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The spatial and community-context of ecological specialisation

Bisschop, Karen

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ecological specialisation

The research reported in this thesis was carried out at the Theoretical Research in Evolutionary Life Sciences group (TRÊS), which is part of the Groningen Institute for Evolutionary Life Sciences (GELIFES) of the University of Groningen (The Netherlands), according to the requirements of the Graduate School of Sciences (Faculty of Science and Engineering, University of Groningen), and Terrestrial Ecology Unit (TEREC) of the faculty of Sciences, Ghent University (Belgium).

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Introduction and outline of the thesis

INTRODUCTION

Introduction and outline of the thesis

Our world is amazingly heterogeneous; from open landscapes to closed forests, from lowlands to highlands, and from arid plains to swamps. Different species adapt to these different conditions and perform best in that specific environment. Think about thorny devils that drink by collecting dew with their scaly skin to survive the aridity or llamas that obtain oxygen more easily at high altitudes. But just being adapted to one condition is not enough as the world is also incredibly dynamic, both in space and time. A tree might fall for instance creating an open spot, excessive rain fall can reshape a landscape, but also anthropogenic influences such as deforestation and eutrophication make the system more dynamic. Biotic interactions within and among species are contributing to the complexity, and the interactions with the bacteria inside the organisms are making the struggle to survive even more puzzling. Fitness, or the contribution of an individual to the next generation (Hunt *et al.*, 2004; Hunt & Hodgson, 2010), is strongly subjected to changes in its biotic and abiotic environment. If species are not able to cope with these environmental changes through phenotypic plasticity or by searching for suitable habitat, they are challenged to genetically adapt to these novel conditions to avoid extinction (Case *et al.*, 2005; Turcotte *et al.*, 2011b; Lindsey *et al.*, 2013). This adaptive evolution can give rise to speciation events, which increase biological diversity. As diversity is known to be important for a variety of ecosystem services (Hooper *et al.*, 2005), gaining insight into local adaptation and in the processes influencing it are more important than ever in a world facing global change (Kokko *et al.*, 2017).

EVOLUTION AND ITS CONDITIONS

Charles Darwin described the principle by which each small change is preserved if it is useful as Natural Selection, which was later termed by Herbert Spencer as the 'survival of the fittest' (Darwin, 1859; Spencer, 1864). It needs to be clear that evolution and natural selection are not the same, because evolution can be established by other processes than natural selection, for example genetic drift. Furthermore, natural selection can occur without a subsequent change in allele frequencies, for instance to maintain the current optimal phenotype (Futuyma, 2009).

Any adaptive evolution to novel challenging environmental conditions depends on the level of genetic variation in traits that are responsible for such adaptations, their heritability, and the strength of the selection pressures (Fisher, 1930; Price, 1972; McGuigan & Sgrò, 2009; Poisot *et al.*, 2011). The pre-existing or standing genetic variation is a key factor for local adaptation. This genetic variation is immediately available for selection to act on and beneficial alleles are normally present at higher initial frequencies (Barrett & Schluter, 2008; Olson-Manning *et al.*, 2012). This standing genetic variation is especially important when a small founder population size is considered (Magalhães *et al.*, 2007). Phenotypic evolution might be facilitated

by the pre-existing but cryptic variation that can be expressed at any time if novel or rare environments are encountered. This variation is present in the genome, but invisible in the phenotype under the native circumstances and hence not subject to natural selection (Gibson & Dworkin, 2004; Le Rouzic & Carlborg, 2007; Schlichting, 2008; McGuigan & Sgrò, 2009). Key innovations and some of the major evolutionary events, such as the evolution from unicellular to multicellular organisms, are now anticipated to be linked with cryptic genetic variation (Schlichting, 2008; McGuigan & Sgrò, 2009).

