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Evolution of ecological specialisation under competition.

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CONTENTS

1. INTRODUCTION

Our world experiences increasing environmental changes at different scales in space and time. In order to cope with these changes, organisms are continuously challenged to adapt to these novel conditions. This process of adaptive evolution is referred to as ecological specialisation (Futuyma & Moreno, 1988). For instance, niche evolution towards changing abiotic conditions, but also towards biotic conditions (Turcotte et al., 2011; Case et al., 2005). Such ecological specialisation can give rise to speciation, which creates biological diversity, in turn being a major driver of a variety of ecosystem services (Hooper et al., 2005). The conservation of biodiversity at the species and genetic level is therefore nowadays, in a world facing global change, more important than ever.

However, to disentangle the evolutionary base of biodiversity, the distinction between the effect of chance and historical coincidence from deterministic events is not completely resolved (Seehausen, 2007). The arrival time of species in certain communities can have an impact on the interspecific relations, known as historical contingency. The priority effects or the magnitude of such historical contingency differ strongly among species and environments (Vannette & Fukami, 2014). For instance, this could possibly explain the fact that some populations can experience radiation, whereas others from the same clade are not capable to achieve this under seemingly the same conditions (Seehausen, 2007). Further, it is expected that convergent patterns are the result of determinism and non-convergent patterns the outcome of chance and contingency, although, Young and others (2009) found that non-convergent patterns may disguise others.

Any adaptive evolution towards novel 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 (Poisot et al., 2011; McGuigan & Sgro, 2009). Genetic variation can be maintained by either ‘de novo’ **mutations** or by migration, such as **gene flow and dispersal** (Poisot et al., 2011). These processes have an impact on the species’ complete genome. Mutations are more common, if big population sizes are considered. For instance, during an extreme demographic context, such as a biological invasion, rapid growth of the population after arriving in new environments with pauperized biological communities is expected, due to the enemy release (less competitors, predators or parasites) in the novel environment, which results in a higher mutation rate (Burns et al., 2011). On the other hand, **genetic drift** counteracts the increase in genetic variation by the loss of certain alleles purely by chance, but its impact can be rescinded by, for instance, high levels of dispersal.

Moreover, the pre-existing or **standing genetic variation**, including recessive rare alleles, is also a key factor for local adaptation. This way to adapt to novel environments is likely to be faster than by mutations, as the variation is immediately and at a higher initial frequency available (Barrett & Schluter, 2007). This makes it more plausible to become fixed in the population and less likely to become lost (Olson-Manning et al., 2012). Besides, as this variation is older, it was previously tested by selection and went through a kind of 'selective filter' (Barrett & Schluter, 2007). Therefore, the standing genetic variation is especially important when a small founder population size is considered in a short time frame (Magalhães et al., 2007). Also, a release of variation that is invisible under the native circumstances, referred to as **cryptic genetic variation**, can occur under new environmental conditions, which can be an important source of local adaptation (McGuigan & Sgro, 2009; Le Rouzic & Carlborg, 2007; Gibson & Dworkin, 2004).

The process of **selection**, which has a more regulated genomic impact than the previous processes, will then act on the existing variation, supposing that certain genotypes are better adapted to the novel environmental conditions. In this case, the individuals having these genotypes possess a higher fitness, i.e. the contribution of their genotype to the next generation compared with the other population members' genotypes (Lawrence, 2008). Since, selection decreases the genetic variation in a population, a weak selection pressure, as for instance experienced during an invasion process, can increase the genetic variation and therefore the frequency of potential beneficial alleles for local adaptation (Pennings & Hermisson, 2006).

The relative importance of selection, genetic drift and mutation is affected by several factors. First, the ideal or **effective population size N_e** matters. The smaller the effective population size, the higher the importance of random genetic drift. In addition, with a stable mutation rate, the prevalence of de novo mutation within a population will logically increase with increasing population size (Olson-Manning et al., 2012). The effective population size will, however, also be impacted by the level of genotypic heterogeneity within the population. When some individuals possess a higher fitness, the effective population size will be lower, since not all the individuals contribute the same to the next generation.

Second, the **strength of selection** is important for local adaptation, which is the magnitude of the advantageous effect of a certain allele. Two models, the infinitesimal model and the major gene model, denote the extremes of the effect sizes. In the first model the variation of a phenotypic trait is determined by many small-effect alleles. Since more alleles are involved, their individual effect is smaller, causing a higher chance to be eliminated due to the lower strength of selection. The second model consists of major alleles which are more rare than the small-effect alleles. Evidence is found for both models (Olson-Manning et al., 2012).

Third, the **allelic initial frequency** plays a major role, which elucidates the importance of gene flow and migration (Olson-Manning et al., 2012). It is expected that a certain amount of gene flow is necessary to create a sufficient gene pool. Adequate migration is especially important to establish populations under competition or bad conditions by restocking the population size and creating more genetic variation. Competition can reduce the population sizes, resulting in the impediment of settlement. With the prevalence of sufficient migration, populations can be demographically rescued and possibly restocked with genotypes that might easily evolve a niche shift that lowers this competition. But, if gene flow is too high, local adaptation will be precluded and the fitness will likely be reduced, which is known as a migration load (Bolnick & Nosil, 2007). In this case, the genetic variation within populations will increase, but a decrease of the variation among populations is likely to be observed. Consequently, it will counteract the evolutionary divergence of populations. Intermediate rates of dispersal from the mainland are advantageous, because this will favour specialisation instead of generalism, which will lead to a better exploitation of the resources and as a consequence a higher productivity (Venail et al., 2008).

Next to the non-selective forces, such as drift, migration and mutation, also the **biotic interactions** are essential, as already mentioned before in case of migration under competition. The adaptation of species to novel environments can thus depend on the community context as well. For that reason, a species can be limited due to the abiotic environment, but also by means of the ensemble of species interactions (e.g. competitors, mutualists and predators) (Case et al., 2005). Under competition, adaptation may even been pushed towards niches that are initially not used. Recently, there has been more attention for indirect interactions, such as indirect competition (Walsh, 2013), which can be caused by induced effects. For instance, Sarmento and colleagues (2011) demonstrated that a higher mortality, a lower oviposition rate and a lower developmental rate of a mite herbivore *T. evansi* are observed on plants that were previously attacked by a closely related, more generalistic species *T. urticae.* As previously highlighted, such an interspecific competition can induce adaptive niche shifts (Turcotte et al., 2012). Alternatively, species in a community can alter the environment experienced by other species, which could possibly lead to ecological specialisation (Lawrence et al., 2012; Turcotte et al., 2012; Poisot et al., 2011). 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 **relatedness** of a focal species to another species in a community is hypothesised to impact the likelihood or 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 comparable (Burns & Strauss, 2011; Violle et al., 2011). This principle has led to the idea of diversity-dependent specialisation (Etienne & Haegeman, 2012). In herbivores for instance, competition between closely related species for the same plant material and nutrients is therefore likely to occur, i.e. exploitative competition (Walsh, 2013). The herbivore spider mites, *Tetranychus urticae* and *T. evansi,* for instance, use needle-like mouthparts to penetrate cells and remove the content of the cells (Salinas et al., 2013; Meck et al., 2012) thereby directly exploiting the same resources. Other herbivores, caterpillars, for instance may consume some specific leaves and are therefore expected to compete less strongly, either because of different feeding niches or the triggering of different plant defence responses (War et al., 2012). The empirical evidence that more related species experience more competition is, however, not completely straightforward. Many unrelated species experienced convergent evolution, which lead to similar adaptations for feeding ecology. For instance, earlier research by Cedola and others (2013) demonstrated that *T. urticae* experiences strong competition with the strawberry aphid, *Chaetosiphon fragaefolii,* resulting in a decrease of the growth rate and fecundity when sharing the same strawberry leaf (Cedola et al., 2013). Both species belong to different classes, Arachnida and Insecta respectively. Some researchers state that competition is not affected by relatedness (Bennett et al., 2013), while others find an even stronger competitive-exclusion pattern between more unrelated species pairs (Beaudrot et al., 2013). It is therefore clear that these patterns may be very context specific, and impacted by for instance other species in the foodweb like predators. In spider mites for instance again, antagonistic interactions may shift to mutual interactions when the competing species benefit each other through the production of defensive structures like silk webs (Yano, 2012). *Tetranychus* ssp. have morphological features that are specific for locomotion on webs (Morimoto et al., 2006). Under predatation, these species thus advantage each other relative to other competitors like *Panomychus* ssp.. These, are at a disadvantage because they lack specialised attributes to move within the complicated webs (Morimoto et al., 2006). However, in circumstances without predators the costs of competition will feasibly overweigh the benefits of web sharing. These specific mechanisms are responsible for the phenomenon of phylogenetic overdispersion, which is a situation often observed in nature, where phylogenetically related species are more biogeographically distributed than by chance (Violle et al., 2011). This is the opposite of the phenomenon of underdispersion, where related species are appearing more together.

Gaining a clear insight into evolution, more precisely into the process of adaptation, is necessary to predict the response of species to climate change, to find better solutions against certain diseases or to regulate pests (Olson-Manning et al., 2012; Turcotte et al., 2012). The two-spotted spider mite or *Tetranychus urticae* is the focal species of our research. This haplodiploid polyphagous mite is a suitable model species for experimental evolution, since the fecundity is really high and the generation time is restricted to about eleven days under 24°C (Hance & Van Impe, 1999; Fry, 1989), which means that a fast growth is expected. The species is extremely polymorphic in its host preference (Agrawal, 2000). Local adaptation to novel host plants can occur extremely fast owing to for example a high standing genetic variation within established populations (Magalhães et al., 2009; Magalhães et al., 2007; Fry, 1989; Gould, 1979). A time frame of 15 generations is known to be sufficient to detect local adaptation (Bonte et al., 2010) and no further increase in oviposition rate and juvenile survival is observed in *T. urticae* at generation 25 (Magalhães et al. 2009). The two-spotted spider mite (*Tetranychus urticae*) is therefore considered as one of the most important pest species that will cause an even more serious problem in the future for agriculture, because rising temperatures will increase their growth rates (Grbić et al., 2011). Besides the relevance to understand the process of ecological specialisation from an applied perspective, we specifically focus on this process from a generic point of view. Insights into the ecological and evolutionary processes that impact the rate of ecological specialisation are crucial for our understanding of the origin of biodiversity and complexity.

2. AIMS

The main topic of this research is to study how gene flow and the presence of a competing species affect the rate of local adaptation in a generalistic arthropod herbivore. In this study, a two-species 'community' is considered, including the two-spotted spider mite and the red tomato spider mite (*Tetranychus evansi*), which is a phylogenetically related species and a big threat to crops belonging to the Solanaceae (Grbić et al., 2011; Boubou et al., 2011). It is supposed that communities with phylogenetically related competitors, such as *T. evansi*, will hinder specialisation. The competitor is likely to perform a lot better on tomato leaves than *T. urticae,* although it is known that also the two-spotted spider mite is a serious pest on tomatoes (Salinas et al., 2013). We implemented different rates of dispersal in a mainland-island mesocosms laboratory system to quantify to which degree dispersal rate (often termed migration in this context*) and the biotic context affect the species' ecological (demography) and evolutionary dynamics (local adaptation). This research will thus provide insights into the community aspect of evolutionary dynamics and the role of biotic interactions (competition) on diversifying or stabilizing evolutionary processes.

3. MATERIAL AND METHODS

Tetranycus urticae and Tetranychus evansi: biology

The haplodiploid *Tetranychus urticae,* or the two-spotted spider mite, and *Tetranychus evansi*, also known as the tomato red spider mite, are both pest species from the class of the Arachnida (Acari: Tetranychidae). The first one is a generalistic herbivore, which is exceptionally polymorphic in its preference for host plants (Agrawal, 2000) and has a cosmopolitan geographic distribution (Raworth et al., 2002; **Figure 2**). On the other hand, *T.*

evansi, is considered to be a specialist on plants from the family Solanaceae, but it is also found on 37 other families and an increasing host range is reported (Navajas et al., 2013). Being a subtropical species, its geographic distribution is less wide, but, it has expanded in the last two decades (Navajas et al., 2013; **Figure 1**).

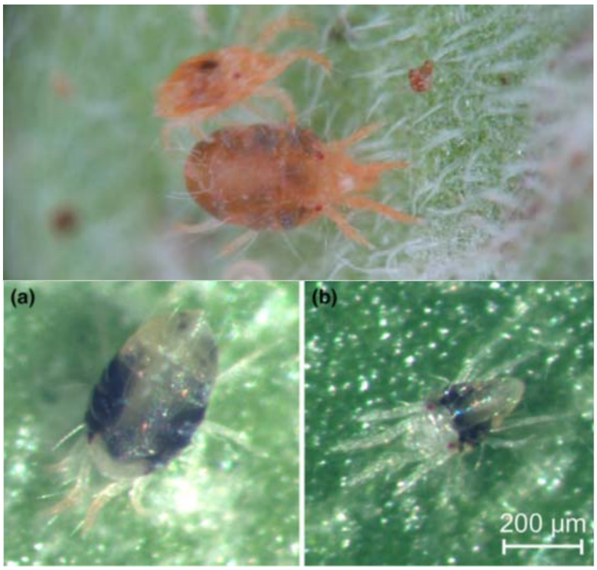


Figure 1: upper figure: *T. evansi* (Migeon & Dorkeld, 2006-2010); lower figure: (a) adult female *T. urticae* (b) adult male *T. urticae* (Oku, 2014)

T. urticae has a female-biased sex ratio going from 2:1 to 3:1, whereas it was rather 4:1 for *T. evansi* (Oku, 2014; Bonato, 1999). But, this operational sex ration (OSR) becomes male biased in a mature colony, since fertilised females disperse from their natal group. Males, who are able to mate multiple, whereas females can mate only once, stay in the colony (Oku, 2014). However, it is known that females can adjust the sex ratio depending on the level of local mate competition (Macke et al., 2012).

Different stages determine the life cycle of these Tetranychus ssp., these are egg, larva, quiescent larva or protochrysalis, protonymph, quiescent protonymph or deutochrysalis, deutonymph, quiescent deutonymph or teleiochrysalis and the adult stages (Oku, 2014; Raworth et al., 2002). The growth cycle of *T. urticae* takes usually 11 days on bean at 24°C (Hance & Van Impe, 1999; Fry, 1989) and 13-15 days on tomato at 21°-27°C (Fry, 1989). For *T. evansi,* the developmental period has an average of 10 days under optimal conditions and it is extremely tolerant do draught and heat (Meynard et al., 2013). Under 22°C a development time of 13,6 days is observed and 6,3 days at 36°C (Bonato, 1999). An adult female *T. urticae* has on average one day without laying eggs, which is referred to as the pre-oviposition time, and, hereafter, a daily fecundity of 1-12 eggs during a period of more than 20 days at 25°C was observed (Oku, 2014). The number of eggs per day for *T. evansi* varies from 10,6 eggs at 36°C until the maximum of 13,4 eggs at 31°C (Navajas et al., 2013). The female longevity for *T.*

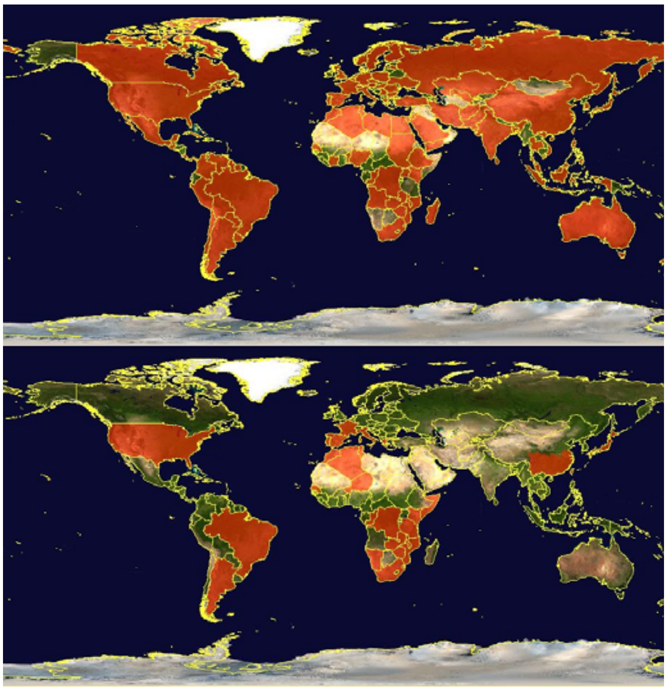


Figure 2: the distribution map of *T. urticae* (upper figure) and *T. evansi* (lower figure) (Migeon & Dorkeld, 2006-2010)

evansi depends on the current temperature and a the maximum was recorded at 21°C with a longevity of 23,8 days (Bonato, 1999).

