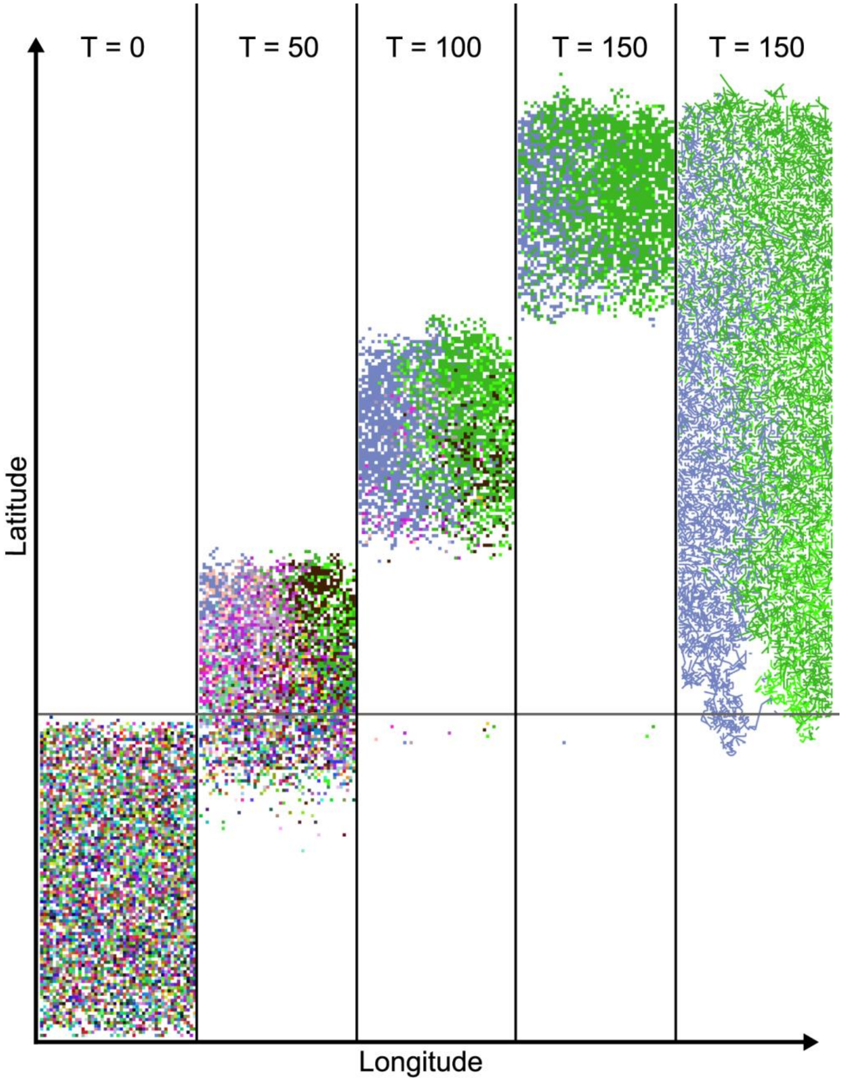


Figure 27: The loss of genetic variance in a neutral model during range expansion. As time progresses (from left to right in graph) more and more unique lineages (i.e. colours) of the original, diverse population (T=O) are lost. The successful lineages all have T=0 ancestors which were close to the original range front (drawn under gray horizontal line) which indicates strong mutation surfing effects. The final figure (rightmost) shows the path of each surviving lineage from the single, original ancestor to all individuals carrying the allele in the current population through time and space. This visualization shows that these two lineages remained spatially segregated throughout most of the range shift although the green lineage seems to have conquered the current range front and will outcompete the blue lineage in subsequent time steps.

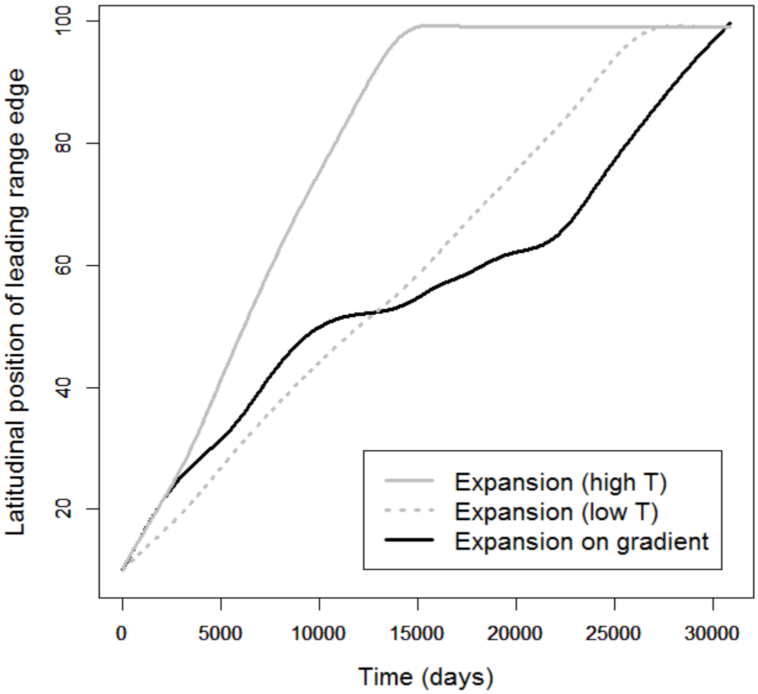


Figure 28: The progression of the leading (i.e. northern) range edge over time for three expansion scenarios, one with and two without a latitudinal gradient in temperature. The scenarios without a gradient either have a temperature regime similar to that of the south (high T) or north (low T) in the with-gradient scenario. This result comes from three simulation runs of the model from chapter 5. The population expands considerably slower and at a less constant rate in the scenario where lineages have to adapt to local conditions.

6.2.5 From theory to practice

"In theory there is no difference between theory and practice. But, in practice, there is."

J. L.A. van de Snepscheut

There is an increasing gap between theory and actual empirical research on the eco-evolutionary consequences of range shifts and expansions. There are theoretical studies on advanced topics such as range contraction after expansion (Kubisch et al 2010; Henry et al 2013), genetic consequences of expansions (Excoffier et al 2009; Slatkin and Excoffier 2012), spatial sorting (Shine et al 2011), mutation surfing (Travis et al 2010a), landscape effects (McInerny et al 2007) and the effects of local adaptation prior to range shifts (Atkins and Travis 2010). Meanwhile, empirical studies on the subject remain rare (Parmesan 2006) and usually don't assess the effects on life-history traits. Examples of such studies can be found on birds (La Sorte and Thompson 2007) Mammals (Beever et al 2003), butterflies (Warren et al 2001), plants (Lenoir et al 2008; Kelly and Goulden 2008) the exceptionally well studied case of the cane toad (Phillips et al 2006; Brown et al 2014) and several others reviewed in (Thomas 2010).

In this work we have contributed mostly to the theoretical aspect of dispersal research. While chapter 3 provides a theoretical framework on optimal kernel shapes and guidelines for application chapter 4 focuses on the consequences of the increase in dispersiveness observed during range shifts. In chapter 5 however, we try to bridge the gap between theory and practice by looking at life history consequences in an actual system at one point in time. Here we find empirical confirmation of what was predicted by chapters 3, 4 and the model in chapter 5: an increase in dispersiveness as a consequence of a recent range shift. However, the particular example of chapter 5 also shows nicely how the degree of specialism of a model trade-offs with the generality of the results. Whereas a generic model would have predicted an increase in developmental speed towards the northern edge of the range as a consequence of the shortening summer season in the north we found a saw-tooth pattern. This interesting pattern in the development time could be explained by the model as a consequence of timing to seasonality and a decrease in the number of generations per season. The repetitive, saw-tooth pattern stems from the fact that the number of generations per season is a discrete variable rather than a continuous one, and the expected northward increase in developmental speed can only be found within each repetition of the pattern. This interesting phenomenon is only relevant for species that have multiple generations per reproductive season (voltinism) and which hibernate or cease reproduction through winter.

6.3 Local density and dispersal, finding the optimal strategy

Both dispersal rates (e.g. Hamilton and May (1977); Metz and Gyllenberg (2001); Poethke and Hovestadt (2002); Matthysen (2005); De Meester and Bonte (2010); Baguette et al (2011)) and distances have been shown to depend on the local density (Wender et al 2005; Bitume et al 2013; Martorell and Martínez-López 2014). However, the theoretically optimal functional relationship between local density and emigration rate has been subject to debate. A comparison between the existing functions was made by Hovestadt et al. (2010). They found the best performance by the asymptotic threshold model (Ruxton and Rohani 1999; Poethke and Hovestadt 2002). This is a model that holds a strategy where individuals only start dispersing once a certain threshold density is reached after which the emigration rate follows an asymptotic increase with density. Our optimality model from chapter 3 confirms this result, we find the asymptotic-threshold functional shape in the probability that our individuals stay at the natal patch. Moreover, our model also incorporates several environmental scenarios and predicts how far dispersing individuals that should go, effectively adding another dimension to current theory.

Unfortunately, our study does not contribute to closing the current gap between theory and empirical work on density dependent dispersal. We strongly emphasize the need for more empirical work on this subject.

6.4 Implementing dispersal, why and when should we use dispersal kernels

Summarizing a dispersal strategy into a single mean dispersal distance neglects biologically relevant variation. This variation is generated by proximate, often stochastic, factors related to the environmental conditions (such as for instance weather and landscape; (Travis 2001) as well as by ultimate factors related to bet-hedging and kin-competition (Bowler and Benton 2005). Therefore, a better approach is to consider the distribution of dispersal distances, which is typically summarized by a probability density distribution, the dispersal kernel (Kot and Schaffer 1986; Nathan and Muller-Landau 2000). The use of kernels to summarize dispersal strategies is a way of incorporating an intermediate amount of detail without going into an actual mechanistic movement approach which requires a lot more detailed parameterization and a small temporal scale to be modelled properly (Travis et al 2012). The spatial scale on which the kernel approach is appropriate furthermore depends on whether dispersal is an active or passive process (see Figure 29). For passive dispersers complex movement is not an option, with the exception of passive dispersers who use actively moving vectors (e.g. D'hondt et al. (2012)). Therefore the kernel approach can be appropriate even at small spatial scales. Another option on relatively small scales is to assume global dispersal where individuals are equally likely to disperse to all patches or positions on the landscape. At very large spatial scales (such as our model in chapter 5) a dispersal rate or a diffusion process coupled with nearest neighbour dispersal may be preferable for reasons of simplicity as on these scales short distance dispersal or movement can be ignored.

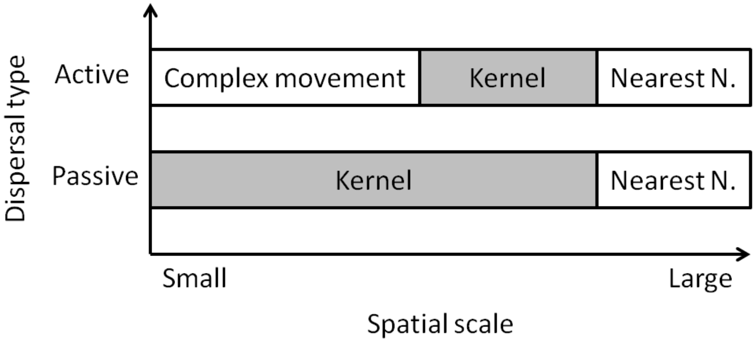


Figure 29: Overview of spatial scales and optimal methods to model dispersal. Nearest N. stands for nearest neighbour dispersal.

6.5 Future prospects

The predictions formulated in this thesis clearly ask for empirical validations. I am looking forward to see more studies on kernel shapes, ideally after different selection regimes have been imposed upon the organisms. Additionally, our model in chapter 5 clearly predicts a decreasing, step wise pattern in voltinism over the latitudinal gradient and a difference between the temperatures at which mites go into diapause in autumn and the one at which they awake from dormancy in spring. Furthermore, the stepwise pattern in voltinism is predicted to be synchronized with the saw-tooth pattern in developmental speed. It would be very interesting, yet challenging, to measure these traits empirically. Finally, I hope that our findings on optimal kernel shapes from chapter 3 will be taken into account by fellow modellers and empiricists.