Genetic variation is further shaped by either 'de novo' mutations or by gene flow due to migration and dispersal (Poisot *et al.*, 2011). With a stable mutation rate, the prevalence of de novo mutations within a population will increase with increasing population size (Olson-Manning *et al.*, 2012). Although there are circumstances resulting in higher mutation rates (Burns *et al.*, 2011), mutation rates are in general very low. A certain amount of gene flow is therefore necessary to create a sufficient gene pool (Holt & Gomulkiewicz, 1996) and essential to maintain viable populations under competition or unfavourable conditions (e.g. small populations or marginal habitats) through demographic and genetic rescue (Brown & Kodric-Brown, 1977; Lenormand, 2002; Garant *et al.*, 2007; Blanquart *et al.*, 2012). But, exaggerated gene flow will counteract evolutionary divergence of populations and ongoing adaptation, which is known as a genetic load (Lenormand, 2002; Cuevas *et al.*, 2003; Bolnick & Nosil, 2007). Excessive dispersal can also lead to population sizes above their carrying capacity resulting in a population collapse (Holt & Gomulkiewicz, 1996; Garant *et al.*, 2007). The ideal rate of dispersal depends on the dispersal-selection balance. Intermediate rates from an ancestral population are usually advantageous for adaptation, favouring specialisation over generalists and leading to better exploitation of the resources and, consequently, higher productivity (Venail *et al.*, 2008; Bell & Gonzalez, 2011; Ching *et al.*, 2012; Forester *et al.*, 2016). Although gene flow is thought to prevent adaptation at small spatial scales, evidence has been provided for microgeographic adaptation (Richardson *et al.*, 2014). One possible mechanism is non-random dispersal or isolation by environment, which may enhance rapid evolution (Jeltsch *et al.*, 2013; Wang & Bradburd, 2014; Jacob *et al.*, 2017).

Genetic drift, on the other hand, counteracts the increase in genetic variation by the loss of certain alleles from generation to generation purely by chance, although its impact can be rescinded by, for instance, high levels of dispersal (Allendorf *et al.*, 2013). Genetic drift is thus a stochastic process and occurs in each population, even in very large ones, but large changes in the allele frequencies from one generation to another are more likely in small populations. Hence, also deleterious alleles can more easily increase in small populations purely by chance.

For a long time it was assumed that natural selection was the only mechanism that can create adaptations which are features that improve the survival chance and reproduction of individuals having these characters (Futuyma, 2009). However, in recent decades, epigenetics and microbiomes have put a spanner in the works.

The changes in the function and expression of genes, which are inherited but cannot be explicated by the DNA sequence (e.g. acetylation or methylation) are within the field of epigenetics (Bossdorf *et al.*, 2007). For instance, Bitume and colleagues (2014) discovered in the two-spotted spider mite that dispersal distance of the offspring is impacted by the parental and grandparental density. These parental effects are thus inherited from the parents and can be seen in the phenotype of the offspring, but are invisible in their genotype. This is known as non-genetic inherited information (Danchin *et al.*, 2011).

Species often host an enormously wealthy community of microorganisms, the microbiome, which is known for influencing different processes such as digestion, detoxification, the immune system, kin recognition, reproductive barriers and tissue development (Berendsen *et al.*, 2012; Huttenhower *et al.*, 2012; Brucker & Bordenstein, 2013; David *et al.*, 2014; Kohl *et al.*, 2014; Lizé *et al.*, 2014; Lewis & Lizé, 2015; Kohl & Dearing, 2016). These findings led to the introduction of the concept of hologenomes, where the microbiome and genome are interacting (Bordenstein & Theis, 2015). This idea is however controversial as microbiome assembly is rather complex causing potential evolutionary conflicts between the microorganisms and their hosts (Moran & Sloan, 2015; Shapira, 2016; Macke *et al.*, 2017). Independent of the correctness of the hologenome concept, these host-microbiota interactions are important and might help to get a better insight into evolution (Franchini *et al.*, 2014). Indeed microorganisms can provide an additional layer of genetic variation and potentially extend the niche width of their host (Zilber-Rosenberg & Rosenberg, 2008).