Sexual dimorphism is a typical feature in spider mites, in which the females are larger and reach a body size of approximately 0,5 mm (**Figure 1**). This difference is already visible in the egg size (Oku, 2014; Macke et al., 2012). Spider mites are able to build complicated silk webs while walking and have specialised morphological features to move on it (Oku, 2014; Morimoto et al. 2006). The visual capacity of the species is limited. It can observe wavelengths from 350 to 600 nm can, although, no images can be resolved (Oku, 2014). Besides, chemicals can be employed to detect information from the environment and the setae on the body are applied to touch and smell (Oku, 2014).

Initial situation

The base population of the two-spotted spider mites (here used as the mainland population, see below) is maintained on green beans (*Phaseolus vulgaris,* prelude) under room temperature conditions in a 16:8 light regime. They were originally cultured at the department crop sciences, faculty of bio-engineering of the University of Ghent and subsequently maintained at the Terrestrial Ecology lab. The population of the phylogenetically related species, the tomato red spider mite, is maintained on tomato plants (*Solanum lycopersicum,* moneymaker), these are preserved in the same room as the population of *T. urticae* and were also originally cultured at the faculty of bio-engineering.

Experimental setup

The experimental setup is arranged as mesocosms in which typical mainland-island dynamics are simulated, with settlement of populations after dispersal from the mainland on novel habitat at the islands. A schematic representation of the populations is given in

Figure 3. Islands can be either occupied by a competitor, or competitor free. The mainland population of *T. urticae* is the base population as described in the previous part. The island populations prevail on separate standardised tomato plants of the same size and all of them are on average four weeks old (three weeks in a small cutting pot of 2 x 2 x 6 cm and, after repotting, one week in a bigger cutting pot of 9 x 9 x 8 cm).

In case a competitor is present, an invasion of a novel, focal, species is simulated. We therefore assumed the competitor to be present before the focal species. Therefore, four adult females of *T. evansi* were put on the plants with competition three days before the arrival of *T. urticae* on the 15th of October 2013. This period should be enough for the establishment of the red tomato spider mites. The transfer of mites is done with a very thin paint brush. Subsequently, depending on the level of gene flow, a certain number of adult female *T.*

urticae (2 immigrants per week, 3 immigrants per week, 5 immigrants per week or 10 immigrants per week) is put on the plants every week during the experiment (**Figure 3**).

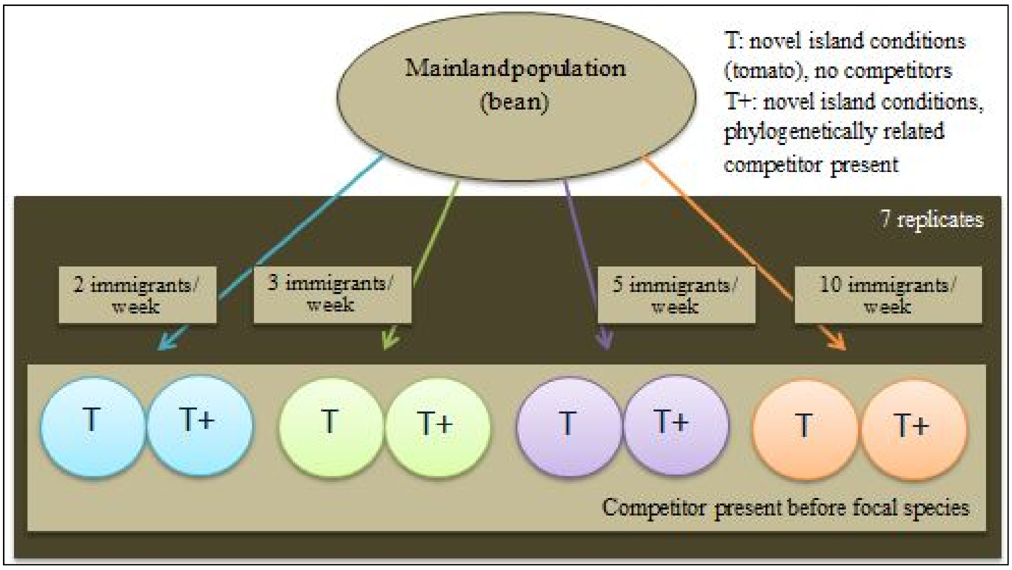


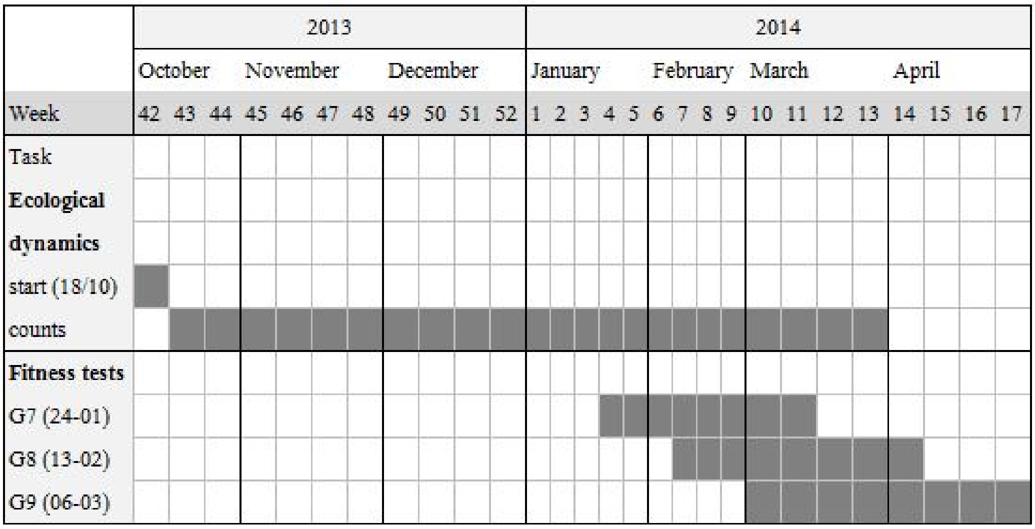
Figure 3: The experimental setup of the mainland-island populations. Four different levels of gene flow are used, indicated in blue (2 immigrants per week), green (3 immigrants per week), purple (5 immigrants per week) and orange (10 immigrants per week). The focal species is *Tetranychus urticae* and the competitor is *T. evansi*.

Figure 4: setting of the plants in one box

In total, 56 tomato plants are used, 28 of these are from the treatment with competition, which means that *T. evansi* is present. The other half is without a competitor. 7 replicates are utilized. These are put in ten plastic boxes, in eight of them six plants are placed together (**Figure 4**) and the last two boxes contain only four plants. All of the plants are separated from each other and supported by skewers to ensure a straight growth. The spider mites cannot reach another plant due to the double-sided sticky paper (Pherobank ®) at the bottom of the box. To preclude the spider mites to escape from the plastic boxes, in case some leaves were accidently touching the edges, Vaseline was spread on the sides of the box. The plants are randomly divided between the boxes by means of drawing cards. But, because the extreme dispersal capacity of *T. evansi*, the islands with the competitor or not mixed with those without competition. The same light regime as the stock populations is used for the islands (16:8) and the temperature in the climate-controlled room is 25 ± 0.5 °C.

At the start of the experiment, the plants of the island are refreshed every two weeks by cutting the leaves with mites on and placing them on the new plant. Like this, the amount of resources is the same in each treatment and pulsed. For allowing *Tetranychus urticae* to establish on the plants under competition, not all the *T. evansi* from the old tomato plant were replaced on the new plant, but it was done in a consistent way for all the replicates. The plants were first screened for leaves containing *T. urticae* and these were placed on the new plant.

Further, also some leaves with only *T. evansi* were replaced, to ascertain a same number of this competitor for the different dispersal levels and replicates. If lower population sizes of the tomato spider mite were measured, all of the individuals were replaced. However, it is logical that some treatments have more resources per capita. This means that overexploitation of the resources can lead to food shortage, but that the next generation is able to grow again, due to the replacement of the host plant. Given that each plant provides the same amount of resources, the sizes of the islands stays equal and there is a certain carrying capacity, *K*. This limitation of nourishment is necessary to ensure that a regulation of the community occurs. Since *T. urticae* is experiencing competition of a phylogenetically related species, *K* is expected to be lower in these treatments compared with the situation without competitors (control), because the available resources are decreasing faster. However, because some plants with *T. evansi* died before the two weeks were past, due to the enormous population sizes, all the plants are refreshed every week and a half starting from the 6th of December 2013. But, the tomato spider mites seemingly took advantage of the faster refreshment, which made them reach even higher population sizes, leading to an even bigger competition pressure for the two-spotted spider mites and, as a consequence, a decrease in their population size (**Figure 7**). Therefore, the plants were refreshed again every two weeks commencing the 17th of January 2014.



	2013											2014																
	October			November				December				January					February				March				April			
Week	42	43	44	45	46	47	48	49	50	51	52	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Task																												
Ecological dynamics																												
start (18/10)	▨																											
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Fitness tests																												
G7 (24-01)															▨	▨	▨	▨	▨	▨	▨	▨						
G8 (13-02)																		▨	▨	▨	▨	▨	▨	▨	▨			
G9 (06-03)																					▨	▨	▨	▨	▨	▨	▨	▨

Figure 5: scheme from the experiments; the fitness from different generations was measured (G7: the first experiment or generation 7, which started at the 24th of January; G8: the second experiment or generation 8, which started at the 13th of February; G9: the third experiment or generation 9, which started at the 6th of March)

Experimental procedure

Three different subjects to control the impact of competition with phylogenetically related species on the evolution of local adaptation are investigated (**Figure 5**).

First, ecological dynamics are followed by measuring the total population twice a week by counting the number of adult females of *T. urticae*. The data are clustered within each generation time of 16 days. Based on the observations, this time frame is likely to be acceptable for the non-competition treatment. But, this subdivision in is rather artificially for the competition treatment, since no real establishment was possible. Further, it is expected that the generation time will decrease if local adaptation is increasing, although, this is not taken into account. Since, we are interested in the impact of the dispersal level and this may not be influenced by the net input of individuals, the number of mites/week (dispersal level) is subtracted from the total numbers in each count and in case the result was less than zero, a zero was used.

Statistics. Generalized linear mixed models (GLMM) were used to discover the effect of the fixed factors, which are treatment (non-competition or competition), dispersal (1: 2 mites/week; 2: 3 mites/week; 3: 5 mites/week and 4: 10 mites/week) and generation (G1-G11). Given that the same replicate is followed during the whole period, this is put as a random factor. For the comparison of the number of adult females between the dispersal treatments, subsets for each generation within each treatment are made and mixed models were used with the Poisson error distribution to analyse the data. The replicate is considered as a random factor. Tukey's HSD test is applied for all pairwise comparisons. Analyses were conducted with R x64 (2.15.2).

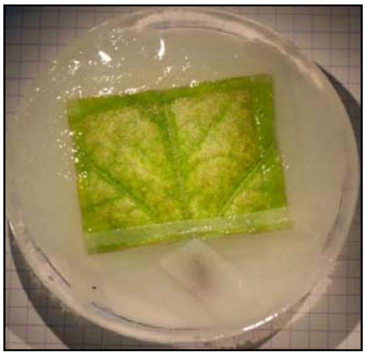

Figure 6: *T. urticae* subject to a common garden in a Petri dish

Second, evolutionary dynamics are assessed by quantifying the magnitude of local adaptation at generation 7, 8 and 9 (**Figure 5**). In **Figure 8** this time frame is indicated with a rectangle. I therefore measured the fitness of the two-spotted spider mites on the novel host relative to the original host.. Fitness is determined by different proxies, such as female longevity, total number of offspring and the growth rate of the population (Bonte et al. 2010; Kawecki & Ebert, 2004). Performance of *T. urticae* from the stock population is compared with the performance on the novel host as present on the islands. Given that the life-history traits of spider mites are sensitive to effects of different environments due to high levels of phenotypic plasticity, the removal of these effects is essential to distinct plasticity and evolutionary effects (Magalhães et al., 2011; Bonte et al., 2010; Kawecki & Ebert, 2004). For this, all the mites were first subjected to a common garden for two generations (**Figure 6**). If more than twenty-five female adults of the two-spotted spider mite are present on the tomato plant, five of them are put alone on a bean leaf for two generations. In case fewer females are found, only four, three, two or one mite is put alone to preclude the risk of collapsing of the population, if respectively more than twenty, fifteen, ten or five mites were available. If less than five mites were available, none of them are used for determining the fitness to avoid the risk of impacting the ongoing eco-evolutionary dynamics. As a control, we also assessed performance of individuals from the mainland stock population after identical common garden conditions. Although these individuals have always been maintained on bean leaves, we performed this treatment, to avoid potential density effects.

Figure 7: F2 generation of *T. urticae* placed on bean leaves (up) and tomato leaves (down)

All mites for the local adaptation assays were put separately on leaves from standardised two weeks old bean plants (*Phaseolus vulgaris,* Prelude) of the same size (4 x 5 cm). These bean leaves are placed in pairs, bordered with strips of paper towel, in a Petri dish (Ø 145 mm) filled with water-soaked cotton wool (Rolta soft), which are placed in a climate-controlled room with a light-regime of 16:8 and a temperature of 25 ± 0.5 °C. On each leaf one of the two-spotted spider mites is placed. After thirteen days, the Petri dishes are controlled and, if possible, four or five adult females from the F1 generation together with some males from the F1 generation are put on a new leaf (4 x 5 cm), coming from a two week old bean plant (*Phaseolus vulgaris,* Prelude), in a Petri dish (Ø 85 mm) filled with water-soaked cotton wool (Rolta soft) and again strips of paper towel are put. These Petri dishes are stocked in the same climate-controlled room as F1 generation. A fresh bean leaf (*Phaseolus vulgaris*, Prelude) from standardised plants of two weeks old is cut in a square of 4 by 4 cm and placed, in the Petri dishes (Ø 145 mm), under the first leaf with the other spider mites from the F1 generation after two weeks. In this way, the second generation is kept alive in order to receive enough *T. urticae* for the genetic analysis.

Afterwards, a quiescent deutonymph female of the F2 generation is put together with some males of the F2 generation on a leaf from an eight weeks old tomato plant (*Solanum lycopersicum,* moneymaker) and a second one on leaf from a two weeks old bean plant (*Phaseolus vulgaris,* prelude). Those leaves are cut into pieces of 2 x 3 cm and placed in a wadded Petri dish (Ø 85 mm). Four leaves are placed in one dish, two tomato leaves and two bean leaves (**Figure 7**). Two different replicates are randomly assigned to a Petri dish. To reduce interfering factors to a minimum one mite on a tomato leaf and the control from the same replicate on a bean leaf are placed in the same dish. However, in some cases the control mite on bean was not in the same Petri dish, given that one of the mites from the pairs did not hatch are died immediately and a new attempt was done. During fifteen days pictures are taken from the Petri dishes and the larvae, protonymphs, deutonymphs, adult females and adult males are counted later by using a self-developed program in MATLAB. These data are collected in an excel sheet, together with the female longevity, the condition of the leaf and the fact whether the female died natural or by drowning. We followed up in total 3 assays to test local adaptation at generation 7, 8 and 9, and followed the faith of almost 50000 adult female spider mites on the experimental populations. But, the same female is probable repeatedly counted, since this was done twice a week. In total, 386 spider mites were put through the fitness tests, however, this number decreased during the procedure because some of the females were inseminated (especially a problem in the common garden) or died too soon.