Summary

The realisation that space is an important factor in a number of key ecological processes has led to an appreciation of the importance of the dispersal process. Recent anthropogenic effects such as climate change, release of invasive species and habitat deterioration further spurred interest in the topic. Moreover, ecologists have begun to realise that under changing conditions dispersal traits can be under strong selection which results in interesting and important eco-evolutionary dynamics. The four research chapters in this thesis offer different insights into the ecological and evolutionary processes that affect and are affected by dispersal.

In chapter 2 we highlight the importance of space as we look into landscape effects on a community level and try to gain insight into the mechanisms maintaining biodiversity. This is an important and ongoing challenge in our changing world. To efficiently protect ecosystem diversity we must understand why and how species coexist, but models explaining species coexistence usually don't incorporate a detailed spatial context. However, spatial structure has been shown to affect species coexistence and habitat deterioration is one of the biggest threats to biodiversity. We therefore explore a spatially explicit two-species model and assess the effects of habitat structure on species coexistence using a wide diversity of fractal landscapes. Each species is specialized in a particular habitat type. We find that landscape structure has a major influence on the stability and constitution of a two species system and may be sufficient to explain the coexistence of two species. Well connected and highly structured habitat configurations allow spatial segregation of both species and this decreases local interspecific competition; in our model this is the most important process stabilizing coexistence. Moreover, we find that more dispersive species are less likely to become spatially segregated and therefore average dispersal distance has a negative effect on the stability of species coexistence.

In chapter 3 we introduce dispersal evolution as we develop a method to find optimal dispersal distance probability functions (dispersal kernels). To maximize their inclusive fitness all organisms have to disperse, or disperse their offspring. While we currently have a good understanding of the selection pressures leading to emigration, we lack a clear understanding on the evolution of dispersal distance strategies, despite its fundamental importance for spatial population dynamics. Dispersal kernels represent the frequency distribution of individual dispersal distance. Insights on the optimal shape of these kernels relative to the prevailing selection pressures and relevant environmental and demographic processes are therefore essential to increase the reliability of predictive methods in spatial ecology. To fill this gap, we followed an optimality approach to theoretically infer

how the relevant cost-benefit balances shape the optimal dispersal kernels. We demonstrate the overall importance of spatial density gradients in determining the optimal kernel shape, ranging from short distance dispersal to unimodal distance probability distribution functions. Consequently, dispersal kernels cannot be described by a single function and need to be adjusted according to the prevailing spatial environmental conditions. Besides yielding novel insights into the evolution of dispersal distances the results from this chapter provide a guide for kernel selection in predictive spatial ecology, which, to date, too often uses arbitrary criteria in this context.

In chapter 4 we look into a potentially important ecological feedback of dispersal evolution. As a consequence of anthropogenic climate change species have to adapt to the new situation or track their preferred conditions polewards. During such a range shift species are simultaneously confronted with a second major anthropogenic disturbance, landscape fragmentation. By implementing a shifting climate window we examine the effect of different rates of climate change on the evolution of dispersal distances through changes in the genetically determined dispersal kernel. In contrast to chapter 3 we assume a particular kernel function (i.e. Gaussian) and let the shape/variance evolve. The results in this chapter demonstrate that the rate of climate change is positively correlated to the evolved dispersal distances although too fast climate change causes the population to crash. When faced with realistic rates of climate change, greater dispersal distances evolve than those required for the population to keep track of the climate, thereby maximising population size. Importantly, these greater dispersal distances induce evolutionary rescue by facilitating the population in crossing large gaps in the landscape. This could ensure population persistence in case of range shifting in fragmented landscapes. Furthermore, this chapter highlights problems in using invasion speed as a proxy for potential range shifting abilities under climate change.

In chapter 5, the final research chapter, we integrate theory and practice as we look into the effects of a recent range expansion on the life history traits of the two-spotted spider mite, *Tetranychus urticae* Koch (Acari, Tetranychidae). Species will experience multiple selection pressures during range expansion and when range expansion takes place along a latitudinal gradient, a straightforward interpretation of the observed evolutionary dynamics is hampered because of the joint action of processes related to spatial sorting and local adaptation. We studied evolutionary divergence related to the recent northwards range expansion and contrasted patterns of evolved life history variation along a latitudinal gradient with theoretical predictions from a simulation model. We demonstrate how spatial sorting and local adaptation synergistically affected life-history evolution. Especially dispersal and development showed contrasting patterns among these two evolutionary scenarios. Development showed typical adaptations towards colder temperatures and shorter breeding seasons at higher latitudes, while dispersal, like in chapter 4, was clearly shaped through genetic sorting along the expanding front. We found no indications for correlated responses between the different life-history traits. Divergence in life history in organisms shifting their range under climate change is consequently jointly determined by contemporary evolutionary dynamics resulting from sorting processes and fast local adaptation to the environmental gradient.

There are important differences between these four chapters. While the model in chapter 2 operates on a community level and focuses on spatial, ecological effects rather than dispersal evolution, the latter effect is incorporated in the other three chapters. These chapters in turn differ in the spatial scale of the study system. Nonetheless all chapters emphasize the importance of dispersal evolution to understand ecological dynamics and call for an appropriate incorporation of space and dispersal in both empirical and theoretical work on this subject.

Samenvatting

Het besef dat ruimtelijke factoren belangrijk zijn voor een aantal ecologische sleutelprocessen verklaart de toegenomen aandacht voor dispersieprocessen. Recente antropogene effecten zoals klimaatsverandering, introductie van invasieve soorten en habitatachteruitgang droegen hier verder toe bij. Bovendien beginnen ecologen te realiseren dat onder veranderende omstandigheden het dispersieproces onder sterke selectie kan staan wat resulteert in interessante en belangrijke eco-evolutionare dynamieken. De vier onderzoekshoofdstukken in deze thesis bieden verschillende invalshoeken op de ecologische en evolutionaire processen die interageren met dispersie.

In hoofdstuk 2 benadrukken we het belang van ruimtelijke factoren, we bekijken landschapseffecten op het niveau van de soortgemeenschap en we proberen inzicht te krijgen in de mechanismen die biodiversiteit in stand houden. Dit is een belangrijke en voortdurende uitdaging in onze veranderende wereld. Om de ecosysteem diversiteit efficiënt te beschermen moeten we begrijpen hoe en waarom soorten samenleven. Modellen die de co-existentie van soorten proberen te verklaren incorporeren gewoonlijk geen gedetailleerde ruimtelijke context. Het is echter geweten dat ruimtelijke structuur de co-existentie van soorten kan beïnvloeden en habitat achteruitgang is een van de grootste bedreigingen voor de biodiversiteit. Daarom onderzochten we een ruimtelijk model met twee soorten. We bepaalden de effecten van habitat structuur op de stabiliteit van co-existentie, gebruikmakend van een grote verscheidenheid aan fractaallandschappen. Elke soort is gespecialiseerd in een specifiek habitat type. We vonden dat habitatstructuur een grote invloed heeft op de stabiliteit en de verhoudingen binnen het systeem met twee soorten. Goed samenhangende en gegroepeerde habitatstructuren laten doe dat soorten ruimtelijk van elkaar gescheiden worden wat resulteert in een minder intensieve lokale interspecifieke competitie. In ons model heeft dit fenomeen de belangrijkste positieve invloed op de stabiliteit van co-existentie. Daarenboven vonden we dat meer dispersieve soorten minder kans hadden om ruimtelijk gescheiden te geraken; gemiddelde dispersieafstand had dus een negatief effect op de stabiliteit van co-existentie.

In hoofdstuk 3 introduceren we evolutie van dispersie en ontwikkelen we een methode om optimale dispersieafstandprobabiliteitfuncties (dispersie kernels) te bepalen. Om hun inclusieve fitness te maximaliseren moeten alle organismen zichzelf of hun nakomelingen disperseren. Hoewel we momenteel een goede kennis hebben van de selectiedrukken die leiden tot emigratie ontbreekt het ons, ondanks het fundamentele belang van dispersieafstand voor ruimtelijke populatie dynamieken, aan een goed begrip van de evolutie van dispersieafstand strategieën. Dispersie kernels vertegenwoordigen de kansendistributie dat een individu naar een bepaalde afstand zal disperseren. Inzicht in de optimale vorm van deze kernels relatief tot de heersende selectiedrukken en relevante omgevings- en demografische processen zijn daarom essentieel om de betrouwbaarheid van voorspellende, ruimtelijke ecologische modellen te verhogen. Om deze leemte in de kennis op te vullen volgden we een optimaliteitsaanpak om theoretisch af te leiden hoe de relevante kosten en baten balans de optimale dispersie kernels vormen. We tonen het algemene belang van ruimtelijke densiteitsgradiënten aan die the optimale kernel vorm bepalen, gaande van korte afstandsdispersie tot unimodale kernels. Dit heeft tot gevolg dat dispersie kernels niet beschreven kunnen worden door één enkele functie en aangepast moeten worden aan de specifieke ruimtelijke omgevingsomstandigheden. Dit werk levert niet alleen nieuwe inzichten in de evolutie van dispersieafstanden maar voorziet ook een gids voor kernel selectie in voorspellende ruimtelijke ecologie waar men, tot op heden, te vaak gebruik maakt van arbitraire criteria in deze context.

In hoofdstuk 4 bekijken we een potentieel belangrijke ecologische feedback van dispersie evolutie. Als een gevolg van antropogene klimaatsverandering moeten soorten zich aanpassen aan de nieuwe omstandigheden of hun originele, voorkeursomstandigheden volgen richting de polen. Tijdens zo’n range shift worden soorten ook nog eens geconfronteerd met een tweede belangrijke antropogene verstoring, landschapsfragmentatie. Met behulp van een opschuivend klimaatsvenster bekijken we het effect van verschillende snelheden van klimaatsverandering op de evolutie van dispersieafstanden via veranderingen in het genetisch bepaalde dispersie kernel. In tegenstelling tot hoofdstuk 3 nemen we een bepaalde kernel functie aan (i.e. Gaussverdeling) en laten we de vorm/variantie evolueren. Onze resultaten tonen aan dat de snelheid van klimaatsverandering positief gecorreleerd is met de evoluerende dispersieafstanden, hoewel te snelle klimaatsverandering voor de ondergang van de populatie zorgt. Wanneer een populatie geconfronteerd wordt met realistische snelheden van klimaatsverandering evolueren er hogere dispersieafstanden dan strikt genomen nodig om het klimaatsvenster te volgen. Hierbij wordt de populatiegrootte gemaximaliseerd. Een belangrijk gevolg is dat de hogere dispersieafstanden kunnen zorgen voor evolutionaire redding van de populatie wanneer ze geconfronteerd worden met onregelmatigheden in het landschap. Dit kan de voortzetting van de populatie verzekeren in geval van range shifts in gefragmenteerde landschappen. Tenslotte brengt dit hoofdstuk mogelijke problemen aan het licht met het gebruik van invasiesnelheden als maatstaaf voor potentiële range shift capaciteiten tijdens klimaatsverandering.

In hoofdstuk 5, het laatste onderzoekshoofdstuk, integreren we theorie en praktijk. We kijken naar de effecten van een recente range uitbreiding op de levensgeschiedenis kenmerken van de bonenspintmijt, *Tetranychus urticae* Koch (Acari, Tetranychidae). Soorten ondervinden hoe dan ook meerdere selectiedrukken tijdens een range expansie. Wanneer de range uitbreiding plaatsvindt langs een latitudinale gradiënt wordt een rechtstreekse interpretatie van de geobserveerde evolutionaire dynamieken bemoeilijkt door de interactie tussen processen van ruimtelijke sortering en lokale adaptatie. We bestudeerden evolutionaire afwijkingen gelinkt aan de recente noordwaardse expansie en contrasteerden de patronen van geëvolueerde levensgeschiedenisvariatie over de latitudinale gradiënt met theoretische voorspellingen van een simulatie model. We tonen aan hoe ruimtelijke sortering en lokale adaptatie tezamen de evolutie van levensgeschiedenis kenmerken beïnvloeden. Vooral ontwikkelingssnelheid en dispersie vertoonden contrasterende patronen tussen deze twee evolutionaire scenarios. Ontwikkelingssnelheid toonde typische adaptaties aan koudere temperaturen en het kortere voortplantingsseizoen op hogere latitudes, terwijl dispersie, net als in hoofdstuk 4 duidelijk beïnvloed was door genetische sortering langs het expansiefront. We vonden geen indicaties van gecorreleerde responsen tussen de verschillende levensgeschiedenis kenmerken. Afwijkingen in levensgeschiedenis kenmerken van organismen die hun range opschuiven tijdens klimaatsverandering worden dus tegelijk bepaald door de evolutionaire dynamieken van sorteringsprocessen en snelle lokale adaptatie aan de omgevingsgradiënt.