Advantageous traits can sometimes have side-effects which are maladaptive under at least some circumstances; this is a cost of adaptation (Futuyma, 2009). Selection might decrease the genetic variation in a population, and hence the potential to diversify into other niches (Buckling *et al.*, 2003). A weak selection pressure might be beneficial for maintaining variation, which is for instance experienced during an invasion process where a species escapes its original competitors and predators. The loss of variation also depends on the type of selection; directional and stabilising selection might decrease variation, while this is not the case for disruptive selection (Pélabon *et al.*, 2010)

i. Spatial Context

Local adaptation depends on the spatial grain of gene flow, hence spatial context; landscapes differ for instance in their degree of heterogeneity, habitat types, and connectivity. Species reaching novel environments through range expansion or invasion usually encounter different conditions than those in their ancestral range. Rapid adaptation will then depend on the number of founders and the strength of the local environmental filter, which together determine the chance to leave the old environment and reach and establish in the new environment (Renault *et al.*, 2017; Szűcs *et al.*, 2017).

As mentioned above, in marginal habitats dispersal might help establishment by creating source-sink dynamics (Kawecki, 2000, 2008; Kawecki & Ebert, 2004), where populations with a negative growth rate are sustained by individuals coming from a nearby population with a positive growth rate. The number, size, and connectedness of habitats strongly influence adaptation through dispersal and drift effects (Fahrig, 2002; Legrand *et al.*, 2017; Bonte *et al.*, 2018). This ecological (demographic) rescue due to restocking of sink populations can only make the sink population viable again if it is complemented with evolutionary (genetic) rescue (Brown & Kodric-Brown, 1977; Carlson *et al.*, 2014; Fitzpatrick *et al.*, 2016). Fitzpatrick and colleagues (2016) found evidence in Trinidadian guppies that even low numbers of immigrants could secure marginal populations via demographic and genetic rescue. Sinks can provide evolutionary stepping stones and hence secure persistence by maintaining connectivity in metapopulations (Furrer & Pasinelli, 2016). Individuals can also end up in a marginal habitat through a competition-colonisation trade-off, where inferior competitors are better suited for colonisation (Calcagno *et al.*, 2006; Bonte *et al.*, 2014). This results in equalising fitness in the metapopulation and hence promoting regional coexistence (Jeltsch *et al.*, 2013; Furrer & Pasinelli, 2016). Evolutionary stepping stones can also be created from less preferred habitat towards harsh environments or extreme stressors. This is especially the case if the former habitat supports genotypes well-suited for multiple environments (Parsons, 1990; Ketola *et al.*, 2013). If the environmental stressor runs along a gradient, for instance a salt gradient, local dispersal can also assist adaptation to extreme environments (Bell & Gonzalez, 2011).

ii. Community context

The adaptation of species to novel environments can depend on the community context because of biotic interactions (Johansson, 2007; De Mazancourt *et al.*, 2008; Lawrence *et al.*, 2012; Urban *et al.*, 2012; De Meester *et al.*, 2016). The idea of co-evolution between multiple species gave rise to the Red Queen hypothesis proposed by Van Valen (1973). He stated that organisms always have to run, and thus evolve, because its competitors, parasites, and predators are doing the same. This means that if some organisms are adapting to a changing environment and thereby increase their fitness, others will have to adapt to avoid being outcompeted and going extinct. For that reason, a species can be limited not only by the abiotic environment, but also by the ensemble of species interactions (e.g. competitors, mutualists, and predators). Interestingly, even the level of phylogenetic relatedness can have an impact on adaptation (Case *et al.*, 2005).

Different interactions exist among competing species (Raven & Johnson, 2002), and their influence on adaptation is to a large extent unpredictable (Rice & Knapp, 2008; Zhao *et al.*, 2018). First, where the species are found (the realized niche) is usually only part of where they are able to live in (fundamental niche) due to interspecific interactions. A classic example is the study of two species of barnacles on the rocks of the coast of Scotland, in which *Chthamalus stellatus* had a much smaller realized niche