Statistics. Since the research design has both fixed and random factors, mixed models were used in R to avoid pseudo replication and to treat these effects appropriately. Data from leaves in bad conditions were removed from the dataset. Also, the data from females that died an unnatural death is not used anymore after the moment they expired. A Poisson error distribution is applied and it was modelled by a generalized linear mixed model fit by maximum likelihood. A control for similarity for females coming from the same host plant was done by putting it as a nested random factor. For the pairwise comparison, a Tukey's HSD test is done and the p value for significance is put at 0.05. Figures are made with the observed data without corrections for random factors. Analyses were conducted with R x64 (2.15.2).

Third, from the second generation of *T. urticae* described above, as much as adult females as possible are put in an Eppendorf tube for a genetical analysis, with a limit of 100. A number between 80 and 100 is sufficient for abstracting DNA from this species, according to previous research. However, this is currently developed at KBIN and is therefore not included in this thesis.

4. RESULTS

I report first on the ecological dynamics by providing results on the total population sizes, and secondly on the evolutionary dynamics by providing results from the GLMM on mite performance. The latter is composed of three parts: a comparison between the treatments, one between the levels of dispersal and an overall comparison between the experiments.

4.1.Ecological dynamics: total population sizes.

The population dynamics as measured by the counts of the total population sizes on each bean island were statistically analysed and summarised in **Table 1**. It is clearly noticeable that the populations reach higher numbers if the competitor is not present (**Figure 8)**. The summaries for the models with dispersal as fixed factor within each generation are given in **Table 7** (appendix) for the non-competition treatment and in **Table 8** (appendix) for the competition treatment.

Significant differences are observed between the levels of dispersal, the different treatments and their interaction. The generation factor alone has no significant effect on the response variable, but its interactions with dispersal and treatment reveal significant effects (**Table 1**). The Tukey's HSD test, which was done between the different levels of dispersal within each treatment within each generation, demonstrated significant differences. I provide for clarity an overview of the ecological dynamics in **Figure 8** by plotting the mean values over time. I do however discuss the results by a careful analysis of the pairwise contrast at each generation time. These results are presented as bar-plots in appendix **Figure 36.**

Table 1: Results for fixed effects form mixed linear models with the total number of females as response variable (Poisson error distributions were used). The number of mites/week (dispersal level) is subtracted from the total numbers in each count and in case the result was less than zero, a zero was used.

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	0,4474999	0,2532601	1,77	0,0772000	.
dispersal2	1,0765373	0,0458002	23,51	< 2,00E-16	***
dispersal3	0,9401608	0,0468455	20,07	< 2,00E-16	***
dispersal4	1,3016542	0,0450254	28,91	< 2,00E-16	***
generation	0,0037598	0,0051837	0,73	0,4683000	
treatmentnC	2,4025972	0,0415124	57,88	< 2,00E-16	***
dispersal2:generation	-0,0006088	0,0003503	-1,74	0,0823000	.
dispersal3:generation	-0,0024520	0,0003493	-7,02	2,23E-12	***
dispersal4:generation	-0,0053557	0,0003420	-15,66	< 2,00E-16	***
dispersal2:treatmentnC	-0,9615768	0,0474881	-20,25	< 2,00E-16	***
dispersal3:treatmentnC	-0,6690639	0,0484429	-13,81	< 2,00E-16	***
dispersal4:treatmentnC	-0,7408714	0,0465642	-15,91	< 2,00E-16	***
generation:treatmentnC	0,0069606	0,0004041	17,23	< 2,00E-16	***

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

The mites from the treatment under competition (C) experience strong difficulties to establish, which can be seen by comparing the numbers of adult females between the different treatments and within C by drawing a parallel between the generations (**Figure 8).**

NON-COMPETITION TREATMENT

Until the 4th generation, the highest level of dispersal is significantly performing better related to the other levels of dispersal. From generation 5 until generation 8, the highest dispersal level is in the best performing group, although not significantly different from some other levels. Starting from generation 9, this level is situated in the significantly worst performing group. The same tendency is occurring for the lowest level of dispersal, which has in the beginning the lowest performance and at the end the best one. The significant differences (see appendix: **Figure 36**) are considered in detail in the following paragraph.

For the first generation, it was not possible to perform the mixed model statistics, due to the many observed zeroes, resulting into a too unbalanced model. In the second generation, the four levels of dispersal are significantly different, in which the higher the level of dispersal is, the more adult females are observed on the tomato plants. In generation three, the highest level of dispersal is still performing significantly better than the others and dispersal level 2 reaches significantly higher numbers than level 1 and 3. Each level is performing significantly different in the fourth generation, in which dispersal level 4 is doing better than 3, which is doing better than 1 and this is, on his turn, performing better than 2.

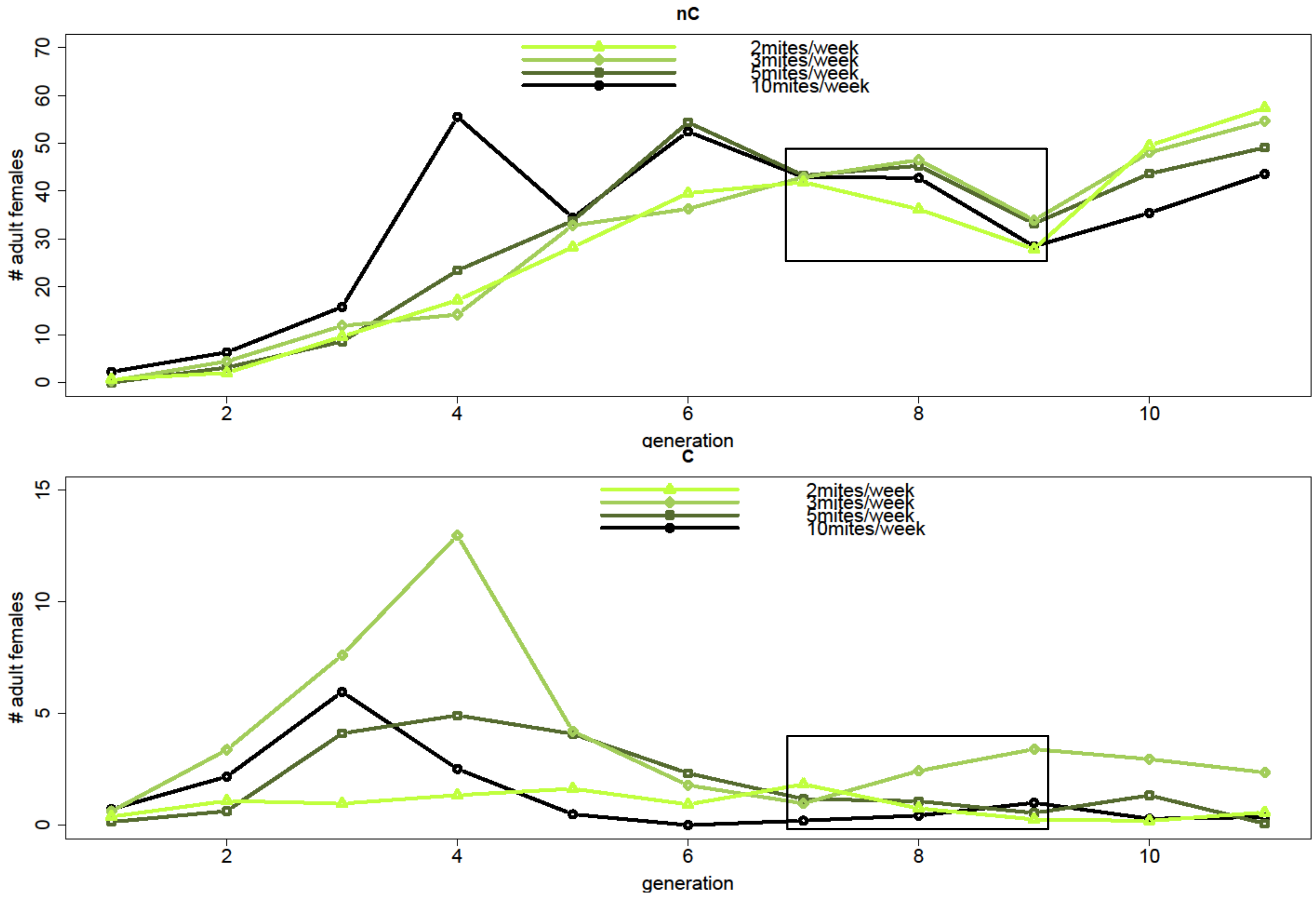

Figure 8: averages of the number of adult females of *T. urticae* for each generation (G: 1 – 11) are plotted, the upper graph presents the situation without competition and the lower graph under competition. Four different levels of dispersal are considered (1: 2 mites/week; 2: 3 mites/week; 3: 5 mites/week; 4: 10 mites/week). The mites for the different fitness experiments are taken from generation 7, 8 and 9, indicated with the rectangle. The figure is made with the observed data.

At generation five, the lowest dispersal rate is significantly doing worse related to the other levels of dispersal. For the sixth generation, dispersal level 3 and 4 are performing better than dispersal level 1 and 2. No significant differences are observed for generation seven and at generation eight the same is occurring as for generation 5, being only the first dispersal is significantly performing worse. In generation nine, dispersal levels 2 and 3 are reaching significantly higher numbers than dispersal level 1 and 4. Dispersal level 4 is, in the tenth generation, performing significantly worse compared with the other levels of dispersal and, within the other dispersal levels, dispersal level 1 is doing significantly better related to level 3. In the last counted generation, generation eleven, dispersal level 1 is has significantly more adult females related to dispersal level 3 and 4, and dispersal level 2, also has a significant higher number of females compared with dispersal level 4.

COMPETITION

No real pattern is visualised for the competition treatment, since it strongly depends on the establishment of some of the replicates. For instance, dispersal level 2 is significantly performing better than the other levels of dispersal from generation 8 until 11. In this period, one replicate was quite well established and this is the replicate that will be used in the treatment comparison for the fitness tests. Also in the beginning of the counts, dispersal level 2 is mostly performing significantly better. A more detailed description is given in the following paragraph (see appendix: **Figure 36**).

For the first generation no significant differences are observed between the different levels of dispersal. In the second generation, dispersal level 2 is significantly performing better than the other levels and dispersal level 4 has a significantly higher performance than level 1 and 3. Dispersal 2 and 4 significantly have the highest number of females in the third generation related to dispersal level 1 and 3, in which the latter one is significantly performing better than the first one. In the fourth generation, all of the dispersal levels show significant differences and the order, started with the best performance, is dispersal level 2, 3, 4 and 1. For generation five, dispersal level 2 and 3 are significantly doing better than the other levels, from which dispersal level 1 has a significant higher number of females related to level 4. No individuals are counted, after the correction for the immigration level, for the highest level of dispersal in generation six. The comparisons between the other levels reveal a significantly higher number of females for dispersal level 2 and 3 related to dispersal level 1. In the seventh generation, the highest dispersal level is performing significantly lower than the other levels and dispersal level 1 has a significant higher number of adult females compared with dispersal level 2. For the eighth generation, the second dispersal level reaches a significant higher number than the other levels of dispersal and dispersal level 3 is significant better than level 4. Also, in generation nine, dispersal level 2 has significantly the best performance, but here dispersal level 4 is significantly performing better related to the lowest level of dispersal. At the tenth generation, dispersal level 1 and 4 are significantly lower than the others and dispersal level 2 is still significantly performing the best. In the last generation, dispersal level 2 has the highest number of adult females, which is a significant difference with all the other levels of dispersal.

4.2 Evolutionary dynamics: Fitness test.

TREATMENT COMPARISON

In this part, the comparison is made between C, nC and the control from the stock population. As mentioned in the previous part, establishment was really difficult for *T. urticae* kept together with their competitor *T. evansi*. Therefore, only one replicate is considered, which had dispersal level 2 (3 mites/week). It was established during the last two experiments (generation 8 and 9) in which local adaptation was measured and it was possible to collect data from this replicate. Consequently, from the treatment without competition the same dispersal level was used. We do not report on results from the assays as followed during the first time period (experiment 1: generation 7), as no replicates for the competition treatment were available.

Total number of individuals as a proxy for the intrinsic growth rate.

Table 2: Treatment. Results for the best model selection from mixed linear models with Poisson error distribution for the total number of offspring (Total). Fixed factors in the full model are the female longevity (FmL), plant species (PlS; bean or tomato), treatment (Trt; with competition, without competition and control), the interaction between plant species and female longevity (FmL:PlS) and the interaction between plant species and treatment (PlS:Trt). The random factors are the several females taken from their respectively replicate. Only one model is presented if the weight is more then 0.50, otherwise the first two models are presented.

<table>
<tr><th></th><th>Model</th><th>df</th><th>logLik</th><th>AICc</th><th>delta</th><th>weight</th><th>R2m</th></tr>
<tr><td colspan="8">Experiment 2: generation 8</td></tr>
<tr><td>Day7</td><td>Total~PlS+Trt+PlS:Trt+(1|Replicate/Sample)</td><td>8</td><td>-148.141</td><td>315.2</td><td>0.00</td><td>0.706</td><td>0.67</td></tr>
<tr><td>Day10</td><td>Total~ PlS+Trt +PlS:Trt+(1|Replicate/Sample)</td><td>8</td><td>-200.997</td><td>421.1</td><td>0.00</td><td>0.444</td><td>0.50</td></tr>
<tr><td></td><td>Total~FmL+ PlS+Trt +PlS:Trt+(1|Replicate/Sample)</td><td>9</td><td>-199.629</td><td>421.3</td><td>0.13</td><td>0.416</td><td></td></tr>
<tr><td>Day15</td><td>Total~FmL+PlS+Trt+PlS:Trt+(1|Replicate/Sample)</td><td>9</td><td>-198.749</td><td>420.5</td><td>0.00</td><td>0.697</td><td>0.60</td></tr>
<tr><td colspan="8">Experiment 3: generation 9</td></tr>
<tr><td>Day7</td><td>Total~PlS+(1|Replicate/Sample)</td><td>4</td><td>-28.209</td><td>65.3</td><td>0.00</td><td>0.477</td><td>0.93</td></tr>
<tr><td></td><td>Total~FmL+PlS+(1|Replicate/Sample)</td><td>5</td><td>-27.939</td><td>67.3</td><td>1.96</td><td>0.179</td><td></td></tr>
<tr><td>Day10</td><td>Total~FmL+PlS+Trt +PlS:Trt+(1|Replicate/Sample)</td><td>9</td><td>-160.081</td><td>343.0</td><td>0.00</td><td>0.672</td><td>0.88</td></tr>
<tr><td>Day15</td><td>Total~FmL+PlS+Trt+FmL:PlS+PlS:Trt+(1|Replicate/Sample)</td><td>10</td><td>-122.721</td><td>275.4</td><td>0.00</td><td>0.964</td><td>0.75</td></tr>
</table>

In **Table 2** a representation of the best model is given, in which an interaction between plant species and treatment is observed for each day in the experiments which was counted, except for the day 7 in the 9th generation. The summary of the models is given in **Table 9** (appendix). Here-under, the details for the separate experiments are provided. These are also visualised in the figures, but it must be taken into account that these are made with the observed numbers, in which the random and nested factors are not included (**Figure 11** – **Figure 16**). Further, the small sample sizes due to low establishment rates for some treatments must be beard in mind when interpreting the results.

Experiment 2: generation 8 (**Figure 11** – **Figure 13**).

Day 7. Pairwise significant differences are observed between the group on bean and tomato for nC and C, with the total number of individuals being lower on tomato. Within the tomato group, the individuals that were under competition are performing significantly better than the control.

Day 10. The significant differences between the plant species are the same as on day 7. Further, the control group does significantly better on bean than C and nC and the reverse pattern is observed for tomato, although, the difference between C and the control is not significantly proven.

Day 15. Pairwise differences between the plant species are measured for each treatment. Treatment C is performing better than nC and the control on bean leaves and the control group is significantly less fit than the others on tomato.

Experiment 3: generation 9 (**Figure 14-Figure 16**).

Day 7. Significant differences are measured between the plant species in the best model, in which the different treatments are not considered. If the pairwise comparisons are made with the treatments included, only the non-competition treatment on bean is significantly performing better than on tomato.