Er zijn belangrijke verschillen tussen deze vier hoofdstukken. Terwijl het model in hoofdstuk 2 op werkt op het niveau van de soortgemeenschap en de nadruk legt op ruimtelijke, ecologische processen in plaats van dispersie evolutie is dit laatste effect wel geïncorporeerd in de andere drie hoofdstukken. Deze hoofdstukken verschillen op hun beurt bijvoorbeeld in de ruimtelijke schaal die ze in rekening nemen. Desalniettemin leggen alle hoofdstukken de nadruk op het belang van dispersie (evolutie) en tonen ze het belang aan van een correcte, aangepaste incorporatie van ruimtelijke factoren en dispersie in zowel empirische als theoretische studies.

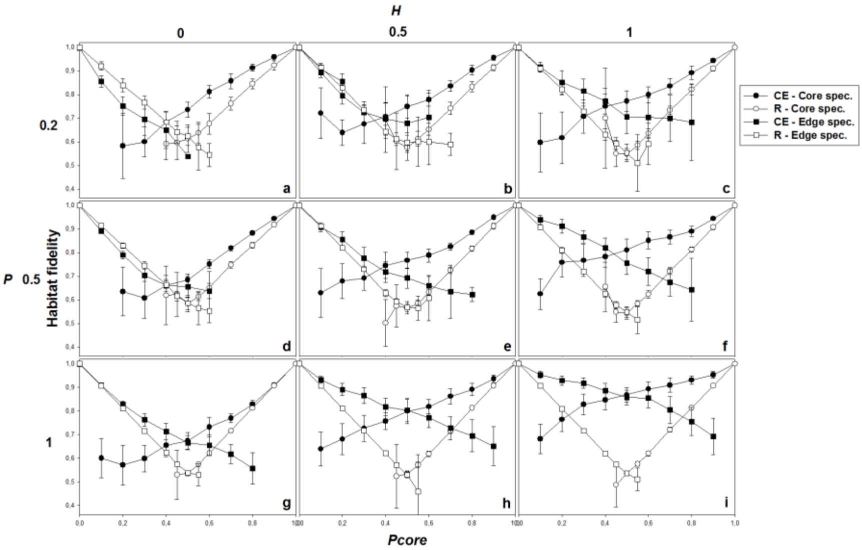
7

Appendices

7.1 Appendix to Chapter 2: Habitat structure mediates spatial segregation and therefore coexistence.

Link 1:

http://www.ecology.ugent.be/terec/JB/A1.gif



Appendix Figure 1: The change in habitat fidelity with Pcore for both species in the random (R) and core-edge (CE) configurations over nine combinations of P and H. The habitat fidelity is calculated as the proportion of individuals from a species that reside in their preferred habitat type. Note that lower levels of H (clumpedness) overall results in fidelities more similar to those found in the random configuration. When P and H increase together they increase the habitat fidelity in the core-edge configuration where overall the fidelity is higher than in the random configuration. One exception to this is the fidelity of the edge specialist in low P and low H conditions. In these conditions the edge habitat is very unattractive because is scattered in very small, isolated patches. When the edge habitat does occur in larger, more viable patches it on average more often lies on the outside (edge) of a such a patch where dispersal mortality is higher. Therefore the edge specialists are found more often in core-habitat in the core-edge configuration than in the random configuration. Off course this puts them in a weak competitive position compared to core specialists who face the same costs but perform better in core-habitat. This is why the edge specialists always go extinct when Pcore is higher than 0.5 whereas core specialist can survive when there is only 20% core habitat available (Pcore 0.2).

7.1.1 ODD protocol for model description

The model description presented here follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al 2006; Grimm et al 2010).

Purpose

To gain detailed insight on how landscape structure influences coexistence and gain understanding of the underlying mechanisms and their relative importance. We hypothesize that when habitat availability and habitat clumping are high, coexistence will be most stable - although species in a weak competitive position might benefit from fragmentation.

Entities, state variables, and scales

The first type of entities we use are individuals which could be insects or plants. State variables are location (x, y coordinates), species (1 or 2), reproductive rate in either habitat type ($\lambda_{preferred} = 2.5$, $\lambda_{unpreferred} = 1.5$) and dispersiveness (i.e. the standard deviation of a Gaussian kernel which is kept constant within simulation runs). Evidently the core and edge specialists prefer core and edge habitat respectively.

The second type of entities are the grid cells which represent the local spatial environment. They have a location (x, y coordinates), a habitat type (0 = unsuitable habitat (matrix), 1 = edge habitat, 2 = core habitat) and a local density (the total number of individuals from both species sharing the same coordinates as the patch) .

Since this is a purely theoretical study the spatial and temporal scales are depending of the specific system we have in mind. We suggest that our model applies to both insects and plants but the scales would differ between them. In order to avoid any further projection on real specific systems of this generic model, we deliberately do not assign very specific units.

Process overview and scheduling

Within one time step individuals disperse and, if they survive the dispersal phase (i.e. if they land in a suitable patch), they reproduce (density dependently), after this they die. The offspring then go on the do the same in the next time step.

A higher level module first loops over all the individuals to handle the dispersal phase. In this phase individual’s locations are updated and unsuccessful dispersers are removed. Hereafter the local density in each grid cell is assessed and assigned to that grid cell. In a subsequent loop the individuals then reproduce according to this local density and the local habitat type.

Design concepts

Basic principles.

The population dynamics used are similar to work by several authors (Travis and Dytham 1999; Poethke and Hovestadt 2002; Kubisch et al 2010; Fronhofer et al 2011; Boeye et al 2013). However, the difference to these models is that our model each individual has very few traits and no evolution or plasticity etc. takes place. The complexity in our model lies in the landscapes structure. On this aspect our approach is most similar to Wiegand et al. (1999) and Wiegand et al. (2005). We try to expand the field of knowledge by combining competition between two species based on simple population dynamics and complex landscape structures.

Emergence.

As the spatial structure of the landscape changes over different simulation results we expect the species abundances and levels of local co-occurrence (see later) to vary.

Interaction.

Each individual indirectly and equally interacts with all other individuals in its patch through increasing the local density. The local density is the only driver of local competition and is negatively correlated to the reproductive output of those in the patch.

Stochasticity.

Both the dispersal and the reproductive process have stochasticity embedded in them. During the dispersal process distances in both x and y direction are randomly selected from a Gaussian kernel. The reproductive output is selected from a Poisson distribution.

Observation.

The first main result observation taken from each simulation run after the 1000th time step are total individual count of both species from which the global coexistence is calculated. The global coexistence is at its maximum (100%) when on a global scale both species are equally abundant whereas a value of 0% indicates the total exclusion of one species. The second value is the percentage of inhabited grid cells occupied by individuals of both species (i.e. the local co-occurrence).

Initialization

During initialization the landscape is created according to the parameters given for: *P* (proportion of suitable habitat, i.e. of the core and edge type),

H (Hurst exponent, level of clumpedness), P_{core} (proportion of the suitable habitat that is of the core type, $P_{edge} = 1 – P_{core}$), the size of the landscape. The landscapes are created with a separate module using the Diamond-square algorithm (Miller 1986) which returns a 2D matrix with the habitat type values (0 = unsuitable habitat (matrix), 1 = edge habitat, 2 = core habitat). Once the landscape is created the main model is initialized with one thousand individuals of each species randomly distributed over the suitable habitat.

Input data

Except for the landscape created by a separate module there is no input data.

Sub-models

Dispersal:

During the dispersal phase a loop goes over all individuals and for each one of them samples a distance in both x and y direction from a Gaussian kernel with a fixed standard deviation. These distances are then rounded to the closest integer. Subsequently the distances are added to the x and y coordinates of the individual. If the new coordinates lie within the boundaries of the landscape and the habitat on that location is of a suitable type (core or edge) then the individual is appended to a list of survivors.

Reproduction:

Before reproduction takes place the local density in each cell is assessed. Next the mean number of offspring μ which each individual will produce in its local patch is calculated as follows:

$$\mu = \lambda(1 + aNt)^{-1}$$

with

$$a = (\lambda - 1)/N^*$$

Here, λ specifies the net reproductive rate which depends on whether the individual prefers the local habitat type ($\lambda_{preferred} = 2.5$, $\lambda_{unpreferred} = 1.5$), N^* is the population equilibrium density for a single patch and is a constant set to 2, Nt is the summed local density of both species at time t; if Nt is higher than N^* the mean number of offspring (μ) will decrease below 1 due to competition and the local population will shrink. The actual number of offspring is drawn from a Poisson distribution with mean μ (Travis and Dytham 2002; Kubisch et al 2011).

7.2 Appendix to Chapter 3: The evolution of density-dependent dispersal kernels

Link 2:

http://www.ecology.ugent.be/terec/JB/A2.gif

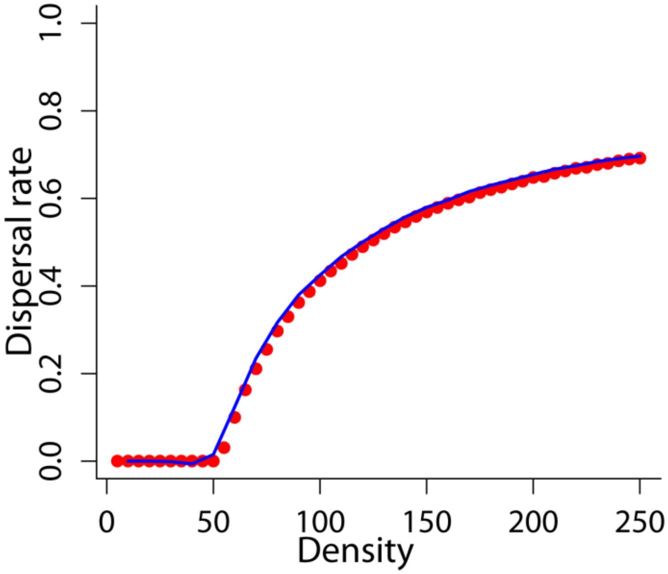
7.2.1 Alternative spatial demography scenarios

As suggested in the methods section there are a number of alternative assumptions one can make compared to the standard scenario described in this article. A first assumption in this scenario is that population dynamics are asynchronous at the metapopulation level, which implies that only individuals in a given, focal patch disperse at one point in time, while individuals in all other patches do not. The result of this assumption is an emerging gradient in densities decreasing from the focal patch outwards as dispersers are more likely to settle close to the natal patch. This gradient provides an incentive to disperse further since individuals can avoid strong competition by doing so. We investigated an alternative scenario where all individuals in all patches in the metapopulation were synchronously dispersing their propagules (i.e. the "equilibrium, synchronous scenario"). Such a scenario is more realistic for species that show synchronous dynamics due to, for example, seasonality. In this scenario no gradient in density away from the natal patch emerges. Consequently, the optimal density-dependent kernels that evolve in this scenario result in short distance dispersal to distance class one at the most (see Appendix Figure 3). The optimal strategy under these conditions is also much less sensitive to changes in both density and mortality (see animation 1 in online appendix). This low sensitivity of the optimal dispersal kernel is not surprising, as, in this scenario, dispersing further hardly bears any benefit --- population densities are very similar everywhere while costs increase with distance (note that for simplicity we have excluded kin-competition from our simulations). For a detailed analysis of different kernel metrics see Appendix Figure 7.