due to the competition of *Semibalanus balanoides* (Connell, 1961). Second, it is impossible for two species to occupy the same niche indefinitely when resources are limiting, without one going extinct; a concept summed in the competitive exclusion principle of Gause (Gause, 1934; Hardin, 1960). Co-existence might occur if the species' niches do not overlap too much. However, it was found that inferior competitors are still able to coexist for many generations (Holmes & Wilson, 1998; Huisman & Weissing, 1999; Lankau, 2011). Third, sympatric species can divide the existing resources and specialise in a genetic or plastic way, which is referred to as resource partitioning (Amarasekare, 2003; Jeltsch *et al.*, 2013). If this is by means of local adaptation to avoid direct competition, it is often denoted as competition-driven character displacement for which the Darwin finches are a classic example. These different ways of interactions are not independent and might occur at the same time (Raven & Johnson, 2002).

Competition can induce several possible scenarios in case resources are limited, resulting in a positive or negative effect depending on the conditions (Johansson, 2007; Urban *et al.*, 2012; Osmond & de Mazancourt, 2013). On the one hand, competitors might accelerate the adaptive process to an abiotic stressor due to a stronger selection pressure as seen in adaptive radiations (Schluter, 1994). Furthermore, competition can even push species towards niches that are initially not used by them, which is an interesting example of character displacement, seen in the Darwin finches or Myzomelid honeyeaters (Diamond *et al.*, 1989; Reznick & Ghalambor, 2001). On the other hand, competition can decrease effective population sizes, which may increase genetic drift effects. As a consequence, the evolutionary potential will be reduced, resulting in higher extinction risks (Johansson, 2007; Lawrence *et al.*, 2012; Osmond & de Mazancourt, 2013; Zhao *et al.*, 2018). Also, it can be harder to track changes in the environment and hence fitness optima due to competition, creating a slowdown in adaptation (Johansson, 2007).

Recently, there has been increased attention to indirect interactions, such as indirect competition (Walsh, 2013), which can be caused by induced effects. Indirect competition occurs when a third species or another link in the ecosystem has an impact on the competition between two other species (Walsh, 2013). Many indirect interactions are for instance seen after a herbivore attack (Zhang *et al.*, 2009; Kant *et al.*, 2015). An example is provided by Sarmiento and colleagues (2011). They observed a lower oviposition rate of a mite herbivore on plants that were previously attacked by a congeneric species, due to the up-regulation of the plant defence. Alternatively, species in a community can alter the environment experienced by other species (e.g. the use of waste products), which could possibly lead to ecological specialisation (Poisot *et al.*, 2011; Lawrence *et al.*, 2012; Turcotte *et al.*, 2012). For instance, host plant specialisation is known to be a widespread phenomenon, due to the arms races between plants and herbivores (Bonte *et al.*, 2010).

The phylogenetic relatedness of a focal species to another species in a community is hypothesised to impact the rate of local adaptation. A higher level of competition is expected between closely related species because they possess similar niches and are hence more ecologically similar, which is called the competition-relatedness hypothesis (Darwin, 1859; Burns & Strauss, 2011; Violle *et al.*, 2011). However, empirical evidence for this hypothesis is not univocal. Bennett and colleagues (2013) stated that competition is not affected by relatedness. Other researchers found an even stronger competitive-exclusion pattern between more unrelated species pairs (Beaudrot *et al.*, 2013). A possible explanation might be convergent evolution experienced by some species, for instance similar adaptations for feeding ecology.

Local adaptation is not only affected by competition between individuals from different species, but also between individuals from the same species; intraspecific competition. This is considered to have a major influence on selection, and hence evolution, because a larger niche overlap is expected than under interspecific competition (Bolnick, 2001; Silvertown, 2004; Svanbäck & Bolnick, 2007). Effects of intraspecific competition are particularly strong in communities experiencing strong indirect interactions (Des Roches *et al.*, 2018). Indirect interactions are interactions where two species do not directly influence each other, but through another species. Apparent competition where one species is predating on two preys, as such the abundance of one prey will affect the other prey (Holt, 1984)

iii. Determinism or chance

The relative contribution of selection, genetic drift, and mutation will affect the predictability of adaptive evolution. This is affected by several factors that may influence each other: the effective population size, the strength of selection and the initial allele frequency (Olson-Manning *et al.*, 2012). The ideal or effective population size (Charlesworth, 2009) is the population size of those individuals contributing to the next generation. The smaller the effective population size, the higher the importance of random genetic drift, which will decrease the predictability. Second, the strength of selection is the magnitude of the advantageous effect of a certain allele. The larger the selection strength, the more predictable the system's behaviour is. Third, the initial allele frequency elucidates the importance of gene flow and migration (Olson-Manning *et al.*, 2012). If the beneficial allele is already available at a high frequency in the population, the predictability of adaptive evolution increases.