Day 10. Pairwise differences are observed between the plant species for each treatment, with individuals on bean leaves performing better, and no differences are visualised within bean. But, on tomato differences are observed between C and the control with the control performing less good.

Day 15. As for day ten all the treatments are performing better on bean and the control is doing significantly better than the others. On tomato, nC is significantly fitter than C and the control.

Female longevity

The longevity of the female is only affected by the random factors and, for generation 8, also by the plant species (**Table 3**). Besides, no significant differences are observed for the plant species, only a marginal value for generation 8, which suggest that the females on tomato are living longer (appendix: **Table 10**). It is illustrated in **Figure 9** and **Figure 10**.

Table 3: Treatment. Results for the best model selection from mixed linear models with Poisson error distribution for the longevity of the female (FmL). Fixed factors in the full model are the plant species (PlS; bean or tomato), treatment (Trt; with competition, without competition and control) and the interaction between plant species and treatment (PlS:Trt). The random factors are the several females taken from their respectively replicate.

Model	df	logLik	AICc	delta	weight	R2m
Experiment 2: generation 8						
FmL~PlS+(1|Replicate/Sample)	4	-130.109	269.1	0.00	0.493	0.06
FmL~(1|Replicate/Sample)	3	-131.720	269.9	0.86	0.321	
Experiment 3: generation 9						
FmL~ (1|Replicate/Sample)	3	-116.609	239.8	0.00	0.694	0

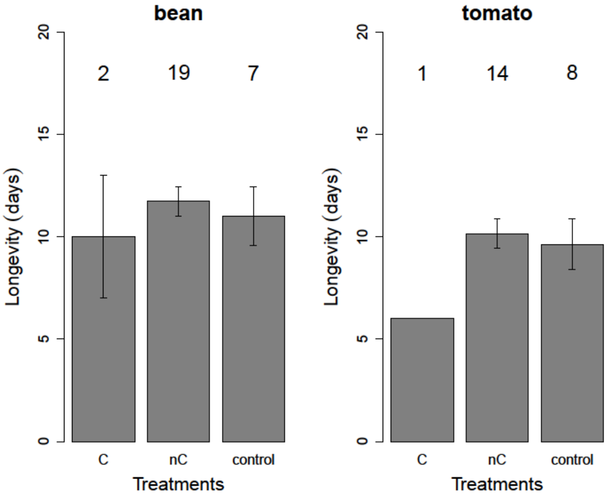

Figure 9: the female longevity for generation 8 compared on bean and tomato for the different treatments, the error bars are plotted on the figure. The figure is made with the observed data.

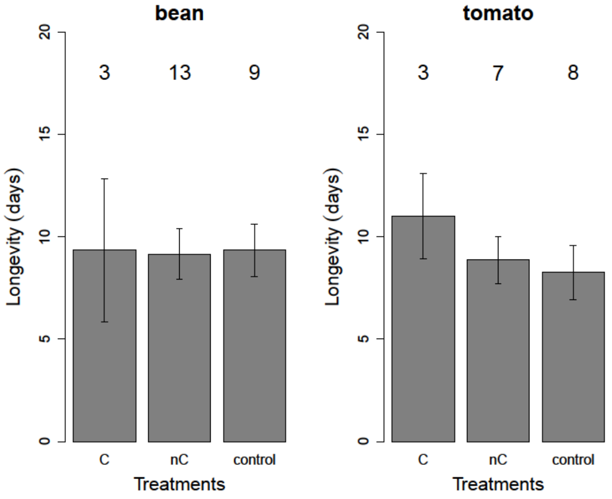

Figure 10: the female longevity for generation 9 compared on bean and tomato for the different treatments, the error bars are plotted on the figure. The figure is made with the observed data.

DISPERSAL COMPARISON

A comparison on the effectiveness of dispersal for local adaptation was derived from the nC and control treatments (the latter are the dynamics from mites from the stock population). The competition treatment is not considered, because of the lack of sufficient replicates for each dispersal level, as not enough females were able to establish in the harsh environment under competition. Therefore only the occurrence of adaptation and the effect of the different dispersal levels affecting this, are measured**.**

Total number of individuals as a proxy for the intrinsic growth rate.

The interaction between plant species and dispersal is observed in each model for day 7, 10 and 15 in the three experiments, in which local adaptation is assessed after respectively 7, 8 and 9 generations, except for day 7 in generation 7 (**Table 4**). The summary of the models is given in **Table 11** in the appendix. The figures are made with the observed data, in which the random and nested factors are not included (**Figure 18 – Figure 26**).

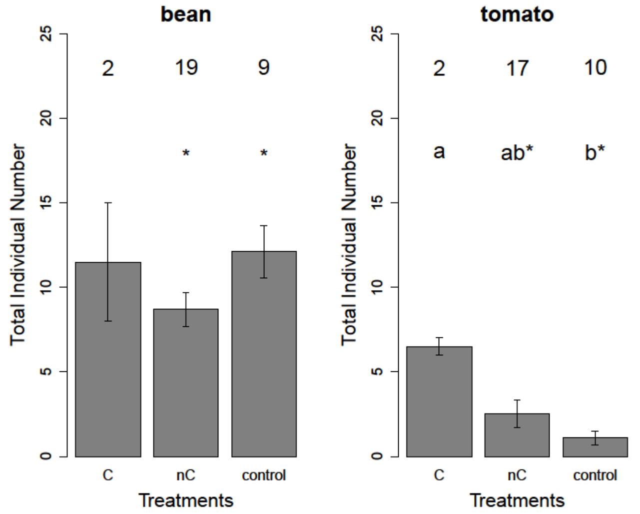

Figure 11: the total number of individuals for the different treatments on day 7 (generation 8).*

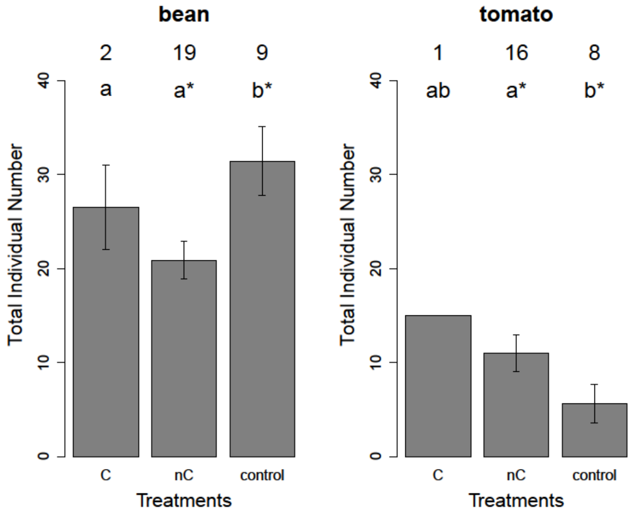

Figure 12: the total number of individuals for the different treatments on day 10 (generation 8).*

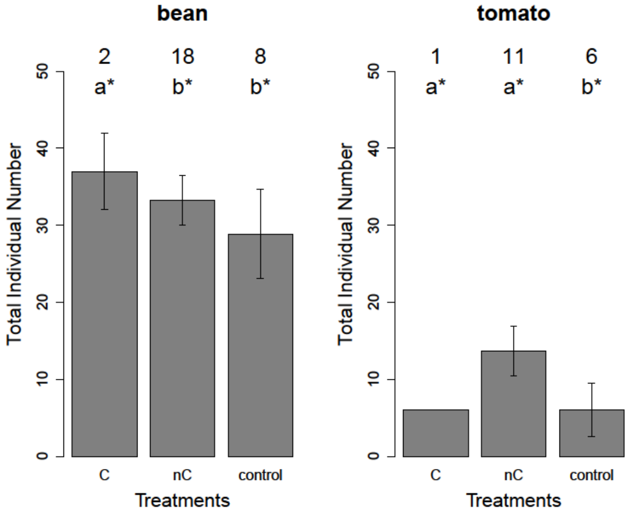

Figure 13: the total number of individuals for the different treatments on day 15 in the (generation 8).*

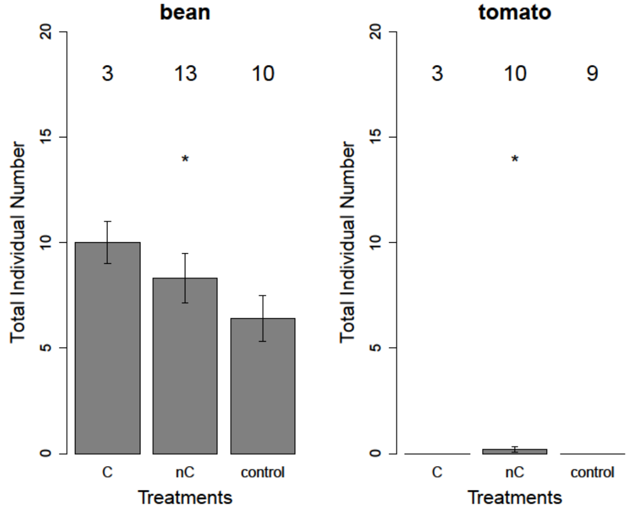

Figure 14: the total number of individuals for the different treatments on day 7 (generation 9).*

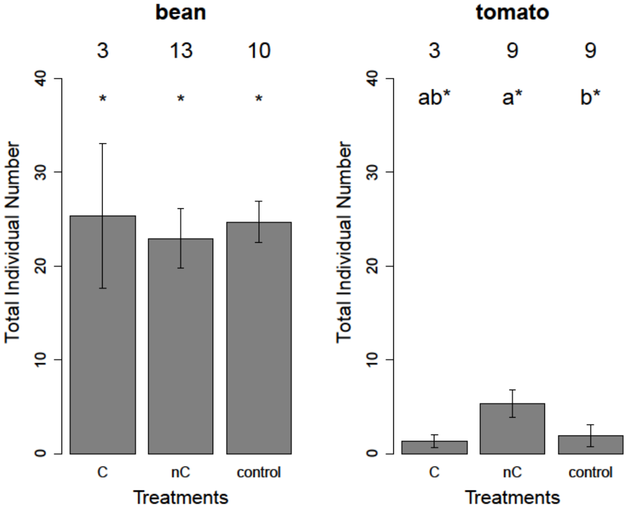

Figure 15: the total number of individuals for the different treatments on day 10 (generation 9).*

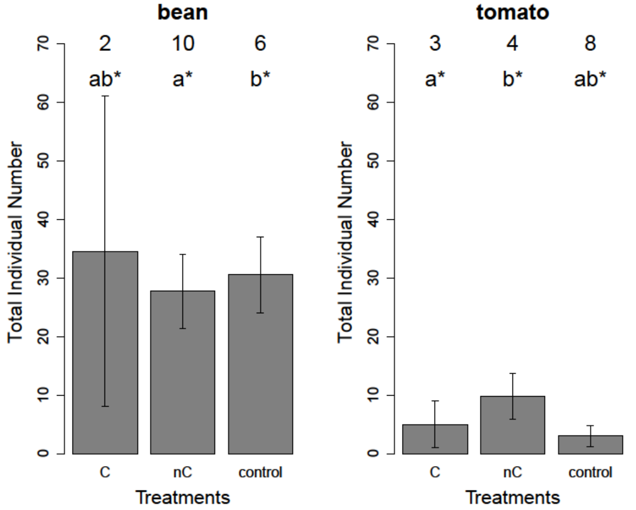

Figure 16: the total number of individuals for the different treatments on day 15 (generation 9).*

***The error bars are plotted in the figure and the sample sizes are on top of the figure. The stars indicate significant differences within the same treatment between the plant species, bean and tomato, and the letter code is used to compare within a certain plant species between the treatments. The figures are made with the observed data.**

Table 4: Dispersal. Results for the best model selection from mixed linear models with Poisson error distribution for the total number of offspring (Total). Fixed factors in the full model are the female longevity (FmL), plant species (PlS; bean or tomato), treatment (Trt; with competition, without competition and control), the interaction between plant species and female longevity (FmL:PlS) and the interaction between plant species and treatment (PlS:Trt). The random factors are the several females taken from their respectively replicate.

	Model	df	logLik	AICc	delta	weight	R2m
Experiment 1: generation 7							
Day7	Total~Dsp+ PlS +(1|Replicate/Sample)	8	-100.208	217.7	0.00	0.482	0.90
	Total~Dsp+ FmL+PlS +(1|Replicate/Sample)	9	-99.875	219.4	1.67	0.209	
Day10	Total~Dsp+FmL+ PlS+Dsp:PlS+ FmL:PlS +(1|Replicate/Sample)	14	-443.029	918.4	0.00	0.979	0.85
Day15	Total~Dsp+FmL+ PlS+Dsp:PlS+FmL :PlS +(1|Replicate/Sample)	14	-408.703	850.5	0.00	0.993	0.84
Experiment 2: generation 8							
Day7	Total~Dsp+FmL+ PlS+Dsp:PlS+(1|Replicate/Sample)	13	-362.014	752.9	0.00	0.488	0.75
	Total~Dsp+FmL+ PlS+Dsp:PlS+ FmL:PlS +(1|Replicate/Sample)	14	-361.696	754.8	1.84	0.195	
Day10	Total~Dsp+FmL+ PlS+Dsp:PlS +(1|Replicate/Sample)	13	-554.475	1138.0	0.00	0.699	0.71
Day15	Total~Dsp+FmL+ PlS+Dsp:PlS+FmL :PlS +(1|Replicate/Sample)	14	-605.284	1242.7	0.00	0.818	0.68
Experiment 3: generation 9							
Day7	Total~Dsp+ PlS+Dsp:PlS+(1|Replicate/Sample)	12	-101.085	228.9	0.00	0.680	0.99
Day10	Total~Dsp+FmL+ PlS+Dsp:PlS+(1|Replicate/Sample)	13	-419.994	869.7	0.00	0.697	0.85
Day15	Total~Dsp+FmL+ PlS+Dsp:PlS+ FmL:PlS +(1|Replicate/Sample)	14	-422.931	879.5	0.00	0.538	0.72

Experiment 1: generation 7 (Figure 18 – Figure 20).

Day 7. No significant difference is observed between the different levels of dispersal and the control, although, pairwise significant differences are observed between plant species for dispersal level 1 and 4.

Day 10. Differences between bean and tomato are detected for each dispersal level, in which the numbers on tomato are significantly lower. For the control no differences are observed between the plant species. Further, performance reached significant higher rates in the dispersal 4 treatment relative to the other dispersal treatments on tomato.

Day 15. On the last day of the follow-up of the population, the same pairwise differences between the plant species are seen as on day 10, but differences occur within the plant species groups. Dispersal 1 performs significantly less good than dispersal 2 and 4 on bean leaves and on tomato, dispersal level 3 is significantly fitter than dispersal 2.

Experiment 2: generation 8 (Figure 21 – Figure 23).

Day 7. The comparison between tomato and bean leaves was significant for the control and each dispersal level. In every case, the individuals on bean were performing better.

Day 10. On bean, the performance was significantly higher for the control relative to the dispersal levels. On tomato, the higher number for dispersal 1 compared with the control was significant. The pairwise comparison between bean and tomato was the same as for day 7.

Day 15. The total number of individuals on bean was significantly lower for dispersal 4 relative to dispersal 2. Further, on tomato, a significant difference was observed between the control in one hand and the different levels of dispersal in the other, which were all doing better. Significant pairwise differences between the two plant species were measured, lower population numbers were achieved.

Experiment 3: generation 9 (Figure 24 – Figure 26).

Day 7. The performance on tomato is in each dispersal level significantly lower than on bean. Within each group no significant values were noticed and also not for the control.

Day 10. As for day 7, the same observations between plant and bean leaves are detected. Also, some significant results were observed within the group on tomato, that is the control is performing worse than dispersal 1, 2 and 3, and, dispersal 3 has a significantly higher number than dispersal 4. On bean no differences were observed.

Day 15. The control group is significantly doing worse on bean relative to dispersal 1, 2 and 4 and is also doing worse on tomato compared with dispersal 2. In general, the individuals on bean are performing significantly better than on tomato.