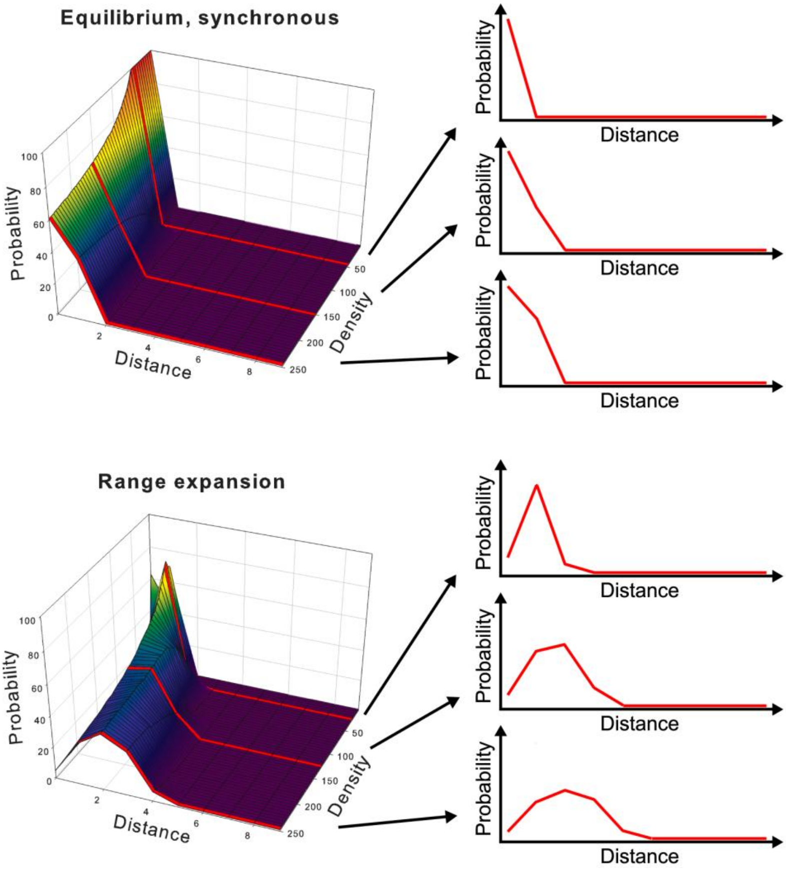
A third and final scenario assumed an empty landscape, apart from the focal patch (no reference model was needed here). This scenario resembles a spatial demographic situation that could occur at an expanding range front where the best dispersers leave the rest of the population behind. It has been shown several times that range expansion processes lead to increases in dispersal (Phillips et al 2008; Kubisch et al 2014), be it caused by spatial sorting (Shine et al 2011) or kin-competition (Kubisch et al 2013). Even though, in this empty landscape competition will be less strong compared to the two equilibrium scenarios, a gradient in disperser density will be present and individuals will have a strong incentive to disperse long distances to reach empty habitat to maximize their reproductive output. We do indeed find the largest dispersal distances in this scenario and the evolution of unimodal kernel shapes at relatively low densities (see Appendix Figure 3). The optimal kernel under these conditions is also the most sensitive to changes in both density and mortality (see online animation through Link 2: in appendix). Following these results, we expect that gradients in population density, as they are likely to occur at expanding range margins, are another factor increasing dispersal due to wider distances travelled. If one includes the (multi-generational) effects of spatial sorting and kin-competition, it is very likely that these forces and their interplay dramatically alter current projections of future range shifts of species. For a detailed analysis of different kernel metrics see Appendix Figure 8.

Kernel shapes do not change fundamentally when we assume asynchronous life-histories (see Appendix Figure 4). Lower dispersal mortality and higher natal population densities lead to a change in kernel shape from decreasing to unimodal and, in the absence of mortality, even to linearly increasing dispersal kernels. Qualitatively this does not change in a scenario of range expansion. Dispersal distances there are generally higher and parameter combinations leading to no emigration at all are restricted to very low densities and high mortalities. These results thus suggest that demographic characteristics of the population will affect the eventual shape of the dispersal kernel in a predictable way.

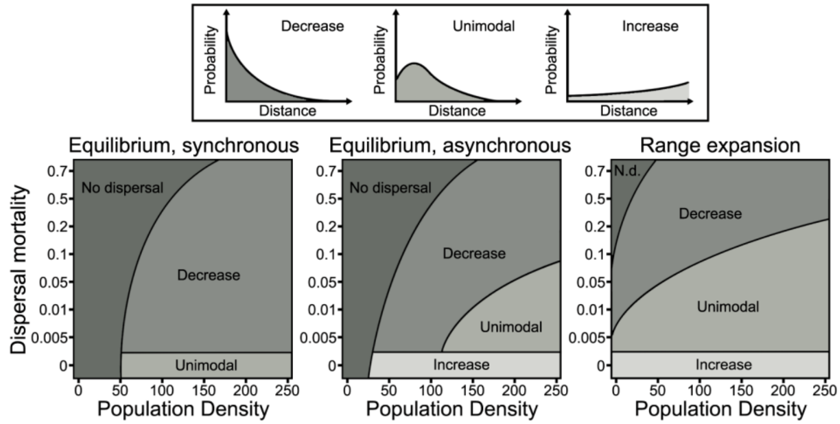
The benefits associated with dispersal differ between the three scenarios and even though the general pattern is similar we find a different sensitivity of the optimal kernel shape to both local density and dispersal mortality in each scenario. In order to describe the range of functional relationships emerging from our simulations quantitatively, we fitted different typical kernel shapes (e.g. negative-exponential, lognormal or Weibull) to the resulting kernels for different parameter combinations and chose the ones with the best statistical fit (Appendix Figure 5).



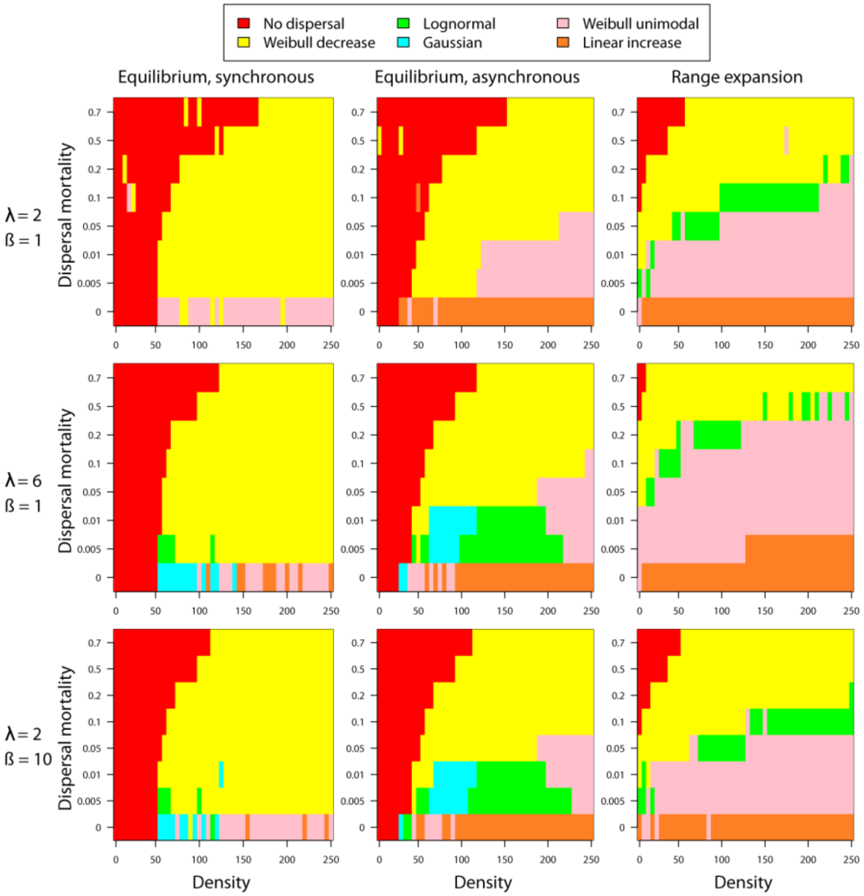
Appendix Figure 2: Comparison of simulated, optimal dispersal rates (red dots) with the dispersal rate predicted by the Poethke-Hovestadt function for each density (blue line). To make our result comparable to those of Poethke and Hovestadt (2002) we used an altered version of the gradient scenario with dispersal rates rather than kernels. Note the nearly perfect fit and the similarity in shape between the figure shown here and the probability to stay at distance class zero over density in Figure 11 (although the dispersal rate is the opposite of the probability not to disperse and therefore shown upside down in this graph).



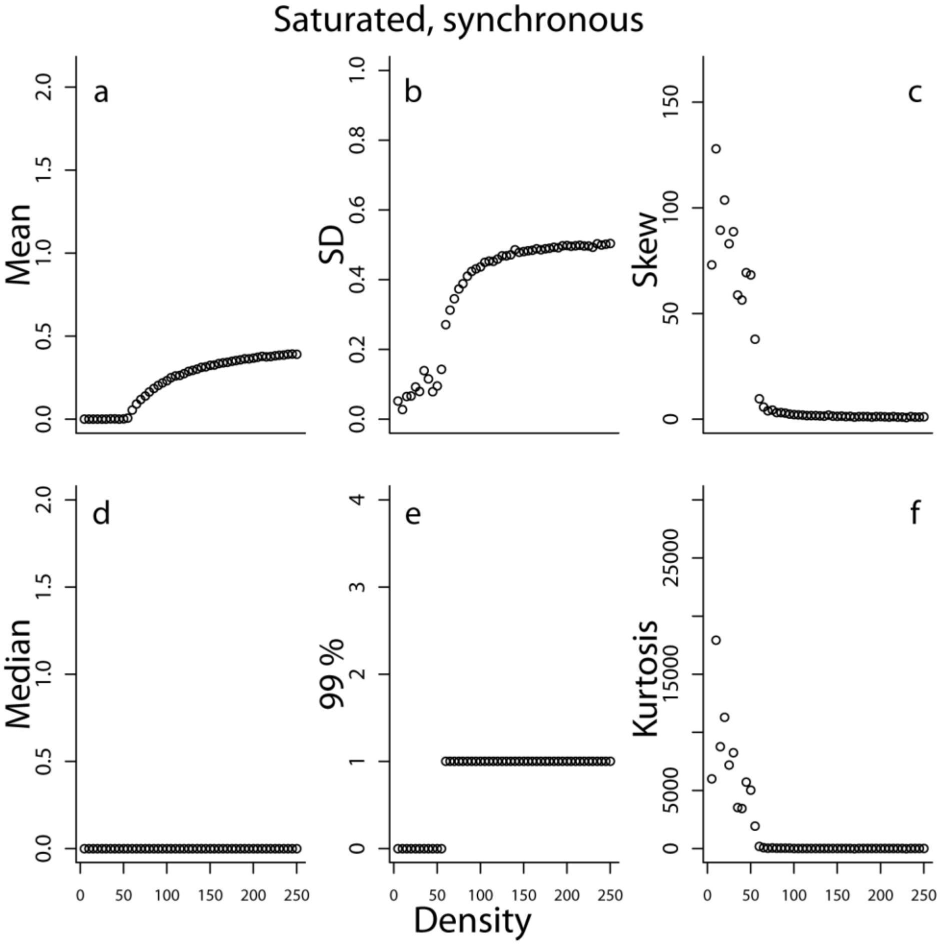
Appendix Figure 3: The optimal kernels for a range of densities and dispersal mortality $m_s = 0.05$ for the scenario with a metapopulation at equilibrium and synchronous dynamics and the scenario of a range expansion. Even though the overall pattern is similar to that in Figure 11, the response to local density is much stronger in the range expansion scenario, resulting in longer dispersal distances.