Processes that seem to repeat themselves in time or at different locations are thought to be the result of determinism, for instance convergent evolution. A nice example of convergent evolution are the colour polymorphisms of spiders from the genus *Selkirkiella* (Cotoras *et al.*, 2016). The authors assume that the parallels in colour morphs between different species are caused by similarity in their niches. By contrast, non-convergent patterns are thought to be the outcome of chance and contingency (Young *et al.*, 2009). The arrival time of species in certain communities can have an impact on the interspecific relations, known as historical contingency (Fukami, 2015).

The priority effects, or the magnitude of such historical contingency, strongly differ among species and environments (Vannette & Fukami, 2014). For instance, the time of arrival could possibly explain why some populations experience radiation, whereas others from the same clade are not capable to achieve this under seemingly similar conditions (Seehausen, 2007). These priority effects could play a role at the population level but also at the level of the community. Furthermore, also early or non-persisting interactions by so-called ghost species can affect current or future dynamics (Law & Daniel Morton, 1996; Miller *et al.*, 2009; Hawkes & Keitt, 2015; Mallon *et al.*, 2018) because they can modify the habitat or induce evolutionary changes for extant species.

ECO-EVOLUTIONARY DYNAMICS

The importance of reciprocal feedbacks between evolution and ecology at contemporary timescales is well-appreciated (Saccheri & Hanski, 2006; Fussmann *et al.*, 2007; Kokko & López-Sepulcre, 2007; Ferriere & Legendre, 2013; Hendry, 2016, 2019; Govaert *et al.*, 2019). Evolution is usually faster and more predictable in the short term than in the long term, which conforms to Simpson's principle of adaptive zones; evolution bounces back and forth in an adaptive zone with large phenotypic shifts occurring only sporadically (Hendry, 2016).

Ecological speciation provides a setting for eco-evolutionary feedbacks, as speciation is driven by ecological differences (eco-to-evo) and speciation events will have ecological consequences (evo-to-eco) (Hendry, 2016). We can hence expect the ecological context to set the scene for both the evolutionary dynamics and its feedback on the ecological context and demography (Govaert *et al.*, 2019; Hendry, 2019). It is obvious that adaptation influences births and deaths, and hence population demography (Pelletier *et al.*, 2007; Schoener, 2011) and many examples of evo-to-eco dynamics are found in predator-prey systems (Yoshida *et al.*, 2003; Hairston Jr. *et al.*, 2005; Becks *et al.*, 2010, 2012; Hiltunen & Becks, 2014; Hiltunen *et al.*, 2014). Finding evidence of these dynamics in more natural situations is, however, not straightforward (Schoener, 2011), because environments are dynamic themselves and change continuously (Kokko *et al.*, 2017; De Meester *et al.*, 2019).

EXPERIMENTAL EVOLUTION WITH MODEL ORGANISMS

Experimental evolution is a research study that follows the evolution of certain populations across generations. This is a great tool to discover the association between adaptation patterns and evolutionary processes, because the initial state and the novel conditions of the populations are known and the ecological and evolutionary dynamics can be monitored in time in multiple replicates (Belliere *et al.*, 2010). Model species can be used for experimental evolution. These are commonly studied species that have several characteristics in common: they are easy to breed and to maintain in a laboratory and have short generation times. Also, they often have relatively small genomes which is advantageous (Grbić *et al.*, 2007) for genomic

analyses. However, caution for generalisations is necessary as the line between model systems and nature can be more blurry than often admitted (Stewart *et al.*, 2013; Zuk & Travisano, 2018; Hendry, 2019).