Female longevity

Plant species was a fixed factor in the best model for the assays from generation 8 and 9 (**Table 5**). The effect was significant for generation 8, meaning that the females did longer live on bean than on tomato. Although, dispersal was not included in the best model, a Tukey's HSD test was done between the different levels of dispersal and the different plant species, but no significant values were revealed. Therefore, no significant values are indicated in **Figure 28**. It is illustrated in **Figure 27 – Figure 29.** The summary of the models is given in **Table 12** in the appendix.

Table 5: Dispersal. Results for the best model selection from mixed linear models with Poisson error distribution for the longevity of the female (FmL). Fixed factors in the full model are the plant species (PlS; bean or tomato), treatment (Trt; with competition, without competition and control) and the interaction between plant species and treatment (PlS:Trt). The random factors are the several females taken from their respectively replicate.

Model	df	logLik	AICc	delta	weight	R2m
Experiment 1: generation 7						
FmL~ 1|Replicate/Sample	3	-293.744	593.7	0.00	0.620	0
Experiment 2: generation 8						
FmL~PlS+(1|Replicate/Sample)	4	-342.862	694.0	0.00	0.847	0.07
Experiment 3: generation 9						
FmL~PlS+(1|Replicate/Sample)	4	-289.382	587.2	0.00	0.636	0.03

COMPARISON OF THE EVOLUTIONARY DYNAMICS AMONG THE DIFFERENT LOCAL ADAPTATION EXPERIMENTS

This part only includes the data from the nC treatment and the control. Data from C are again not considered due to the lack sufficient replicates. A comparison is made for each day between the three experiments. The factor experiment, which stands for the different generation times, is observed in each model (**Table 6**). The summary of the models is given in **Table 13** in the appendix. The figures are made with the observed data, in which the random and nested factors are not included (**Figure 17; Figure 30 – Figure 31**). Here-under, the results for each day will be provided.

Table 6: Results for the best model selection from mixed linear models with Poisson error distribution for the total number of individuals (Total). Fixed factors in the full model are the level of dispersal (Dsp; 1 – 4), the experiments (Exp; 1 – 3), the female longevity (FmL), the plant species (PlS; bean or tomato) and some of their interactions (Dsp:Exp; Dsp:PlS; Exp:PlS; FmL:PlS). The random factors are the several females taken from their respectively replicate.

Model	df	logLik	AICc	delta	weight	R2m
Day 7						
Total~Exp+PlS+Exp :PlS+(1|Replicate /Sample)	8	-789.618	1595.7	0.00	0.398	0.92
Total~Exp+FmL+PlS+Exp :PlS+(1|Replicate /Sample)	9	-788.607	1595.8	0.09	0.380	
Day 10						
Total~Dsp+Exp+FmL+PlS+Dsp:Exp+Exp:PlS+FmL:PlS+ (1|Replicate /Sample)	19	-1344.906	2730.4	0.00	0.623	0.89
Day 15						
Total~Dsp+Exp+FmL+PlS+Dsp:Exp+Dsp:PlS+Exp:PlS+FmL:PlS+ (1|Replicate /Sample)	22	-1403.728	2855.6	0.00	0.770	0.90

Day 7 (Figure 17).

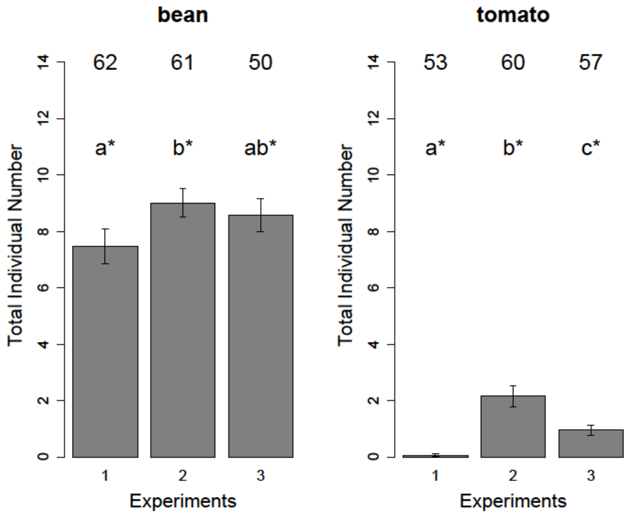

Figure 17: the total number of individuals on day 7 for the different dispersal levels (D: 1 – 4; 1: 2 mites/week, 2: 3 mites/week and 3: 5 mites/week, 4: 10 mites/week) and experiments (E: 1 – 3; 1: generation 7, 2: generation 8 and 3: generation 9) on bean and tomato. The letter code on top indicates the differences between the experiments within each dispersal level.

Given that the factor dispersal is not included in the best model for this day (**Table 6**), only the plant species and the different experiments, performed at generation 7, 8 and 9, are compared. At all measured generations, the performance on bean is significantly higher compared with tomato. Further, some significant values are observed within the plant species. The total number of individuals is significantly higher for experiment 2 related to experiment one in both plant species and, on tomato, the value of the third experiment is in the middle of experiment 1 and experiment 2.

Day 10 (Figure 30).

The same dispersal level within the same experiment is compared between bean and tomato and significant values are observed in all cases. Also, the comparison is made between the experiments within a certain dispersal level on a certain plant species. The only measured significant value within the group on bean is between the experiments for dispersal level 1, in which the third experiment (generation 9) is performing significantly better than experiment 1 (generation 7). On tomato, the same pattern is observed for dispersal level 1 and 2. Namely, the three experiments are significantly different from each other, with a better performance of experiment 2 (generation 8) and 3 (generation 9) related to experiment 1 (generation 7) and with experiment 3 doing significantly worse compared to experiment 2. The total number of individuals, observed for dispersal 3, is significantly lower for experiment 1 than for 2 and 3. Further, within dispersal 4, experiment 1 and 3 are significantly worse performing related to experiment 2.

Day 15 (Figure 31).

All pairwise comparisons for the same dispersal level within the same experiment are significant between bean and tomato. Besides, the same pattern is perceived for each dispersal level on tomato, in which experiment one (generation 7) is performing significantly less good than the last two experiments. On bean, significant differences are observed for dispersal 1, experiment 2 reaches lower number related to experiment 3, and for dispesal 4, experiment 2 has a significantly lower performance compared with the other two experiments.

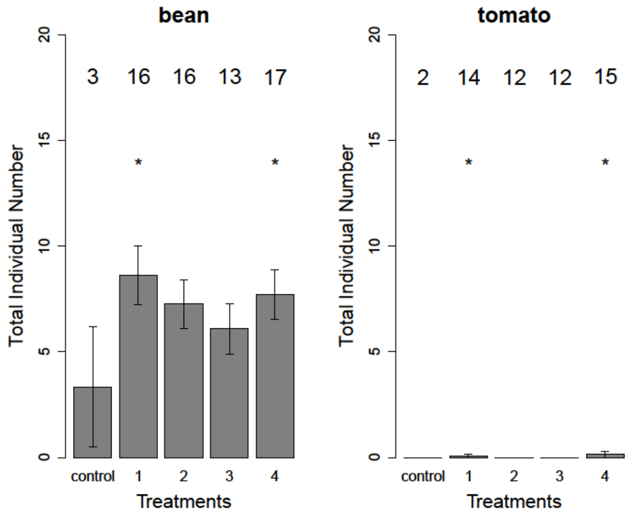

Figure 18: the total number of individuals for the different levels of dispersal on day 7 (generation 7).*

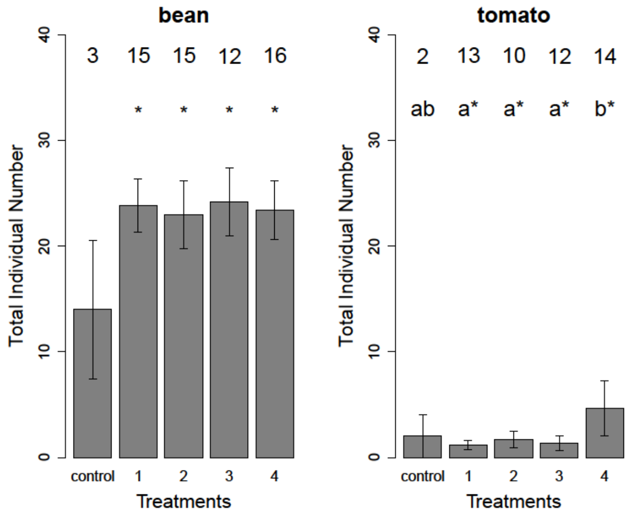

Figure 19: the total number of individuals for the different levels of dispersal on day 10 (generation 7).*

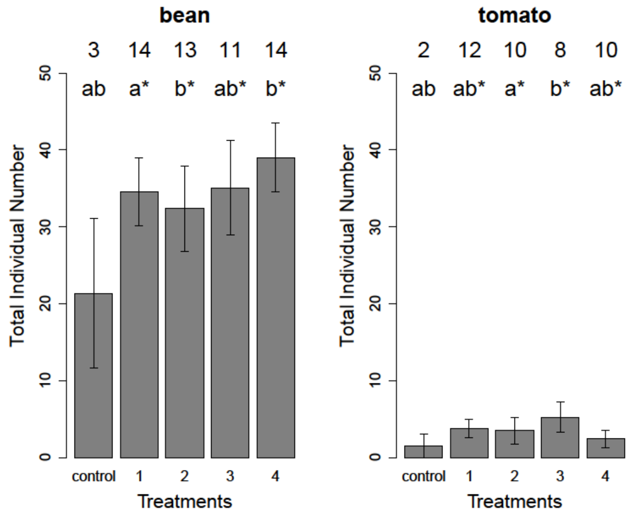

Figure 20: the total number of individuals for the different levels of dispersal on day 15 (generation 7).*

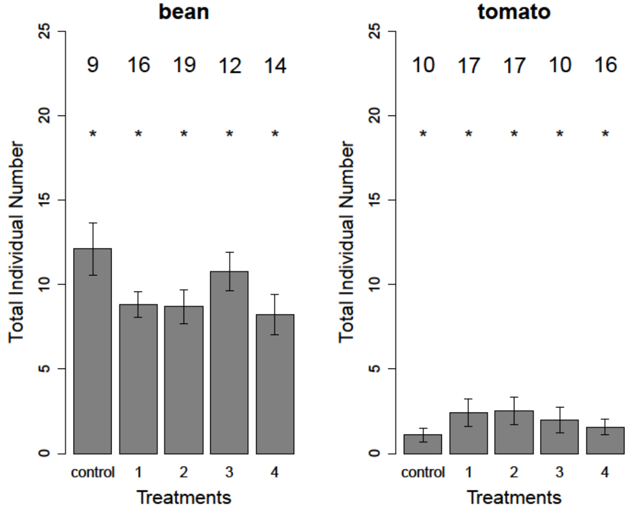

Figure 21: the total number of individuals for the different levels of dispersal on day 7 (generation 8).*

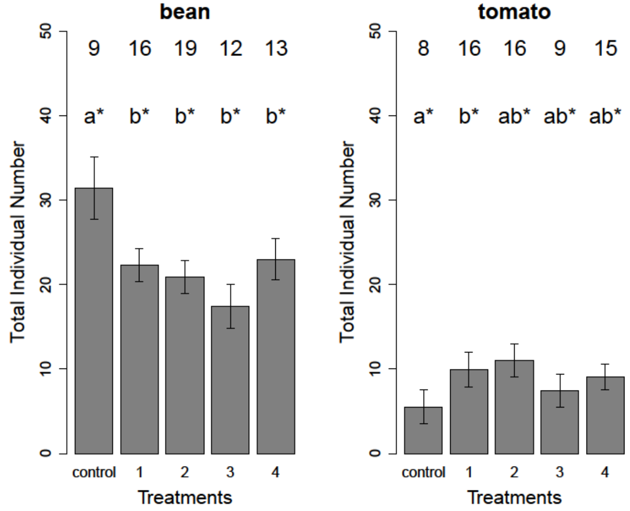

Figure 22: the total number of individuals for the different levels of dispersal on day 10 (generation 8).*

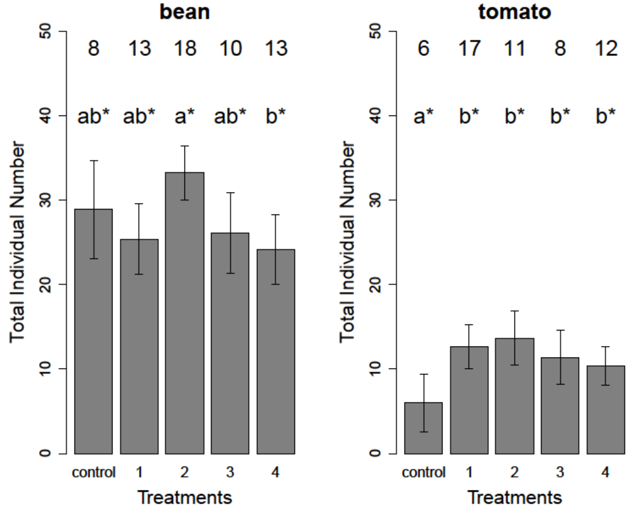

Figure 23: the total number of individuals for the different levels of dispersal on day 15 (generation 8).*

***The error bars are plotted in the figure and the sample sizes are on top of the figure. The stars indicate significant differences within the same treatment between the plant species, bean and tomato, and the letter code is used to compare within a certain plant species between the treatments. The figures are made with the observed data.**

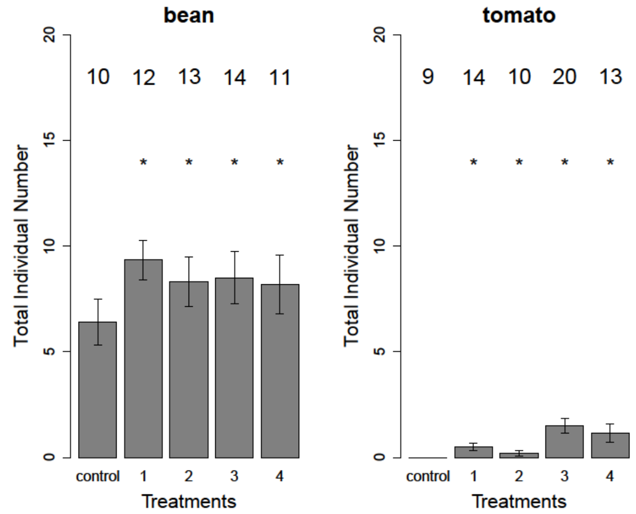

Figure 24: the total number of individuals for the different levels of dispersal on day 7 (generation 9).*

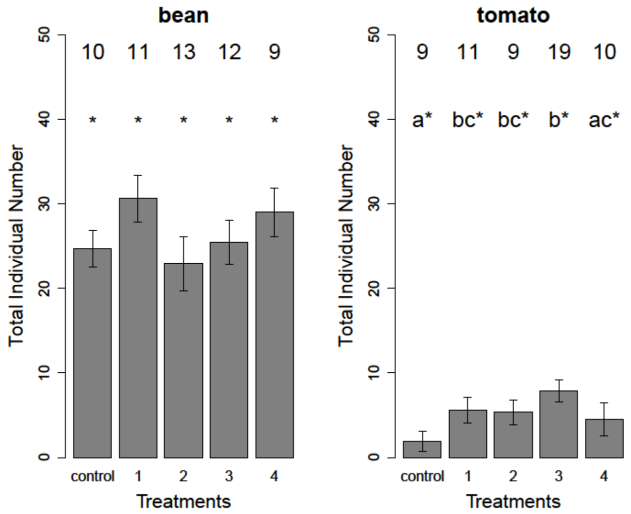

Figure 25: the total number of individuals for the different levels of dispersal on day 10 (generation 9).*