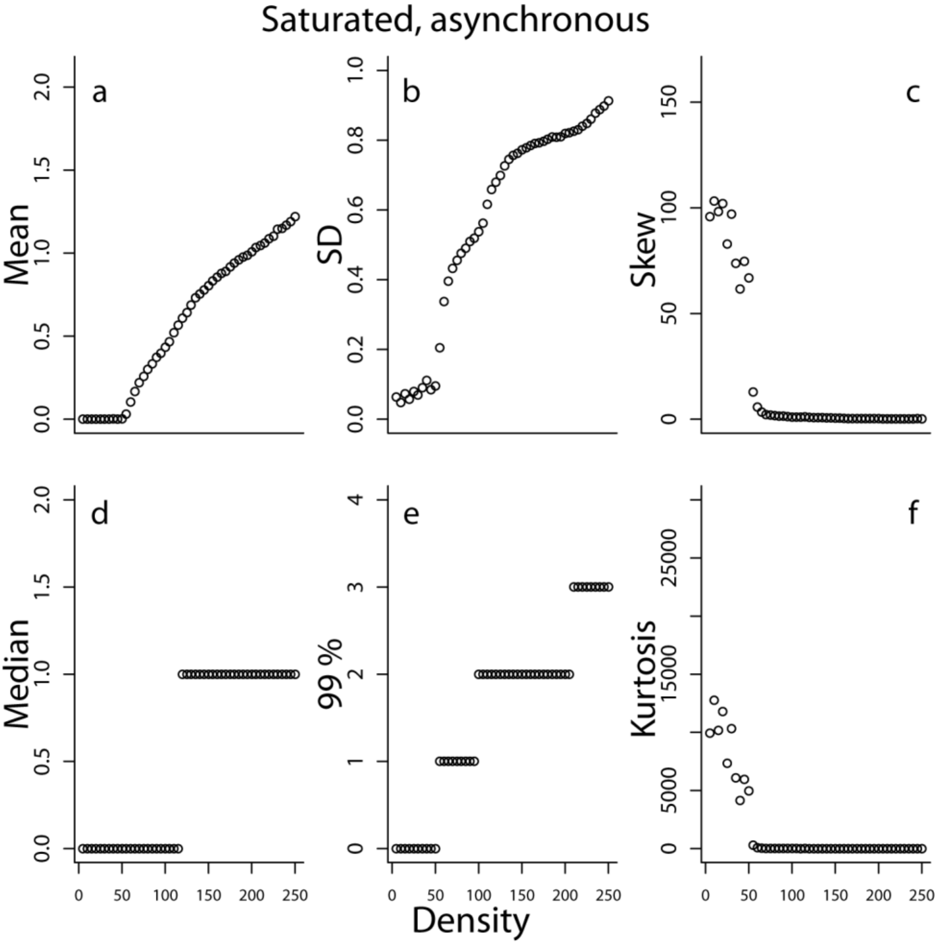
Appendix Figure 4: A summary describing the optimal kernel shapes qualitatively over the explored range of local densities and dispersal mortalities in the three scenarios. The sensitivity to both dispersal mortality and local density increases from left to right as do the potential benefits of (longer distance) dispersal. The `no dispersal' category comprises kernels with less than 3% dispersal. Note that the dispersal mortalities on the y-axis do not decrease linearly. For an overview of which probability function fits best to each kernel shape represented here see Appendix Figure 5.



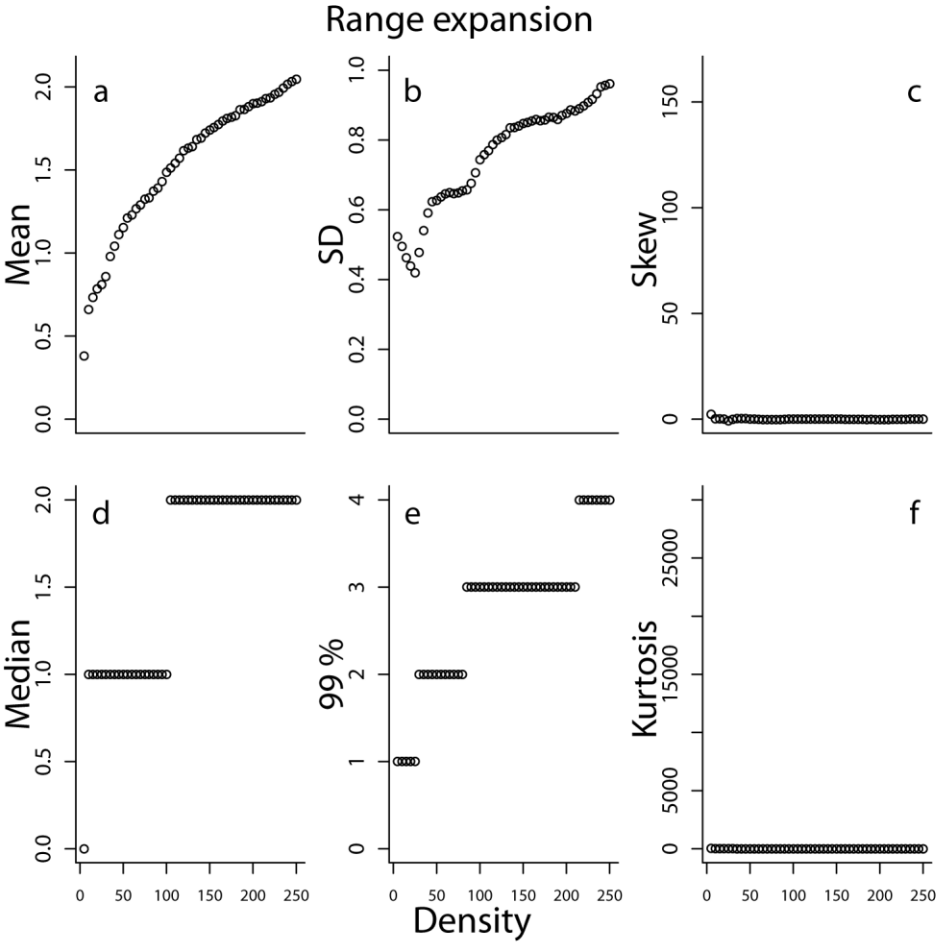
Appendix Figure 5: Overview of the function types fitting best to the simulated optimal kernel shapes over combinations of local density and dispersal mortality for the three different scenarios. For the top and bottom row the growth rate λ = 2 while for the centre row λ = 6. For the top and centre row the strength of competition β = 1 while for the bottom row β = 10. The average dispersal distance always increases with population density. In accordance with our other results the kernel shapes associated with longer dispersal distances are most abundant in the expansion scenario followed by the asynchronous, equilibrium metapopulation scenario. The `no dispersal' category holds kernels with less than 3% dispersal. Note that the dispersal mortalities on the y-axis do not decrease linearly.



Appendix Figure 6: The change of six kernel metrics over density for a dispersal mortality of m_s = 0.05 in the equilibrium metapopulation with synchronous dynamics scenario. The metrics are, (a) the average dispersal distance, (b) the standard deviation on the average dispersal distance, (c) the skewness of the kernel, (d) the median dispersal distance, (e) the dispersal distance of the 99% percentile and (f) the kurtosis of the kernel. The mean dispersal distance gradually reaches a maximum of 0.5 and the standard deviation stabilizes after an initial increase. Both skewness and kurtosis rapidly decrease with density.



Appendix Figure 7: The change of six kernel metrics over density for a dispersal mortality of m_s = 0.05 in the equilibrium metapopulation with asynchronous dynamics scenario. The metrics are, (a) the average dispersal distance, (b) the standard deviation on the average dispersal distance, (c) the skewness of the kernel, (d) the median dispersal distance, (e) the dispersal distance of the 99 % percentile and (f) the kurtosis of the kernel. Before the local density reaches the carrying capacity (50) the average distance remains zero; after this threshold is reached the average dispersal distance increases almost linearly; the standard deviation too increases but this trend weakens with higher densities. The skew and kurtosis are quite similar to the no gradient scenario with a long, weakening decrease.

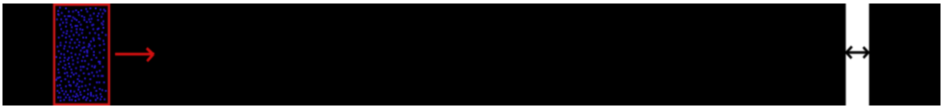


Appendix Figure 8: The change of six kernel metrics over density for a dispersal mortality of $m_s = 0.05$ in the range expansion scenario. The metrics are, (a) the average dispersal distance, (b) the standard deviation on the average dispersal distance, (c) the skewness of the kernel, (d) the median dispersal distance, (e) the dispersal distance of the 99% percentile and (f) the kurtosis of the kernel. In contrast to the other scenarios the mean dispersal distance starts to increase even at the lowest densities. The standard deviation starts at a higher value than in the other scenarios and after an initial dip starts to increase up to a value of 1 (just like the gradient scenario). Unlike in the other scenarios the skew and kurtosis are very low (close to zero).

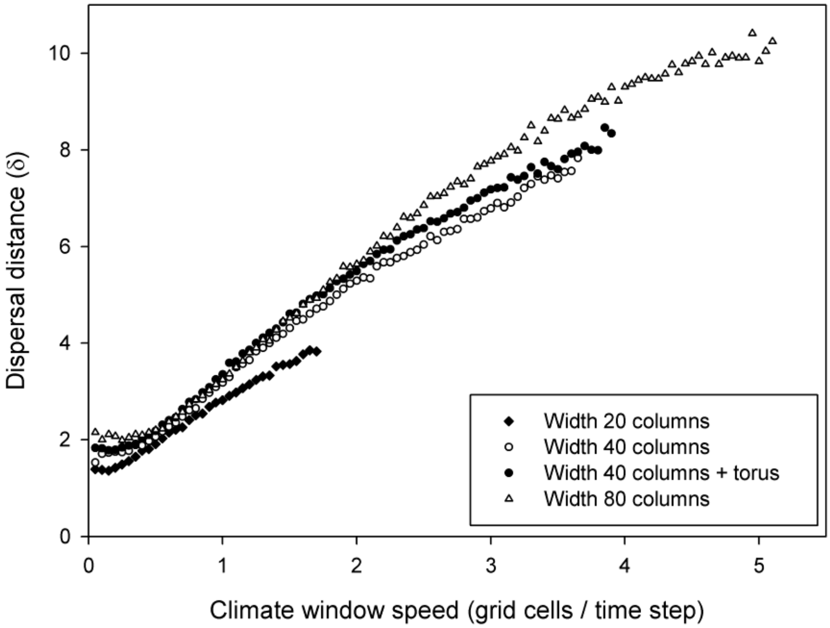
7.3 Appendix to Chapter 4: More rapid climate change promotes evolutionary rescue through selection for increased dispersal distance.

Link 3:

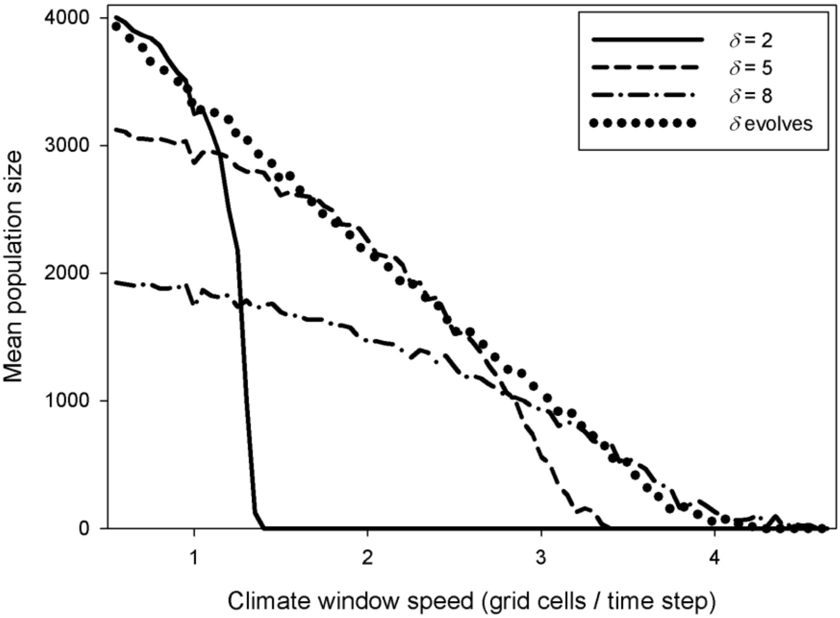
http://www.ecology.ugent.be/terec/JB/A3.gif



Appendix Figure 9: A schematic representation of the modelled landscape. Individuals (blue dots) can survive and reproduce in a patch that both consists of suitable habitat (black) and is located in the moving climate window (red rectangle). In some cases the population is confronted with a gap of unsuitable habitat (white) at the end of the landscape. The width of this gap is fixed during a single simulation but is systematically varied over several runs.