In this thesis, three species of spider mites or Tetranychidae (Arachnida, Acari) are considered as model organisms: *Tetranychus urticae* Koch, 1836 (Fig. 1), *T. evansi* Baker and Pritchard, 1960, and *T. ludeni* Zacher, 1913 (Table 1). They are aboveground herbivores feeding on the cell content of plants. Different stages determine the life cycle of these spider mites (hemimetabolous); these are egg, larva, quiescent larva or protochrysalis, protonymph, quiescent protonymph or deutochrysalis, deutonymph, quiescent deutonymph or teleiochrysalis, and the adult stages (Raworth *et al.*, 2001; Zhang, 2003; Oku, 2014). These haplodiploid arthropods can reproduce by means of parthenogenesis, meaning that unfertilized eggs develop into haploid males (Zhang, 2003; Kaimal & Ramani, 2011; Clemente *et al.*, 2018). Fertilized eggs develop into diploid females (Macke *et al.*, 2011).

Especially the two-spotted spider mite or *T. urticae* is known to respond very fast, mostly within fifteen generations, at a certain selection pressure due to a high standing genetic variation and hence it is a good candidate species for experimental evolution (Gould, 1979; Fry, 1989; Agrawal, 2000; Egas & Sabelis, 2001; Magalhães *et al.*, 2007, 2009; Kant *et al.*, 2008; Bonte *et al.*, 2010; Bitume *et al.*, 2014). Also, most studies do not show adaptation costs; even if mites adapt, they still perform well on the ancestral host (Van Leeuwen *et al.* 2008, Magalhães *et al.* 2009, Tien *et al.* 2010; but see Gould 1979, Fry 1989, Agrawal 2000).

Figure 1: *Tetranychus urticae* (left) and *T. ludeni* (right) (Pictures: Karen Bisschop)

Tetranychus sp. are known to both upregulate and downregulate plant defenses, which could influence other herbivores on the shared host plant (Sarmiento *et al.*, 2011a; b; Godinho *et al.*, 2016). Also, evidence for reproductive interference among our species has been found (Sato *et al.*, 2014; Clemente *et al.*, 2018).

	<i>T. urticae</i>	<i>T. evansi</i>	<i>T. ludeni</i>
Common name	Two-spotted spider mite	Tomato red spider mite	Red-legged spider mite
Appearance	yellowish-greenish with two black spots	Orange to dark red	Dark red with dark red legs
Body size (adult ♀)	0.4 – 0.5 mm	0.5 – 0.6 mm	N.A.
Daily fecundity	1 – 12 eggs	10.6 – 13.4 eggs	1 – 11 eggs
Oviposition peak	7 th day	4 th day	Between 6 th and 9 th day
Generation time (depends on temp. and host plant)	Between 11 and 15 days	Between 6.3 and 13.6 days	About 10 days
Host species	Extremely polymorphic, >1100 plant species	Specialist on Solanaceae, but also found on 37 other families	Bean, eggplant, hibiscus, potato, pumpkin and other Cucurbitaceae
Distribution	Cosmopolitan; develops above 12°C; optimal temperature 30-32°C	Subtropical; tolerant for drought and heat	(Sub)tropics; only develop above 14.7°C
Operational sex ratio	Female-biased, 2:1 to 3:1	Female-biased, 4:1	N.A.
Literature	(Fry, 1989; Navajas, 1998; Hance & Van Impe, 1999; Agrawal, 2000; Raworth <i>et al.</i> , 2001; Zhang, 2003; Grbić <i>et al.</i> , 2007, 2011; Kaimal & Ramani, 2011; Macke <i>et al.</i> , 2012; Oku, 2014)	(Bonato, 1999; Zhang, 2003; Kaimal & Ramani, 2011; Meynard <i>et al.</i> , 2013; Navajas <i>et al.</i> , 2013)	(Zhang, 2003; Adango <i>et al.</i> , 2006; Kaimal & Ramani, 2011)

Table 1: Overview of the three model species *Tetranychus urticae*, *T. evansi* and *T. ludeni*

THESIS OUTLINE

INTRO

Several questions concerning both the spatial- and the community-context of ecological specialisation are addressed in this thesis. Below I give an overview of the different chapters and the main objectives and goals.