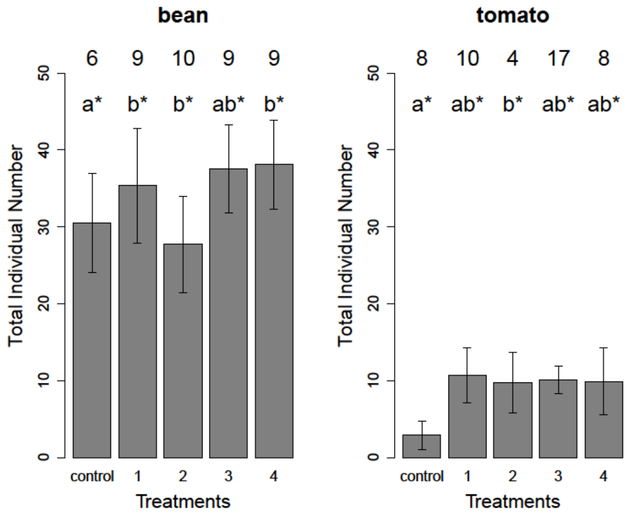

Figure 26: the total number of individuals for the different levels of dispersal on day 15 (generation 9).*

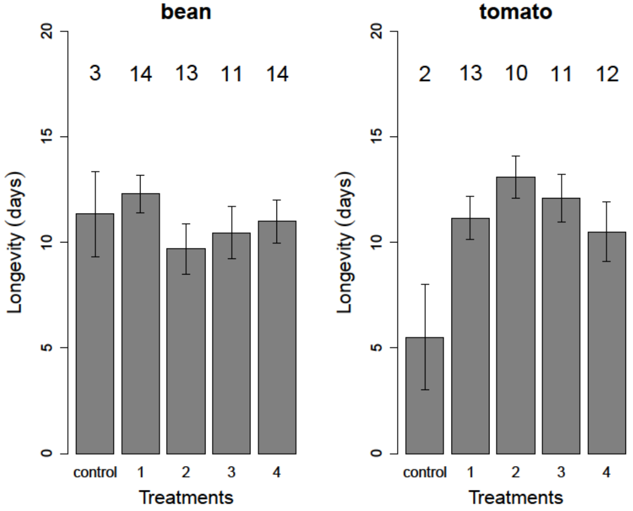

Figure 27: the female longevity on bean leaves for generation 7 related to tomato leaves for the different treatments.*

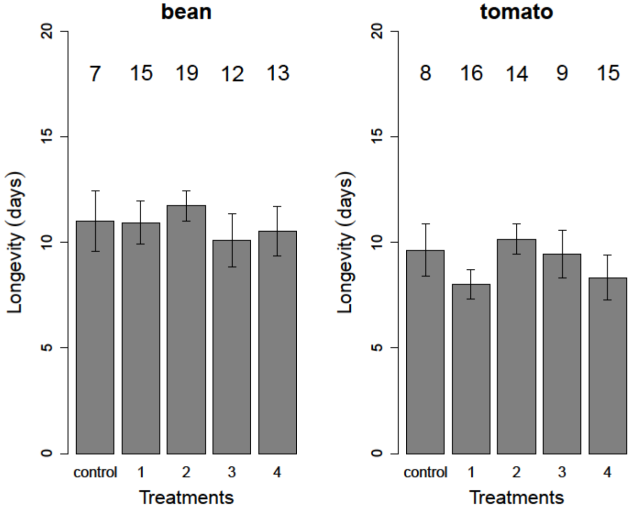

Figure 28: the female longevity on bean leaves for generation 8 related to tomato leaves for the different treatments.*

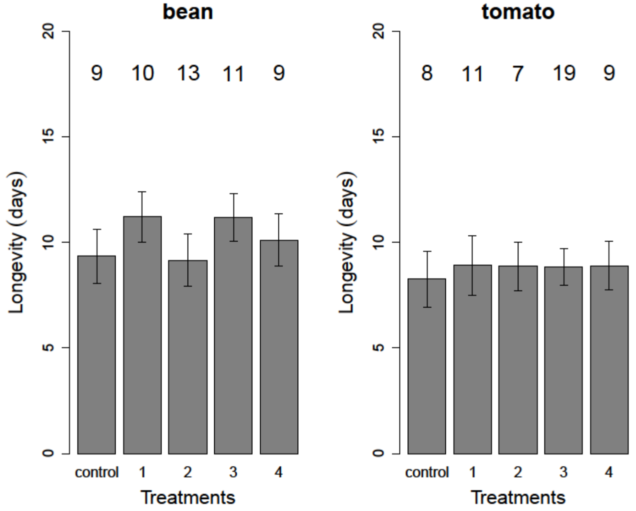

Figure 29: the female longevity on bean leaves for generation 9 related to tomato leaves for the different treatments.

***The error bars are plotted in the figure and the sample sizes are on top of the figure. The stars indicate significant differences within the same treatment between the plant species, bean and tomato, and the letter code is used to compare within a certain plant species between the treatments. The figures are made with the observed data.**

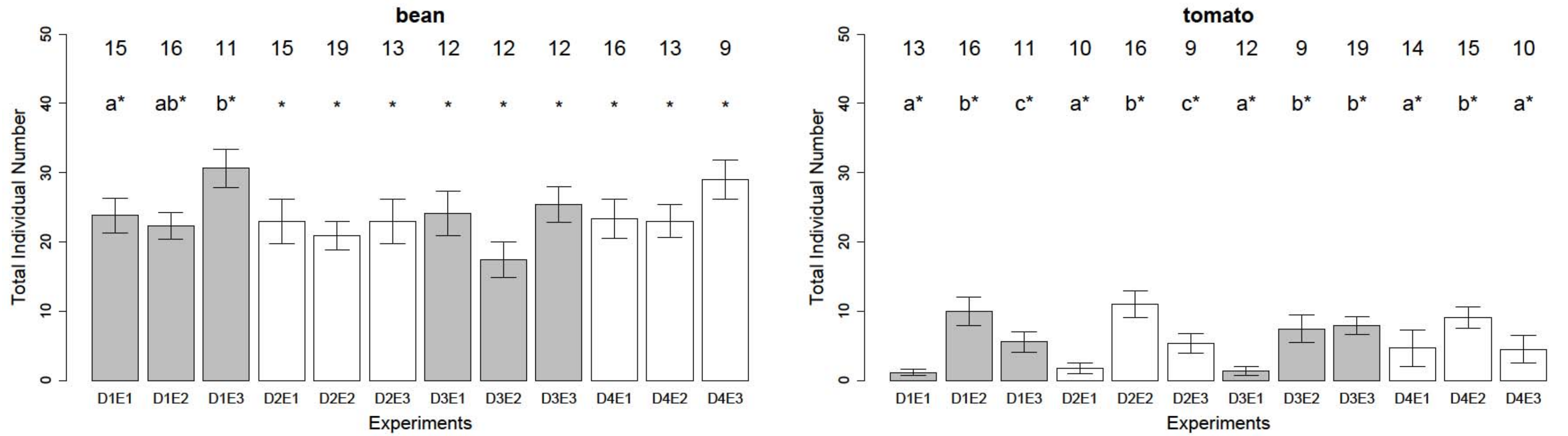

Figure 30: the total number of individuals on day 10 for the different dispersal levels (D: 1 – 4; 1: 2 mites/week, 2: 3 mites/week and 3: 5 mites/week, 4: 10 mites/week) and experiments (E: 1 – 3; 1: generation 7, 2: generation 8 and 3: generation 9) on bean and tomato. The letter code on top indicates the differences between the experiments within each dispersal level.

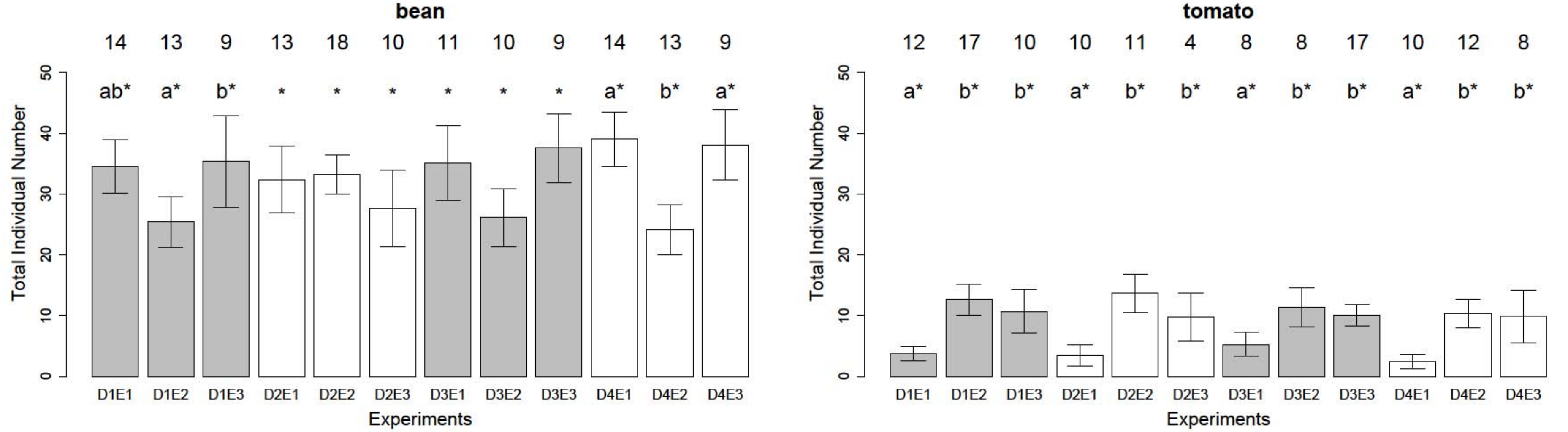

Figure 31: the total number of individuals on day 15 for the different dispersal levels (D: 1 – 4; 1: 2 mites/week, 2: 3 mites/week and 3: 5 mites/week, 4: 10 mites/week) and experiments (E: 1 – 3; 1: generation 7, 2: generation 8 and 3: generation 9) on bean and tomato. The letter code on top indicates the differences between the experiments within each dispersal level.

***The error bars are plotted in the figure and the sample sizes are on top of the figure. The stars indicate significant differences within the same treatment between the plant species, bean and tomato, and the letter code is used to compare within a certain plant species between the treatments. The figures are made with the observed data.**

5. DISCUSSION

The hypothesis that **phylogenetically related competitors** will hinder specialisation is confirmed in the considered two-species ‘community’, given that the establishment of the two-spotted spider mite could only be achieved for shorter periods. These cases were probably affected by the current level of lower interspecific competition and the introduction of successful founders. Although the dispersal rate might reduce the chance for extinction, referred to as rescue effect (Gotelli, 1991), it cannot compensate for the much higher growth rate of *T. evansi.* Olsen and Klanderud (2013) demonstrated that, even there is dispersal, a local environmental filter, such as micro-climate or biotic interactions, becomes more important during establishment and could even preclude it. Although, this research is done in plant communities, the same conclusion might be drown for this ‘community’ of arthropod herbivores.

The competitor performed better than the focal species, which was expected. But, the extreme option, the impediment of establishment, was rather unpredicted, since, some populations of the two spotted spider mite are known to be a serious pest on tomatoes (Salinas et al., 2013). However, in Ferragut and others (2013) the impact of the invasion of *T. evansi* on the natural spider mite community was studied, in which a competitive displacement of *T. urticae* by the red tomato spider mite was observed. Possible responsible factors are the resistance against acaricides, the release of native enemies, the manipulation of plant defences and the same type of complicated silk webs which can be used. Furhter, *T. evansi* is rather considered as a specialist species on plants from the family Solanaceae, of which the tomato plant is a member (Navajas et al., 2013). This indicates that, even if our focal species would be adapted, the tomato spider mite is an extremely strong competitor.

In this research, the **ecological dynamics** for the non-competition treatment reveal quite interesting results (**Figure 8)**

The number of mites, which were dispersed every week, are each time subtracted from the total number of females and in case the result would be less than zero, a zero was used. This correction was done to determine whether the dispersal level has an impact on the population growth, since the potential differences should be higher than the net input of immigrants. The most striking outcomes are visualised for the highest dispersal rate (10 mites/week). Until the fourth generation, the number of adult females for this dispersal level was significantly higher related to the other dispersal levels. At the generation five and six, no significant difference is revealed between, respectively, the highest three and two immigration rates, but these were still significantly performing better than the lower ones. A quite surprising result is seen at the seventh generation, since none of the dispersal levels seems to be different from each other at this time point. From generation eight onwards, the populations receiving the highest number of immigrants are doing worse. This is clearly noticeable from the ninth generation onwards. In this generation a turning point is detected, in which the highest dispersal level is even significantly performing worse than the following two levels (3 and 5 mites/week). The same tendency is observed for generation 10 and 11. In fact, in these periods, a significantly lower performance is observed related to each other level of dispersal level, although, in the last generation no significant differences were detected between the highest two levels.

Comparing with the fitness tests, the turning point at generation nine, came together with the indication of migration load, which will be discussed further. Besides, this turning point is visible for all the different levels of dispersal. So, in the beginning the principle the higher the dispersal the better is followed, but at a sudden generation, the lower ones are better. It is supposed that at this turning point the input of potential beneficial alleles to increase the initial allelic frequency, which plays a major role for local adaptation (Olson-Manning et al., 2012), is less important than the existing beneficial alleles under selection. Further, the effective population size is possibly big enough to counteract genetic drift and, if a stable mutation rate is expected, to increase the total number of mutations in the population (Olson-Manning et al., 2012). This might be an example of **eco-evolutionary dynamics**, in which an evolutionary change, caused by natural selection, can influence the survival or reproductive success and, consequently, has an impact on the population dynamics in a short time-scale (Turcotte et al., 2011; Pelletier et al., 2009). This indicates that the link between ecology and evolution is not a one-way traffic, in which ecology affects evolution, but rather a reciprocity between these two processes (Turcotte et al., 2011).

Some other notable features in **Figure 8** are the increase in the number of adult females for the highest level of dispersal at the fourth generation and the sudden decrease in the number of adult females for all the levels of dispersal at generation ten. The increase could potentially be the result of selection on life-history traits, impacting for instance the developmental rate or the number of offspring, leading to this spectacular increase. Further, a drop in the population size is detected in the next generation, followed by an increase which reaches almost the same height as in the fourth generation. A possible explanation could be the exceeding of the carrying capacity, *K*, which is the number of individuals in a population that can be sustained in a certain environment, shaped by the biotic and abiotic conditions. Such an increase could lead to overexploitation of the resources and, consequently, starvation. The decline in the fifth generation could be the result. Another possible explanation might be that more resources were available, because the plants for the highest dispersal level had grown faster related to the other plants. However, this is not very convincing, since seven replicates were used and, therefore, the chance that all of them had a faster growth rate is rather small. Unfortunate, the size of the plants is not recorded in the data. Such an explanation is more plausible for the sudden decrease at the tenth generation, because the plants were selected to provide the same amount of resources.

Few conclusions can be drawn about the performance of the individuals under competition compared with those of the control and those from the treatment without interspecific competition, due to the absence of enough replicates. I will discuss some outcomes and possible tendencies based on the low amount of established populations that could be compared . The discussion is therefore rather speculative but nevertheless important in light of our research questions. Only the comparison from the competition treatment with the others will be considered, since the differences between the non-competition treatment and stock population will be discussed in following paragraphs. Also, the competition treatment is referred to as generation 8 and 9, but, this is rather artificially, since the effective establishment was much later compared with the non-competition treatment (**Figure 8**).

The comparison among the individuals from the different treatments at generation eight on bean indicate a possible ecological release effect (**Figure 13**). Within this generation, no significant differences are revealed at day seven on bean and, for day ten, the stock population is performing significantly better related to the competition treatment (**Figure 11** – **Figure 12**). This result could be explained by a cost of adaptation. But, this is not very convincing evidence, since only two individuals are considered for the competition treatment. A better example is visualized in the comparison between the different levels of dispersal, therefore, this effect will not be explained here. At day fifteen, exactly the reverse is obtained, in which the competition treatment is performing significantly better than the control and the non-competition treatment. This occurrence could be explained by the ecological release, in which the ecological opportunity is a more hospitable environment with more accessible resources which can be consumed in the bean common garden compared with the tomato experiment plants (Des Roches et al., 2011). Also, since a two-species ‘community’ is considered, this ecological opportunity is further shaped by the enemy release effect. Besides, some researchers state that certain generalistic species are actually a heterogeneous group of relatively specialised individuals, referred to as individual specialisation (Bolnick et al., 2007). So, it is reasonable that the individuals which were most individually specialised on bean leaves who went through strong selection on tomato, experienced less intraspecific competition, leading to an increase of the population. But, as already mentioned before, only two individuals are used for this analyses, which is way too low to make real conclusions. In the other measured generation, generation 8, no significant differences between, on the one hand, the competition and, on the other hand, the other treatments is revealed (**Figure 14** – **Figure 16**).