Appendix Figure 10: Sensitivity analyses according to landscape and climate window properties. The evolved dispersal distances as a response to different sizes and velocities of the climate window. The distance between the leading and trailing edge of the window was varied. Larger climate windows allow populations to persist in environments that change faster. Usually climate windows are 40 grid cells wide in the x-direction (direction of movement) and 100 grid cells long in the y-direction, if we make the length of the climate window infinite in the y-direction (i.e. a torus) there is only a small positive effect on evolved dispersal distances and maximal rate of climate change the population can track.



Appendix Figure 11: Mean population size over several rates of climate change for fixed and evolving δ. When dispersal distances (δ) are fixed there is a clear trade-off between population size at low rates of climate change and the capacity to cope with high rates of climate change. This is due to higher mortality of dispersive individuals in slow moving climate windows and high mortality of poor dispersers in faster moving climate windows. When the dispersal distance (δ) is allowed to evolve there is a selection for the dispersal distance that finds an optimal balance between dispersal mortality and resilience to the shifting climate window. This results in a maximization of the population size for each rate of climate change.

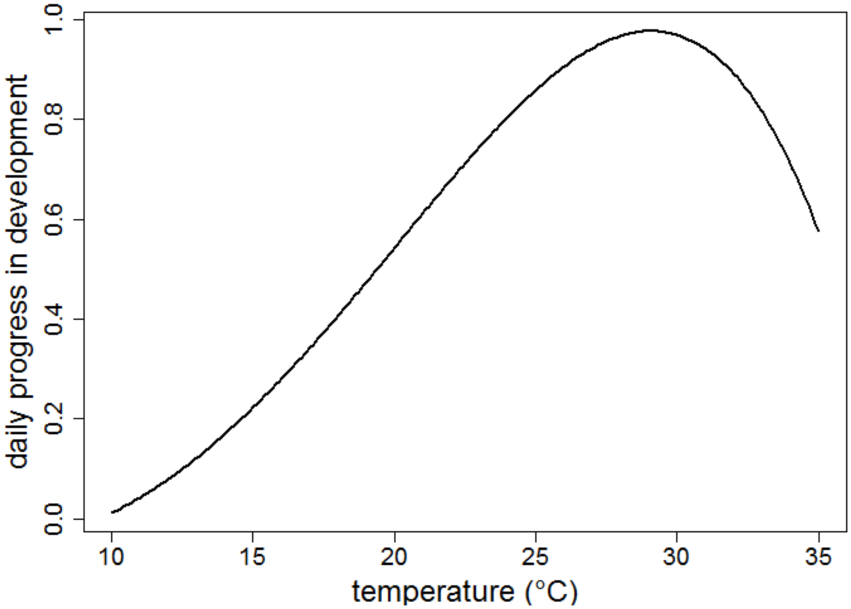
7.4 Appendix to Chapter 5: Integrating empirical and theoretical approaches to understand life history evolution during range expansion along a latitudinal gradient.

7.4.1 Development as a function of temperature

The development of juvenile spider mites depends on the local temperature and lasts about seven days under optimal conditions [±28°C (Sabelis 1981). We calculated this effect of temperature on the daily progress in development (E), using data by Sabelis (1981). Our calculations were based on formulas developed by Logan et al. (1976) and Lactin et al. (1995), and used by Bancroft & Margolies (1999) to determine how well development is progressing under certain temperatures (*e.g.* E=1 is an optimal development; E=0.5 is 50% slower). E was calculated as:

$$E = \beta\left(e^{(\rho T_{cur})} - e^{\rho(T_{opt}-(T_{max}-T_{cur}))/(T_{opt}/T_{max})} + \lambda\right)$$

Where β (0 -1) is used to scale the development rate; ρ is the constant growth multiplier below the optimal temperature; Tmax is the maximum temperature at which development can take place (38.1°C); Tcur is the local ambient temperature; Topt is the optimal temperature for development (28.17°C); and λ (-1.74) allows the curve to intersect the abscissa at suboptimal temperatures (Bancroft and Margolies 1999). Each day, the daily progress in juvenile development (E) is calculated and added to the value so far (*i.e.* the sum of all E-values of the previous days). When this summed E-value surpasses 7 (e.g. after seven days under optimal conditions), the individual becomes an adult.

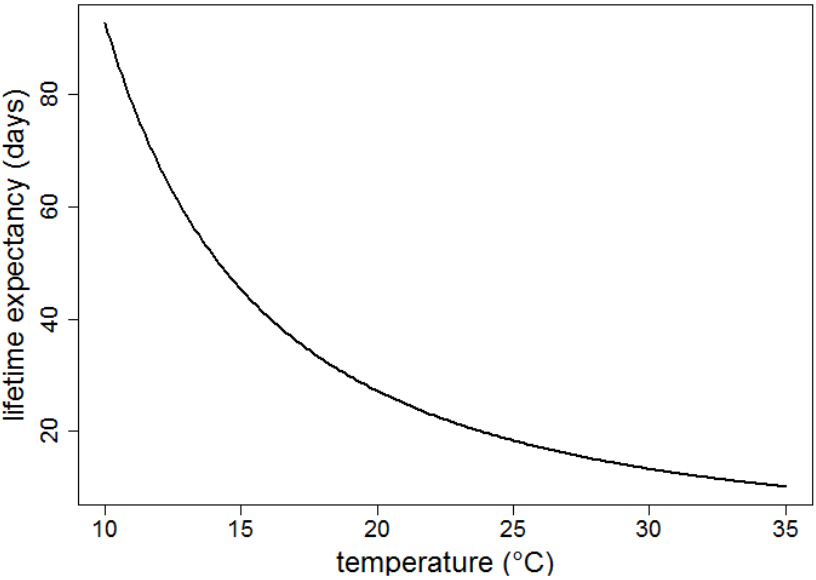


Appendix Figure 12: development as a function of temperature.

7.4.2 Longevity as a function of temperature

Using the data from Sabelis (1981), we calculated the lifetime expectancy for an adult mite (N_{days}). The fit between these data and our predicted values was high ($R^2 = 0.9779$):

$$N_{days} = 5459.7 {T_{cur}}^{-1.77}$$



Appendix Figure 13: Expected longevity as a function of temperature.

7.4.3 *Juvenile and adult mortality as a function of temperature.*

To assess mortality caused by suboptimal temperatures (a mortality additional to the mortality due to age), we fitted nonlinear functions to the data from Sabelis (1981). We did this for both juveniles and adults.

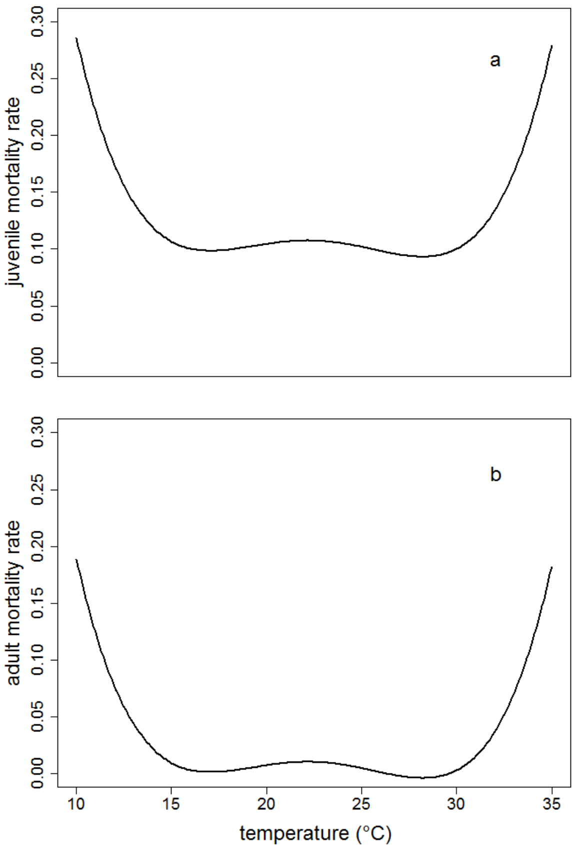
Juvenile temperature-dependent mortality function (fit between used data and our predicted values: $R^2 = 0.9996$):

$$M = 2.781464 - 0.508014T_{cur} + 0.035370{T_{cur}}^2 - 0.001072{T_{cur}}^3 + 0.000012{T_{cur}}^4$$

Adult temperature-dependent mortality function (fit between used data and our predicted values: $R^2 = 0.9996$):

$$M = 2.684464 - 0.508014T_{cur} + 0.035370{T_{cur}}^2 - 0.001072{T_{cur}}^3 + 0.000012{T_{cur}}^4$$

To calculate the daily probability of a temperature-induced death, we divided the mortalities for each stage (juvenile or adult, *cfr*. calculations above) by the presumed length of that stage given the current local temperature.



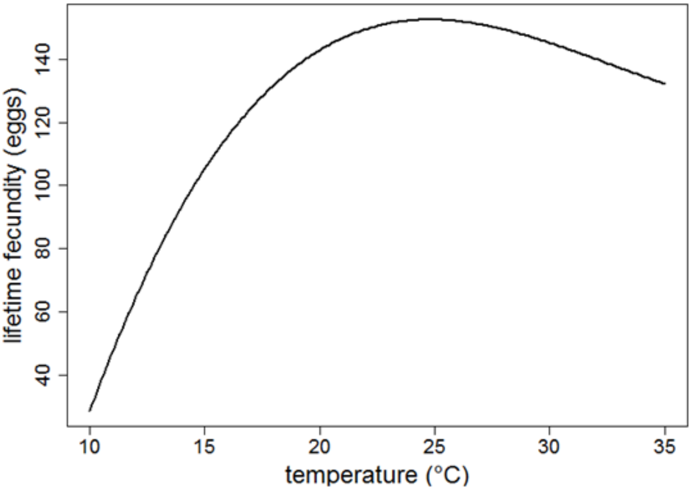
Appendix Figure 14: Juvenile (a) and adult (b) mortality rate as a function of temperature. Note that adults also have an age-dependent mortality factor, and that longevity in turn depends on temperature (see Appendix Figure 13).

7.4.4 Fecundity as a function of temperature

We estimated the (potential) number of eggs produced during a mite's lifetime (N_e), depending on the current local temperature. The calculations were performed using data from Sabelis (1981).The fit between these data and our predicted values was high ($R^2 = 0.9777$).

$$N_e = -287.52 + 44.68T_{cur} - 1.4563{T_{cur}}^2 + 0.0149{T_{cur}}^3$$

To calculate the daily fecundity, we divided this lifetime fecundity by the expected longevity of the mite (which both depend on the local temperature).