The main topic of the first chapter is how different rates of dispersal and the presence of a competing specialist species affect the rate of local adaptation in a generalist arthropod herbivore, *T. urticae*. We discovered that high dispersal from an ancestral population towards a novel challenging environment was detrimental for local adaptation due to genetic load. However, under interspecific competition a higher number of immigrants was necessary as the competitor reduced population sizes and increased extinction risks, so the negative effect of high dispersal was counteracted under the competition scenario. The joint influence of dispersal and competition on adaptation has never been experimentally investigated before. Our results illustrate the importance of combining the community context with landscape connectivity for gaining insight into the process of local adaptation.

Adaptive evolution to a novel host plant can result in a higher food uptake or a more efficient resource consumption. Both outcomes create changes in population demography and will therefore be an example of evo-to-eco dynamics. In chapter two we use empirical data of *T. urticae* to test this hypothesis with a discrete-time model of population dynamics similar to the Ricker model. Our work shows a clear effect of adaptation on the population's carrying capacity and the intrinsic growth rate. We suggest that adaptation has led to an increased food uptake where the surplus acquired energy can be allocated to population growth.

The third chapter deals with performance in a novel environment subject to early selection pressures, such as ghost competition. The interspecific competitor was outcompeted by the focal species, *T. urticae*, after about four generations, which gave us the opportunity to show a lasting evolutionary signal of ghost competition. We

found a significantly positive interaction between oviposition rates of the superior species and the initial densities of the ghost competitor. The correlation was independent of time and hence still visible even after 25 generations. This emphasises the value of unsuccessful ghost competition on long-term performance.

In the fourth chapter, I present results from an evolutionary experiment investigating local adaptation influenced by interspecific competition and a homogeneous or heterogeneous landscape consisting of a challenging and/or a more benign but still suboptimal environment. The competitor went extinct soon after the start of the experiment, but it had a long-term negative effect on the performance of the focal species, *T. urticae*. We demonstrate that a heterogeneous environment can facilitate adaptation to a harsh environment by providing an evolutionary stepping stone. However, this adaptation was only temporary. When the populations on the more benign environment expanded, a large spill-over from these populations to the harsh environment was generated, and hence a genetic load. Our study highlights that adaptation in heterogeneous landscapes strongly depends on the nature of source-sink dynamics.

Microbiomes are engaged in all kind of processes, such as immunity, detoxification, and digestion. They thus affect the fitness of their eukaryotic host and can be involved in local adaptation to novel host plants, which is the topic of chapter five. The microbiome is created through vertical (from parent to offspring) and horizontal (from the environment) transfer of bacteria. For adaptive evolution, heritability is a necessary component. In this study, we created strains of *T. urticae* and transferred them to their initial host plant and two novel hosts. Fecundity and longevity were measured during adaptation to the novel host plants and after about twelve generations the microbiome was assessed through 16S rRNA sequencing. We found that ancestry was a key element for microbiome composition, indicating its potential for selection. Furthermore, the level of specialisation or generalisation of the host was a significant explanatory variable of the microbiome. Although only little of the microbiome variation was explained in this study, the results point out the importance of taking the bacterial community within hosts into account for local adaptation.

Triggered by the results of the previous chapter, I was interested in the role of the microbiome in the field (chapter six). More precisely, we investigated the interactions between host communities, diet, and microbiomes. To answer this, we had the opportunity to test this using microsnails on limestone outcrops as a model. We found no or at most a weak negative correlation between the host communities and their diet. By contrast, the microbiome correlated positively with both the hosts and their diets. Also, environmental factors such as the habitat size, the presence of caves, and especially anthropogenic activity affected those correlations between communities.

All chapters are jointly discussed in the final synthesis of the thesis, including some final remarks and general conclusions.