The results between the different treatments on tomato are inconsistent (**Figure 11** – **Figure 16**). Only day seven will be discussed for generation 8 on tomato, since the groups for the other days consists of only one individual (**Figure 11**). A surprising tendency is obtained for day 7, in which the competition treatment seems to reach higher number than the other treatments, although it is only significant different from the control population. But, the p value attained for the difference between non-competition and competition is marginal.

However, no real conclusions or hypothesis could be assumed with this low sample size, although, there are some indications that a stronger selection pressure could lead, in this case, to a higher rate of local adaptation. On the other hand, no such results were obtained for generation 9 on tomato (**Figure 14** – **Figure 16**). At day seven, no differences were measured between the treatments. The competition treatment was performing lower compared with the other treatments on day ten and, if also the marginal values ($0.05 < p < 0.10$) are considered, there was no difference with the control and it was significantly performing worse related to the non-competition treatment. The same result was obtained at day fifteen, except that the comparison between the competition treatment and the non-competition treatment already shows significant differences at the 0.05 significance level. Therefore, it is supposed that local adaptation did not occur. Since, the two generations show completely reverse results, both possible tendencies should be considered and more research is necessary to unravel the effect of competition for the rate of local adaptation.

Further, it was tested whether a difference for the trait female longevity did occur between bean and tomato and, consequently, if this could reveal some adaptation. Magalhães and others (2009) investigated the same trait and detected no significant differences for female longevity. The same result was obtained for generation 7 and 9 (**Figure 27** and **Figure 29**), but in generation 8 significant differences were observed between bean and tomato. This is not indicated in **Figure 28**, because the figure reports also the different levels of dispersal and, therefore, no significant differences were measured. However, the best model did not take the different levels of dispersal into account (**Table 5**) and the summary of the model did show a significant difference between the plant species bean and tomato (appendix: **Table 12**). Nevertheless, the lack of significant differences between the control and the levels of dispersal indicates only that the females on tomato are less fit, considering their longevity, related to those on bean leaves. Also, the explained variance of the treatments (R^2 values with female longevity as a response variable) is extremely low with respectively 0%, 7% and 3% for generation 7, 8 and 9, meaning that almost no variation could be explained by the fixed factors in the model and that it is just random or could be explained by a factor, which was not measured in this study (**Table 5**).

The different rates of dispersal that were considered in the fitness tests reveal clearly that spatial dynamics have the potential to affect the rate of ecological specialisation. I will fist discuss the performance of tomato/island mites on their original host plant from generation seven on bean (**Figure 18** – **Figure 20**). The females, which were collected from the non-competition treatment, performed seemingly better than the stock population. Although, we have to pay attention to the fact that no significant differences were observed. The lack to detect significant differences can be the result of the very small sample size of the stock population, since the *p* value is depending on it, and the huge variation between the individuals. Obviously, it is also possible that there are no real differences.

However, there is evidence that the stock population is performing worse during this assay, which is demonstrated in **Figure 32** and **Figure 33**. In both days, the performance of the population on bean is significantly worse in the first measured period. Besides, the huge variation makes it even not possible to detect a significant difference between tomato and bean on day 15. A possible explanation for this result could be that the stock population had suffered from inbreeding and genetic drift, resulting in a decreased fitness of the population by means of inbreeding depression (Reed & Frankham, 2003). This effect is known to have a big impact and is especially caused by the reduction of heterozygosity (Charlesworth & Charlesworth, 1987). Even though, inbreeding is less likely in haplo-diploid organisms, it does happen (Oku, 2014). A possible remedy for this phenomenon is migration (Reed & Frankham, 2003), which did not occur in the utilized stock population. However, Tien and others (2011) demonstrated a female preference for mating in *T. urticae*, implying a recognition of kin and, as a consequence, a possible way to avoid inbreeding. But, knowing that fertilised females disperse from their natal colony and can on their own be the founder of new populations, refusing mating with relatives might not be very advantageous. Given that her offspring could otherwise not reproduce. Therefore, the avoidance of inbreeding is possibly not subjected to a strong selection pressure (Oku, 2014).

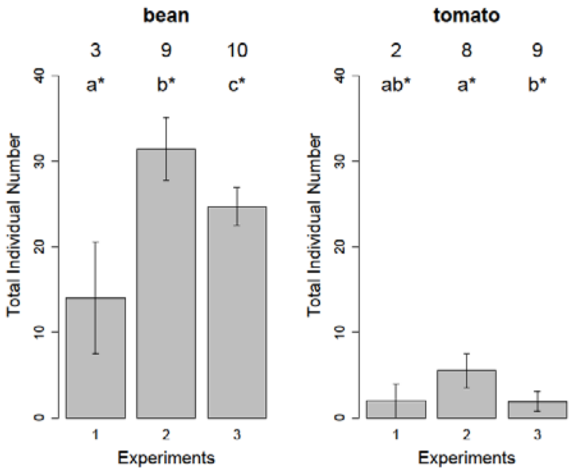

Figure 32: the total number of individuals on day 10 for the stock population, a comparison between the different experiments on bean and on tomato. The letter code on top indicates the differences between the experiments and the stars indicates the differences between bean and tomato within the same experiment. The figure is made with the observed data.

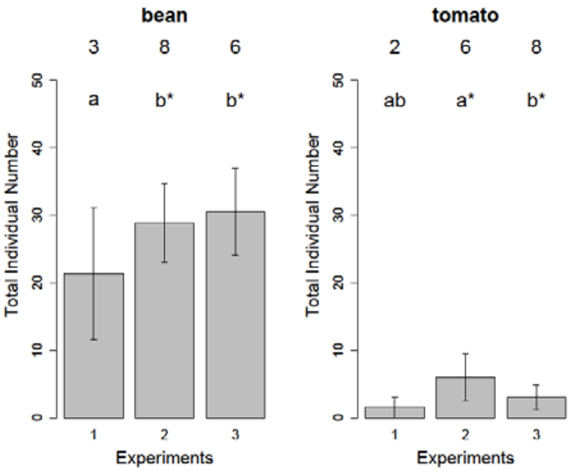

Figure 33: the total number of individuals on day 15 for the stock population, a comparison between the different experiments on bean and on tomato. The letter code on top indicates the differences between the experiments and the stars indicates the differences between bean and tomato within the same experiment. The figure is made with the observed data.

The considered populations are evidently not yet well adapted to the new host plant in generation 7 (**Figure 18** – **Figure 20**). There is a tendency for local adaptation in the last measured day, though, it is not significant. This time frame is apparently not sufficient to detect local adaptation, which was predictable. Despite this short time frame, some significant differences are observed between the different levels of dispersal. The performance of the highest level of dispersal (10 mites/week), was significantly better than the other dispersal regimes on day 10. By comparing this result with the ecological dynamics (**Figure 8**) this number of migrants seems suitable to achieve higher population sizes until about generation 7. Since, more founders are arriving each time, the effect of bottlenecks is reduced by enhancing the genetic variation and replenish the local population size (Dlugosch & Parker, 2008). As a consequence of the bigger genetic variation, more chance for beneficial alleles to become expressed. Besides, bigger population sizes also increase the total number of advantageous mutations, considering a constant mutation rate (Olson-Manning et al., 2012). The tendency on day 15, in which the higher the dispersal is, the better the performance, is more or less consistent with the population sizes obtained from the ecological dynamics, although no significant differences are measured at this generation. This is especially the case for dispersal 3, which has in both situations the best performance (**Figure 8** and **Figure 20**). Further, the total number of individuals for the highest dispersal level is lower at day fifteen compared with five days before, which could be an indication for a high mortality during the development of the offspring. In Boggs (2009) differences for resource acquisition and allocation are stated between specific life stages in insects and also the influence of harsh and benign environments is considered. Although, spider mites belong to the class of the Arachnida, such differences could also be the explanation for the sudden decrease in the total number of individuals. Besides, the longevity for dispersal 4 is slightly lower, although not significant, related to the other dispersal levels (**Figure 27**), which reduces the chance for new larvae to hatch between day 10 and 15. If the juvenile mortality differs between the life stages, a better measurement of the real fitness might be the number of adult females on the last observed day. Unfortunate, no adult females are already perceived for the 7th generation at day 15.

The most striking feature on bean for generation 8 is the lower performance for the different levels of dispersal related to the stock population, potentially indicating a cost of adaptation (**Figure 21** – **Figure 23**). This is observed on day 10 and the same pattern is detected for day 7, but here the performance of the control is not significantly better. The observed pattern could indicate a cost of adaptation. Conversely, Magalhães and others (2009) found that no costs are involved in the adaptation toward novel host plants. In this study, the experimental evolution of *T. urticae* was implemented on cucumber, which was their original host, pepper and tomato. The performance of the spider mites was compared between the three plant species after 15 and 25 generations. However, our results indicating a possible cost of adaptation were from generation 8, in which the mites were on average 4 months on tomato. Besides, the spider mites in the research of Magalhães and others (2009) were about 8 months on their new host plants, which denotes that a potential cost at generation 8 is not contradicted by this previous research. On the other hand, Fry (1990) discovered trade-offs for

T. urticae. The two-spotted spider mites that were originally maintained on tomato plants and placed on bean plants for more than ten generations, showed significant declines in survival rates when placed back on tomatoes. Further, the observed trend on day 7 and 10 is not visible anymore in day 15. But, if only the adult females are considered as a response variable, the control is still performing better on day 15 (**Figure 34**). Although, it is not known whether the difference in performance is significant, given that the used methods are not sufficient to deal with the data. A zero inflated model should be used in the future. Another explanation for the lower performance of the dispersal treatments related to the control, can be that the control is overachieving at day 10. In **Figure 32** a significant difference with the other two assays is observed for the control on bean, while on the other hand, the individuals from the dispersal treatments are not doing worse related to the other trials, except perhaps for dispersal 3 (**Figure 30**). Following the interpretation of the potential inbred stock population observed in the 7th generation, this could be the result of outbreeding, which is known to be a potential cure for inbreeding depression. This could be achieved by the female preference for unrelated mating partners (Tien et al., 2011). But, the intermixing could also lead to certain problems, such as the disruption of beneficial gene interactions (Edmands & Timmerman, 2003). This seemingly did not occur. Further, the second lowest dispersal level (3 mites/week) is in both cases, with only the females or with all the offspring as response variable, performing better than the other levels of dispersal. This is consistent with the results of the ecological dynamics (**Figure 8**), in which the highest number of adult females is obtained for the second dispersal level, though not significantly different from the two highest levels of dispersal (5 and 10 mites/week). This level of dispersal is supposed as an intermediate level of dispersal and can, therefore, possibly favour specialisation instead of generalism (Venail et al., 2008).

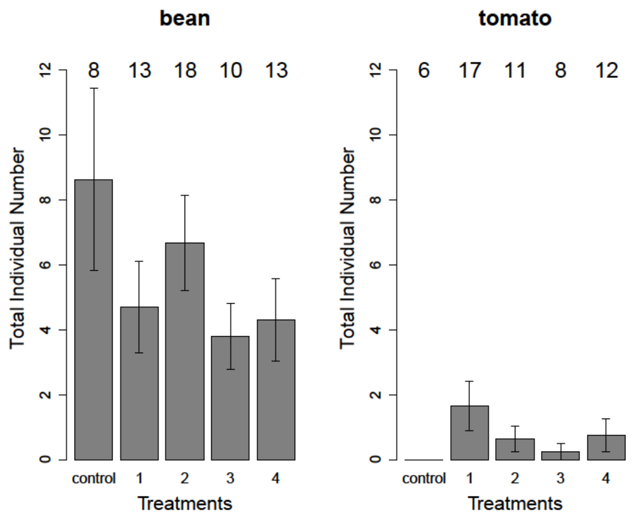

Figure 34: the total number of females on day 15 for generation 8, comparison between the different experiments on bean and on tomato. The letter code on top indicates the differences between the experiments and the stars indicates the differences between bean and tomato within the same experiment. The figure is made with the observed data.

From generation 8 onwards, signals of local adaptation become prevalent (**Figure 21** – **Figure 23**). The different dispersal levels from the non-competition treatment are in each case, although not always significantly, performing better than the control on tomato, indicating **local adaptation**. Only at the last day of measurement this complete phenomenon is significant. But, if also the marginal significance values are taken into account, not only the lowest dispersal level (2 mites/week), but also the dispersal level consisting of 3 mites/week reaches in day 10 significant higher values for the total number of individuals related to the control. This means that already at generation 8 a possible indication for local adaptation can be visualised, which is almost half of the generation time previous known to be sufficient to detect local adaptation in *T. urticae* (Bonte et al., 2010; Magalhães et al. 2009). The pattern in **Figure 23**, in which the performance is getting lower for highest level of dispersal, could indicate the effect of genetic load. This will be discussed later, since it is not significantly proven in this assay, which means that at generation 8, the highest dispersal level used, 10 mites/week, is still not too high. Besides, the fact that the only measured significant difference at day ten was for the lowest dispersal level on tomato (**Figure 22**) is rather unexpected compared with the ecological dynamics (**Figure 8**), in which this dispersal level was the only one which was significantly different, in a way that it had the lowest performance. Therefore, it was expected to have the lowest number. However, no significant differences were obtained between the different levels of dispersal from the non-competition treatment. So, for this generation it is clear that all the used dispersal levels provide sufficient genetic variation, necessary for local adaptation.

Patterns in generation nine were generally similar as during the previous generation, but signatures of migration load become visible (**Figure 24** – **Figure 26**). The performance on bean did not reveal significant differences on day 7 and 10. Only the last day revealed significant differences, but, since the figure is made with the observed values, which does not consider the random and nested factors, the significant letters are counter-intuitive with the figure. Therefore, a figure is made with the calculated expected values, by using the output from the best model (**Figure 35**). Here, the tendency which was observed in the previous generation, is retained, indicating a **cost for local adaptation**.

On tomato, as in generation 8, the different levels of dispersal are performing better than the control in generation 9 (**Figure 24** – **Figure 26**). Further, another interesting occurrence is observed, **migration load** (Bolnick & Nosil, 2007). The higher level of migrants counteracts the evolution of local adaptation, due to more non-adapted alleles. This effect is also referred to as gene swamping (Bridle & Vines, 2007). This principle is especially visible at day 10, since all

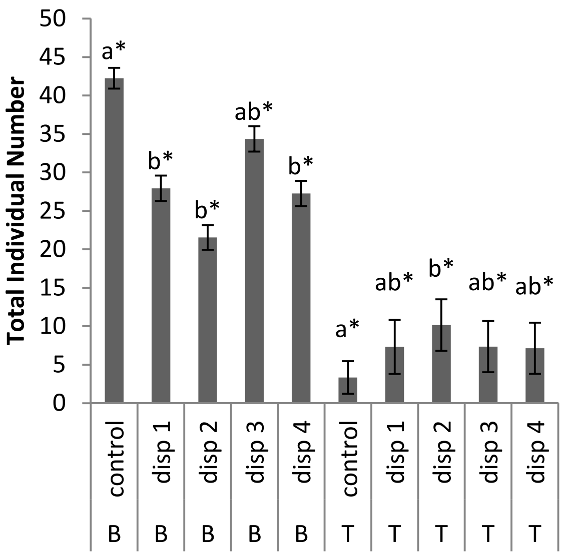

Figure 35: the total number of individuals on day 15 for generation 9, comparison between the different experiments on bean and on tomato. The letter code on top indicates the differences between the experiments and the stars indicates the differences between bean and tomato within the same experiment. The figure is made with the expected data.

the dispersal levels are significantly different from the stock population, except for the highest level of dispersal. Moreover, if also the marginal values ($0.05 < p < 0.10$) are considered, the same is occurring at day 15. Therefore, it is concluded that at generation 9, the highest dispersal is no longer suitable. Besides, it would be interesting to measure the lowest possible level of dispersal, since it is expected that a certain amount of dispersal and, subsequently, gene flow is obligated to achieve sufficient genetic variation (Poisot et al., 2011). Unfortunately, it was not possible in this research, because at this way a chance to establish under the competition of *T. evansi* was totally excluded.