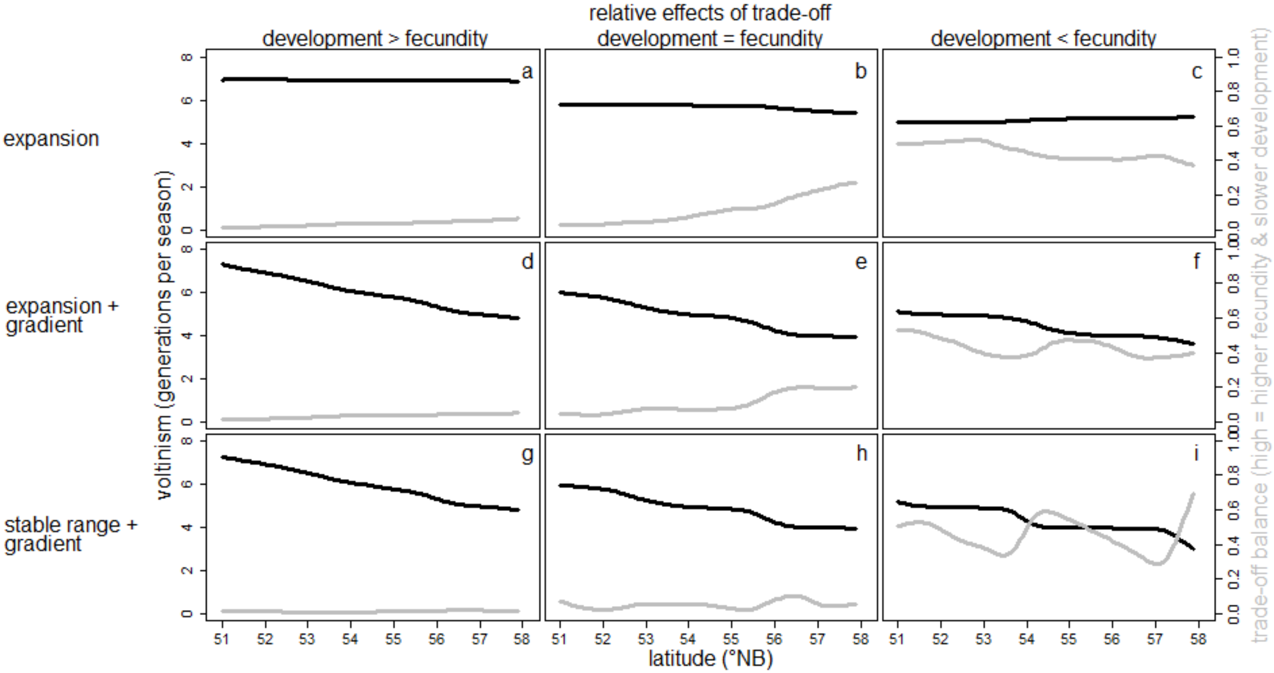
Appendix Figure 15: Expected lifetime fecundity as a function of temperature

7.4.5 Sensitivity analysis trade-off fecundity vs. development

We tested nine different settings for the trade-off between development time and fecundity by varying the maximal costs and benefits for either trait (all combinations of 10, 20, and 50%). From this sensitivity analysis (see Appendix Table 1) we picked a smaller subset of models to explore visually and discuss in more detail (see Appendix Figure 16, grey lines). The variation in the trade-off balance had important consequences, as the preference of mites to invest in either a faster development or a higher fecundity greatly depends on this trade-off. In the first visually explored trade-off setting (Appendix Figure 16: a, d, g), the trade-off could maximally induce a 50% increase/decrease in the development speed at the cost/benefit of a 20% decrease/increase in fecundity. (In other words, a trade-off balance value of zero would result in 150% development speed and 80% fecundity, while a trade-off value of 1 would decrease development speed to 50% and increase fecundity to 120%. A trade-off value of 0.5 would leave both traits at 100%.) With this setting, mites evolved a rather uniform strategy over the whole latitudinal range: a near maximal investment in development in all scenarios. Logically, this investment in a faster development resulted in a higher voltinism compared to the other two trade-off settings. In the second visually explored trade-off setting (Appendix Figure 16: b, e, h), the costs and benefits of the trade-off were identical for both traits; both maximally increasing or decreasing 20%. This resulted in different patterns for the different scenarios. Although mites prefered investing in development rather than fecundity (trade-off balance <0.5) in all scenarios, there was an increasing investment in fecundity in the scenario with solely range expansion whereas this was not the case in the stable range scenario (the scenario with expansion along a gradient laid somewhere in between). In the third visually explored trade-off setting (Appendix Figure 16: c, f, i), a maximal increase/decrease of 50% in fecundity came with the cost/benefit of a 20% slower/faster development. Under this setting, we got the lowest number of generations per season due to a reduced investment in development. In the stable range scenario, we here observed a saw-tooth pattern in the trade-off balance, completely in synchrony with the step-wise decrease in voltinism from south to north. In contrast, there was a small and almost steady decrease in the trade-off balance (*i.e.* faster development) from south to north in the scenario with solely range expansion. Again, the scenario with expansion along a gradient was situated somewhere in between.

Model settings				Fitting analysis results (% best fit)					
Gradient present	Max. % develop. time trade-off effect	Max. % fecundity trade-off effect	Range dynamics	Dispersal	Fecundity	Develop. time	Wavelength develop. time	Amplitude develop. time	Average
Yes	10	50	Expansion	2.98	31.77	7.06	3.49	12.8	11.62
Yes	10	20	Stable	0	0.42	9.41	26.78	17.58	10.838
Yes	20	50	Stable	0	9.48	27.44	14.3	1.3	10.504
Yes	20	50	Expansion	4.15	24.03	9.84	8.26	5.08	10.272
Yes	10	50	Stable	0	0.35	1.13	3.21	41.26	9.19
No	20	50	Expansion	9.32	18.22	2.02	2.42	5.11	7.418
No	10	20	Expansion	6.88	4.16	7.39	3.2	4.8	5.286
No	10	50	Expansion	3.98	9.38	10.01	2.47	0	5.168
Yes	10	20	Expansion	2.55	2.07	7.57	5.7	3.86	4.35
No	20	20	Expansion	13.18	0.01	2.34	3.04	0.99	3.912
Yes	50	10	Expansion	10.88	0.02	1.56	5.28	0.94	3.736
No	50	20	Expansion	11.99	0	2.9	2.67	0.81	3.674
No	20	10	Expansion	11.17	0	1.49	2	0.41	3.014
No	10	10	Expansion	9.41	0.02	2.67	2.26	0.58	2.988
Yes	50	20	Expansion	8.27	0.01	2.1	2.95	0.66	2.798
Yes	10	10	Expansion	2.14	0.05	4.41	5.68	1.43	2.742
Yes	20	20	Expansion	3.1	0.01	0.66	6.29	2.39	2.49

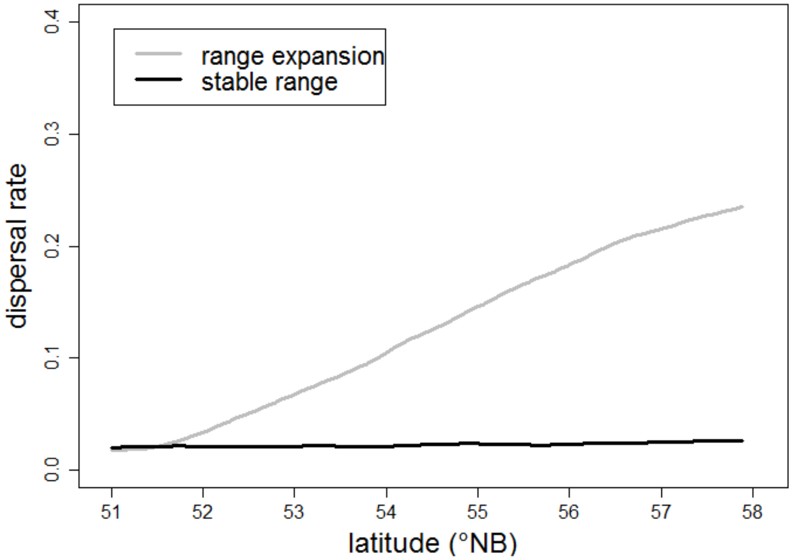
Appendix Table 1: Results of a sensitivity analysis on model settings. Four model parameters were varied (4 left columns) and each parameter combination was simulated 100 times. This resulted in a distribution of outcomes for each evolving variable (5 in total, columns 5-9). The fit of this simulated distribution to the empirical value was compared among different models with different settings. The table above shows the probability (in %) that a model will provide the best estimate for a particular empirical variable. This analysis shows that models with a gradient in latitudinal temperature and a trade-off that has a larger effect on fecundity than development time have the highest overall fit. Only models with a range expansion scenario have a good fit with the empirical dispersal trait. A number of poor performing models were omitted from this table.



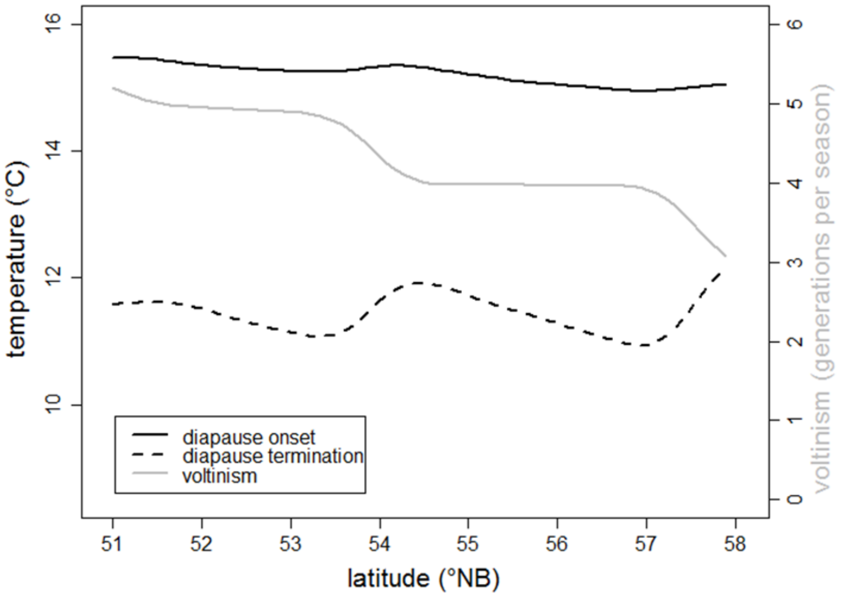
Appendix Figure 16: The number of generations per season (black) and the trade-off balance between fecundity and development (gray) over the latitudinal range for three scenarios (one for a stable range along an environmental gradient, one with range expansion along this environmental gradient and one with range expansion in a homogeneous landscape) and three trade-off settings. The three trade-off settings vary the costs and benefits for development *versus* fecundity. In the left column, the effect on development (*max.* ±50%) is larger than the effect on fecundity (*max.* ±20%). In the central column, both effects are equal (*max.* ±20%). In the right column, the effect on development (*max.* ±20%) is smaller than the effect on fecundity (*max.* ±50%). The trade-off function between both traits is linear. In other words, when the trade-off balance is 0.5, there is no effect on either trait. When the trade-off balance is 1, however, both the positive effect on fecundity and the negative effect on development are maximal (*e.g.* +20% and -50%, respectively, for the left column).

7.4.6 Patterns emerging from the model

Due to a number of assumptions (*e.g.* the strength of the trade-off between development and fecundity –see Appendix Figure 16), we had to simulate a large parameter space. Nonetheless, three consistent (*i.e.* consistent over all the trade-off settings) patterns emerged. The first emerging pattern was the presence of a steep increase in dispersiveness from south to north in both the expansion scenarios, while this increase was absent under the stable range scenario (Appendix Figure 17). The second pattern was a clear decrease in the number of generations per season (voltinism) from south to north (Appendix Figure 16, black lines). The third pattern concerned the temperatures at which mites terminated diapause in spring and entered diapause in autumn. The former temperature consistently evolved to lower values than the latter (Appendix Figure 18). Most probably, this is because eggs laid at the very end of the season will not have the time to mature, while the very first eggs of the season are very important for population growth. Therefore, entering diapause later can be expected to be less advantageous than terminating diapause earlier, resulting in a higher evolutionary pressure on the latter. Under conditions where a clear step-wise decrease in voltinism occurred, a saw-tooth pattern moreover emerged in the temperature at which mites terminated diapause but not in the temperature at which they entered diapause (Appendix Figure 18).

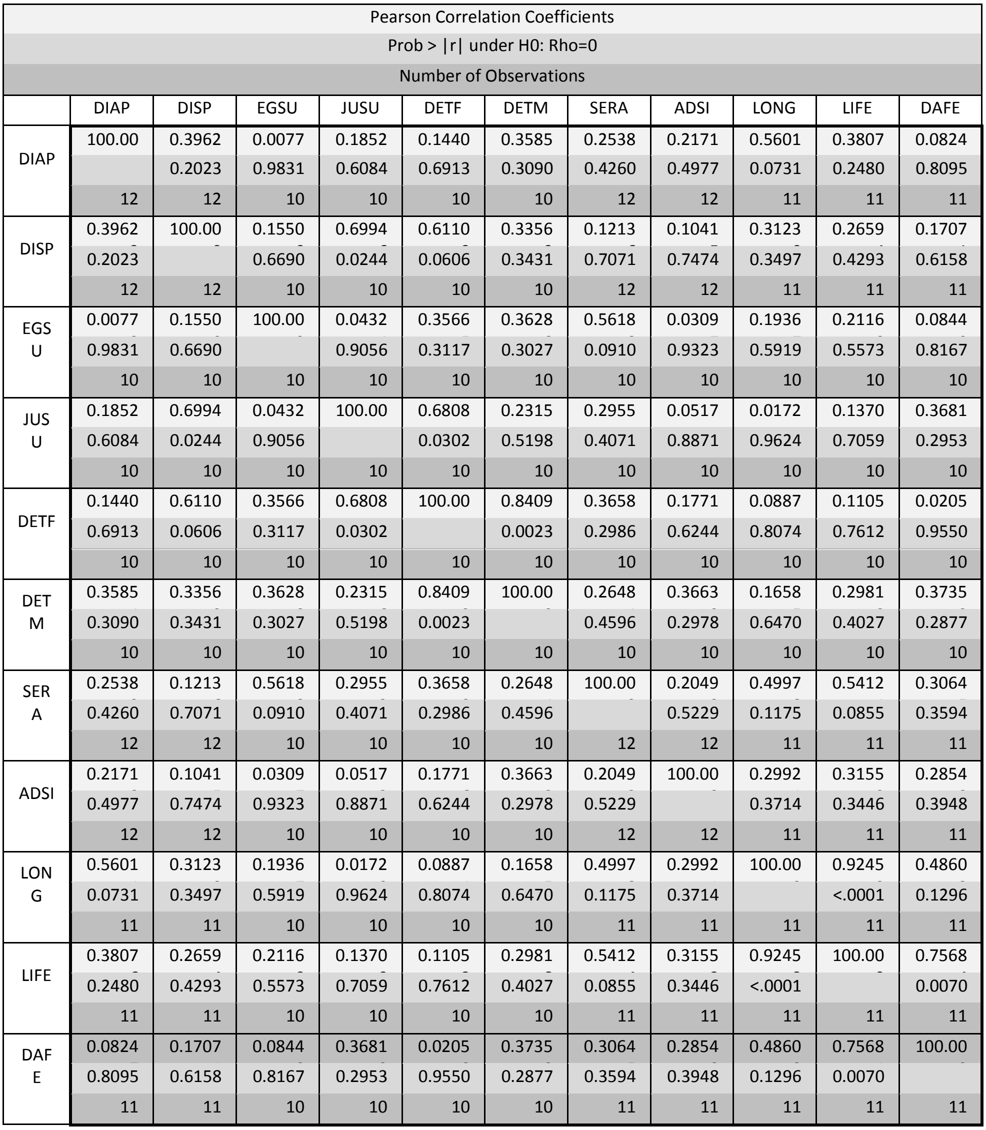


Appendix Figure 17: Evolution of the dispersal rate over the latitudinal range for the model scenarios with range expansion *vs.* the model scenario with a stable range (for a trade-off setting of *max.* 20% development, *max.* 50% fecundity –see Appendix Figure 16: c,e). There is no latitudinal effect on dispersal in the stable range scenario, while there is a clear increase in dispersal for the range expansion scenarios.



Appendix Figure 18: Voltinism (gray line), the temperature of diapause onset (black line), and the temperature of diapause termination (dashed black line) over the latitudinal range (here only shown for a stable range scenario with a trade-off setting of *max.* 20% development, *max.* 50% fecundity –see Appendix Figure 16: c,e). The temperature to terminate diapause is always lower than the temperature to enter diapause. Furthermore, a saw-tooth pattern emerges in the temperature of diapause termination –in synchrony with the step-wise decrease in voltinism.

Appendix Table 2: Pairwise correlations between all the life-history traits: DIAP (diapause), DISP (dispersal), EGSU (egg survival), JUSU (juvenile survival), DETF (development time for females), DETM (development time for males), SERA (sex ratio), ADSI (adult size), LONG (longevity), LIFE (lifetime fecundity) and DAFE (daily fecundity). All (marginally) significant correlations are in bold. Only the positive correlation between longevity and lifetime fecundity, however, remained after performing a Bonferroni correction.

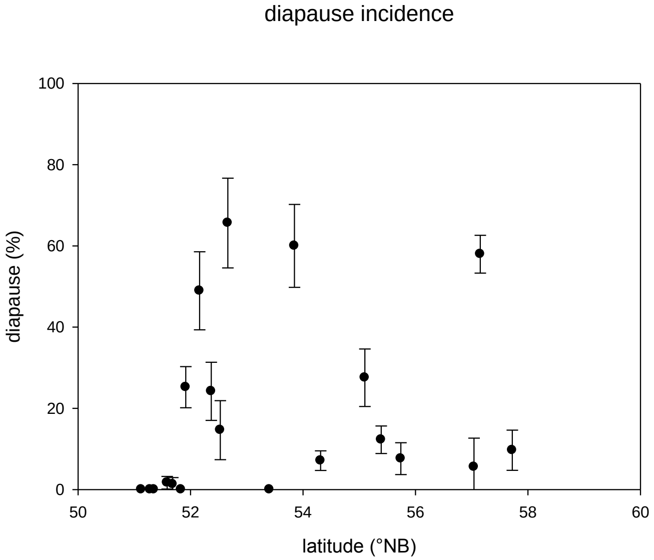


Pearson Correlation Coefficients

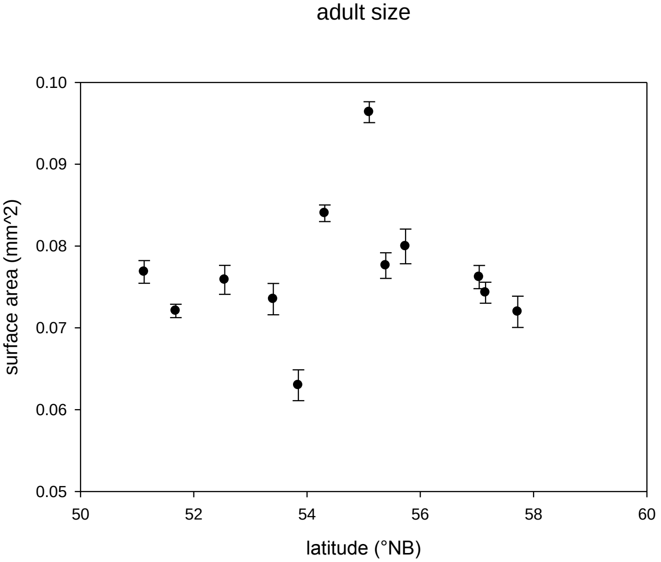
Prob > |r| under H0: Rho=0

Number of Observations

	DIAP	DISP	EGSU	JUSU	DETF	DETM	SERA	ADSI	LONG	LIFE	DAFE
DIAP	100.00	0.3962	0.0077	0.1852	0.1440	0.3585	0.2538	0.2171	0.5601	0.3807	0.0824
		0.2023	0.9831	0.6084	0.6913	0.3090	0.4260	0.4977	0.0731	0.2480	0.8095
	12	12	10	10	10	10	12	12	11	11	11
DISP	0.3962	100.00	0.1550	0.6994	0.6110	0.3356	0.1213	0.1041	0.3123	0.2659	0.1707
	0.2023		0.6690	0.0244	0.0606	0.3431	0.7071	0.7474	0.3497	0.4293	0.6158
	12	12	10	10	10	10	12	12	11	11	11
EGSU	0.0077	0.1550	100.00	0.0432	0.3566	0.3628	0.5618	0.0309	0.1936	0.2116	0.0844
	0.9831	0.6690		0.9056	0.3117	0.3027	0.0910	0.9323	0.5919	0.5573	0.8167
	10	10	10	10	10	10	10	10	10	10	10
JUSU	0.1852	0.6994	0.0432	100.00	0.6808	0.2315	0.2955	0.0517	0.0172	0.1370	0.3681
	0.6084	0.0244	0.9056		0.0302	0.5198	0.4071	0.8871	0.9624	0.7059	0.2953
	10	10	10	10	10	10	10	10	10	10	10
DETF	0.1440	0.6110	0.3566	0.6808	100.00	0.8409	0.3658	0.1771	0.0887	0.1105	0.0205
	0.6913	0.0606	0.3117	0.0302		0.0023	0.2986	0.6244	0.8074	0.7612	0.9550
	10	10	10	10	10	10	10	10	10	10	10
DETM	0.3585	0.3356	0.3628	0.2315	0.8409	100.00	0.2648	0.3663	0.1658	0.2981	0.3735
	0.3090	0.3431	0.3027	0.5198	0.0023		0.4596	0.2978	0.6470	0.4027	0.2877
	10	10	10	10	10	10	10	10	10	10	10
SERA	0.2538	0.1213	0.5618	0.2955	0.3658	0.2648	100.00	0.2049	0.4997	0.5412	0.3064
	0.4260	0.7071	0.0910	0.4071	0.2986	0.4596		0.5229	0.1175	0.0855	0.3594
	12	12	10	10	10	10	12	12	11	11	11
ADSI	0.2171	0.1041	0.0309	0.0517	0.1771	0.3663	0.2049	100.00	0.2992	0.3155	0.2854
	0.4977	0.7474	0.9323	0.8871	0.6244	0.2978	0.5229		0.3714	0.3446	0.3948
	12	12	10	10	10	10	12	12	11	11	11
LONG	0.5601	0.3123	0.1936	0.0172	0.0887	0.1658	0.4997	0.2992	100.00	0.9245	0.4860
	0.0731	0.3497	0.5919	0.9624	0.8074	0.6470	0.1175	0.3714		<.0001	0.1296
	11	11	10	10	10	10	11	11	11	11	11
LIFE	0.3807	0.2659	0.2116	0.1370	0.1105	0.2981	0.5412	0.3155	0.9245	100.00	0.7568
	0.2480	0.4293	0.5573	0.7059	0.7612	0.4027	0.0855	0.3446	<.0001		0.0070
	11	11	10	10	10	10	11	11	11	11	11
DAFE	0.0824	0.1707	0.0844	0.3681	0.0205	0.3735	0.3064	0.2854	0.4860	0.7568	100.00
	0.8095	0.6158	0.8167	0.2953	0.9550	0.2877	0.3594	0.3948	0.1296	0.0070	
	11	11	10	10	10	10	11	11	11	11	11



Appendix Figure 19: Diapause incidence along a latitudinal gradient. The mean value (averaged over replicates) for diapause incidence is given for each sampled population. Standard errors are represented by bars.



Appendix Figure 20: Adult size along a latitudinal gradient. The mean value (averaged over replicates) for adult size is given for each sampled population. Standard errors are represented by bars.

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Projects not included in this thesis

As (shared*) first author:

Boeye, J., C. Dytham and D. Bonte., (in prep.) The spatial distribution of contributing ancestors during range expansions.

Boeye, J., J. Hillaert* and D. Bonte, (under review) The evolution of thermal performance and dispersal during range shifts

As collaborator (model creator):

Hovestadt et al. (in prep.) Species abundance and the characteristics of spatial patterns in neutral communities.

Van Noorwijck et al. (under review) A multi-generation perspective on functional connectivity for arthropods in fragmented landscapes

De Roissart et al. (in prep.) Eco-evolutionary feedbacks in the spider mite Tetranychus urticae.

Lehouck et al. (in prep.) Direct and indirect effects of habitat loss on seed dispersal and early recruitment of a bird-dispersed tree: a modelling approach.

Master thesis:

Van Damme et al. (submitted) Digit ratios in two lacertid lizards: sexual dimorphism and morphological and physiological correlates.