The comparison between the different generations divulges the effect of local adaptation towards tomato on each measured day (**Figure 17**; **Figure 30 – Figure 31)**.

At day seven, the seventh generation is performing worse on tomato compared with the eighth and ninth generation, indicating local adaptation. Further, it is remarkable that the last measured generation is performing worse related to the second measured generation, given that it was expected that it would perform better. Several possible explanations are suggested.

First, the time when the pictures when taken, could lead to potential differences. The pictures for generation eight were taken between 3.30PM and 9.30PM and those for generation nine between 9AM and 5PM. This means that the spider mites could have had more time to hatch in generation eight, leading to the higher observed number of individuals in this generation. But, also the exact time when the quiescent deutonymph hatched is important to know whether they really had more time, which is almost impossible to measure due to the big number of replicates. Therefore, it could have been better to include time in the full model, but the real time spend on the leaf is impractical.

Second, the tomato plants for the last generation were almost one week older, resulting in a possible better resistance against herbivores, for instance more toxic substances, more multicellular hairs and glandular trichomes, etc. Research about the influences of the age of the leaves was done for *T. urticae* on cotton plants. Although, some disagreement occurs in the literature. Wilson (1994) concluded that the lowest fecundity was found for cotyledons and old leaves and he suggested that the younger leaves were preferred because of the higher levels of nitrogen. Besides, Karban and Thaler (1999) discovered a higher growth rate on the cotyledons, possibly because of the higher rate for photosynthesis or other related processes, but no real differences were found between younger and older leaves. A possible way to overcome this problem is by analysing the pictures and adding more factors to the model, for instance the level of existing trichomes.

Third, in the ecological dynamics (**Figure 8**), there is also a drop in the population size. In case these two effects are related with each other, it is suggested that the origin should be found in the experimental room and that the population size did affect the evolutionary change. The other direction of the eco-evolutionary dynamics is rather implausible, since in that case, all the different replicates needed to evolve in a way resulting in a decrease in the population size. Before, it was argued that the plants maybe did not grow enough due to a general incident, leading to a smaller possible population size. For instance, a possible explication might be a change in growing conditions in the experimental room.

At day ten there is again the indication of local adaptation, since the last two generations are performing significantly better. The same tendency as for day seven is visible in the lowest two levels of dispersal, for which the same explanations could be considered. Although, the time the pictures were taken was not strikingly different for this day. For the third level of dispersal (5 mites/week) no significant differences were found between generation 8 and 9. The migration load, which was seen for the highest level of dispersal in the dispersal treatment at generation 9 (**Figure 25**), is also visible in this comparison between the different experiments.

The significant differences visualised for the last measured day did reveal local adaptation, given that the last two generations were both performing significantly better than the first one.

The spider mites which were put on bean from generation seven produced a significant lower number of offspring related to generation eight. The third experiment on this day did not significantly differ from the other two.

At day ten, the only measured significant difference is within the lowest level of dispersal between generation seven and eleven. This could be the result of eco-evolutionary dynamics (Pelletier et al., 2009). In **Figure 8** it is seen that a strong increase in population size is measured after the ninth generation. Therefore, it is assumed that an evolutionary change, which increases the total number of offspring, has resulted to this abrupt increase in the counted number of adult females. This is possibly the change, which is measured in the evolutionary dynamics.

The cost of local adaptation, which was especially observed at generation eight, is the potential cause of the observed pattern for day fifteen. The lowest dispersal level at generation eight is significantly performing worse compared to the last measured generation. Further, the last dispersal level revealed the same tendency, but here also generation seven is significantly performing better than generation eight.

CRITICAL REFLEXIONS AND CONSEQUENCES FOR FURTHER RESEARCH

Due to the extreme interspecific competition, it was not possible to achieve establishment during the whole period of measurements in the competition treatment. However, it remains to be seen whether adapted populations of the two spotted spider mite, instead of populations which were originally maintained at another host plant, could establish in this strong competitive environment. Therefore, it would be interesting to use the adapted spider mites as mainland population to disperse from. Parsons (1990) argued that an environmental stress, such as a novel host plant, can induce general stress responses, due to the contribution of the same underlying molecular mechanisms in an evolutionary change. For instance, the evolution towards a more efficient food strategy, such as a sigmoid functional response (Holling's Type III), for which a change to alternative food sources is a possible mechanism (van Baalen et al., 2001). Because of this, it is plausible that the establishment under interspecific competition can be easier, because of the adaptation towards the novel host plant, a general adaptation towards stress, or because of a mixture of the two. To determine whether a locally adapted species did rather evolve its competitive abilities instead of adapt towards a novel host plant, a comparison of the fitness under interspecific competition can be made between a population, which has been recently under stress by the adaptation towards a novel host plant, and a population, which has been maintained on the same host plant for several generations.

Further, it is not known which number of immigrants would be necessary to achieve establishment under such level of interspecific competition. Therefore, the design could be extended by using a higher number of immigrants and, perhaps, also another sequence of introduction. In this way, it can be determined if, in such a system under a strong phylogenetically related competitor, the range boundaries will disappear or maintained by the interspecific competition. Further, it would be interesting to see if local adaptation can occur, because two possible explanations for failures are considered. If the connection between the mainland, bean, is not sufficient, small populations with high genetic drift, Allee effects and a lower chance for beneficial mutations will lead to the obstruction of local adaptation. On the other hand, migration load could occur, which washes out the possible adaptation (Bridle & Vines, 2007).

Also, the priority effects of historical contingency could possibly has an impact (Vannette & Fukami, 2014). In the design used for this research, the competitor was present before the focal species. In this way, *T. urticae* was at the start of the competition under a strong interspecific competition. Since, indications of local adaptation of *T. urticae* are, under the current conditions, noticeable at generation 8, an interesting case would be, to introduce the competitor at this moment. Besides, other levels of interspecific competition can be investigated by using, next to phylogenetically related competitors, also less related species.

6. CONCLUSION

1. The general conclusion for this research is that competition with phylogenetic related species can limit the process of specialisation, given that in the considered two-species 'community' the focal species was not even capable to establish during the whole measurements of the ecological dynamics.

2. Indications for local adaptation can already occur at the eighth generation for the *Tetranychus urticae,* which was originally maintained on bean and adapting towards tomato.
3. Evidence was found for eco-evolutionary dynamics in which an evolutionary change, caused by natural selection, impacts the survival and reproduction of a population in a small time-scale.
4. Migration load for the highest considered level of dispersal (ten mites per week) and a cost of local adaptation on bean are revealed in the evolutionary dynamics.
5. Female longevity can be affected by different plant species, in a way that a lower performance might occur on a host plant to which the species is not adapted.

7. DUTCH SUMMARY

Hoewel het leven op aarde altijd al veranderingen in tijd en ruimte onderging, worden heel wat organismen vandaag meer op de proef gesteld door de klimaatsverandering. Om te kunnen blijven bestaan, is het voor deze organismen noodzakelijk zich aan te passen aan de heersende omstandigheden. Aangezien lokale adaptatie kan leiden tot biodiversiteit en hierover geweten is dat het één van de belangrijkste drijfveren is voor verschillende ecosysteemdiensten, is onderzoek naar de factoren die het adaptatieproces beïnvloeden uitermate belangrijk. In dit onderzoek wordt gekeken naar de invloed van verschillende niveaus van dispersie, en bijgevolg ‘gene flow’, en naar de invloed van competitie in een kleine gemeenschap bestaande uit twee soorten. Er werd geopteerd voor Tetranychus urticae als modelsoort en voor zijn fylogenetisch verwante competitor, Tetranychus evansi. Deze laatste staat bekend als een pestsoort op planten van de Solanaceae, zoals de tomatenplant.

De experimentele setup bestaat uit verschillende ‘mesocosms’ waarbij de typische ‘mainland-island’ dynamieken gesimuleerd worden. Het hoofdeiland bestaat uit verschillende bonenplanten met *T. urticae* of de bonenspintmijt. De eilanden bestaan elk uit een individuele tomatenplant, waarvan de helft de competitor *T. evansi* bevat en de andere helft als controle dient. Wekelijks worden op deze twee groepen van tomatenplanten bonenspintmijten overgezet naargelang het niveau van dispersie (twee mijten per week, drie mijten per week, vijf mijten per week of tien mijten per week). In totaal wordt gewerkt met zeven replica’s en om de twee weken worden de populaties overgezet op nieuwe tomatenplanten, zodat steeds voldoende voedsel beschikbaar is.

Om de impact van competitie aan te tonen worden zowel de ecologische als de evolutionaire dynamieken nader onderzocht. Het eerste onderdeel bestaat uit de ecologische dynamieken, waarvoor tweemaal per week het aantal volwassen vrouwtjes op de planten geteld wordt. Deze tellingen worden dan later gegroepeerd per generatie voor de verdere analyse. Voor de evolutionaire dynamieken wordt de ‘fitness’ bepaald van de verschillende populaties door individuen uit de populaties af te zonderen en voor twee generaties in een ‘common garden’ te plaatsen. Van deze tweede generatie wordt er telkens een volwassen vrouwtje, vergezeld van een aantal mannetjes, op een bonenblad gezet en een ander van dezelfde populatie op een tomatenblad. Hierdoor kan een vergelijking worden gemaakt tussen het totale aantal nakomelingen en de levensduur van het oorspronkelijke vrouwtje op de aanvankelijke waardplant en op de nieuwe tomatenplant. Dit proces werd in totaal drie keer doorlopen, namelijk voor generatie zeven, acht en negen. Telkens zijn er ook individuen van het ‘hoofdeiland’, verder wordt verwezen naar de stockpopulatie, onderworpen aan dezelfde behandeling, om eventuele lokale adaptatie vast te kunnen stellen.

In het onderzoek is duidelijk geconstateerd dat fylogenetisch verwante competitie het adaptatieproces kan verhinderen, aangezien het voor de bonenspintmijt zelfs niet mogelijk was om zich tijdens de volledige duur van het experiment te vestigen op de tomatenplanten onder competitie. Enkelingen waren toch in staat zich te vestigen voor kortere periodes, wat wellicht te wijten is aan een beïnvloeding door een toevallig lager niveau van interspecifieke competitie. Dus zelfs het hoogste niveau van dispersie, waarbij wekelijks tien mijten overgezet worden, is niet voldoende om de veel hogere groeisnelheid van *T. evansi* te compenseren. Door de zeer kleine populatiegroottes was het spijtig genoeg niet mogelijk om voldoende data te verzamelen en konden dus geen echte conclusies worden getrokken over de invloed van competitie op het adaptatieproces.

In vorig onderzoek werd aangetoond dat de plantensoort de levensduur van het aanvankelijke vrouwtje niet beïnvloedt en dat deze eigenschap dus geen lokale adaptatie kan aantonen. In dit onderzoek is echter aangetoond dat, ten minste voor de achtste generatie, er wel een invloed is. Aangezien er echter enkel een verschil waargenomen werd tussen boon en tomaat en niet tussen de stockpopulatie en de verschillende niveaus van dispersie, kan niets geconcludeerd worden in verband met adaptatie.

Het onderzoek naar de ecologische dynamieken bij de populaties zonder competitie, waarbij gekeken is naar de verschillen in populatiegrootte tussen de differente niveaus van dispersie, geeft opmerkelijke resultaten weer. Bij de start van het experiment bereiken de populaties die het grootste aantal immigranten krijgen de grootste populaties. Dit verschijnsel blijft ongeveer zeven generaties van kracht. Daarna beginnen er zich verschillen voor te doen tot een duidelijk keerpunt bekomen wordt bij de negende generatie. Hierna zijn het net de laagste niveaus van dispersie die de hoogste populatiegroottes bereiken. Dit keerpunt valt samen met de geobserveerde ‘migration load’ voor het hoogste niveau van dispersie bij de evolutionaire dynamieken. Dit is mogelijk een voorbeeld van eco-evolutionaire dynamieken, waarbij een evolutionaire verandering de overleving en reproductie van een populatie kan beïnvloeden op een korte tijdschaal en hierdoor dus ook de populatiedynamieken.

Naast ‘migration load’ zijn er ook enkele andere interessante patronen waar te nemen, zoals een kost van adaptatie, die het duidelijkst zichtbaar was in generatie acht. Hier werd significant aangetoond dat de stockpopulatie het duidelijk beter doet op de bonenbladeren dan de populaties die onderworpen waren aan de stress van een nieuwe omgeving door de experimentele procedure. Al vanaf de achtste generatie zijn er ook duidelijke signalen voor lokale adaptatie zichtbaar. Dit is ongeveer de helft van de tijd die voordien nodig werd geacht om adaptatie te detecteren bij de bonenspintmijt.

Ten slotte kan geconcludeerd worden dat competitie een groot effect heeft op de mogelijkheid om lokaal te adapteren, evenals de verschillende niveaus van adaptatie.

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10 APPENDIX

Table 7: Ecological Dynamics (non-competition treatment). Results for fixed effects form mixed linear models with the total number of adult females as response variable (Poisson error distributions were used).

Factor	Estimate	Std. Error	z value	Pr(>|z|)	
Generation 2					
(Intercept)	0,55080	0,25660	2,15	0,03187	*
dispersal2	0,78070	0,14330	5,45	5,11E-08	***
dispersal3	0,43780	0,15230	2,88	0,00403	**
dispersal4	1,13550	0,13640	8,32	< 2,00E-16	***
Generation 3					
(Intercept)	2,12657	0,20428	10,41	< 2,00E-16	***
dispersal2	0,21042	0,08204	2,57	0,0103	*
dispersal3	-0,11407	0,08880	-1,29	0,1989	
dispersal4	0,49660	0,07733	6,42	1,35E-10	***
Generation 4					
(Intercept)	2,73550	0,18100	15,11	< 2,00E-16	***
dispersal2	-0,19167	0,06061	-3,16	0,00156	**
dispersal3	0,30783	0,05369	5,73	9,82E-09	***
dispersal4	1,17173	0,04665	25,12	< 2,00E-16	***
Generation 5					
(Intercept)	3,29839	0,11804	27,94	< 2,00E-16	***
dispersal2	0,14894	0,04336	3,44	0,000593	***
dispersal3	0,17726	0,04308	4,11	3,88E-05	***
dispersal4	0,19736	0,04289	4,60	4,19E-06	***
Generation 6					
(Intercept)	3,65648	0,08788	41,61	< 2,00E-16	***
dispersal2	-0,08668	0,04344	-2,00	0,046	*
dispersal3	0,31747	0,03949	8,04	9,06E-16	***
dispersal4	0,28134	0,03980	7,07	1,55E-12	***
Generation 7					
(Intercept)	3,71956	0,07259	51,24	< 2E-16	***
dispersal2	0,02428	0,03673	0,66	0,509	
dispersal3	0,03290	0,03665	0,90	0,369	
dispersal4	0,02494	0,03672	0,68	0,497	
Generation 8					
(Intercept)	3,56619	0,08690	41,04	< 2,00E-16	***
dispersal2	0,25000	0,04188	5,97	2,39E-09	***
dispersal3	0,22354	0,04213	5,31	1,12E-07	***
dispersal4	0,16591	0,04268	3,89	0,000101	***
Generation 9					
(Intercept)	3,29686	0,09813	33,60	< 2,00E-16	***
dispersal2	0,19572	0,04321	4,53	5,91E-06	***
dispersal3	0,17443	0,04342	4,02	5,88E-05	***

dispersal4	0,02028	0,04504	0,45	0,653	
Generation 10					
(Intercept)	3,86325	0,10980	35,19	< 2,00E-16	***
dispersal2	-0,03026	0,04419	-0,68	0,49347	
dispersal3	-0,12696	0,04531	-2,80	0,00508	**
dispersal4	-0,33494	0,04802	-6,98	3,05E-12	***
Generation 11					
(Intercept)	4,03668	0,06930	58,25	< 2,00E-16	***
dispersal2	-0,04848	0,05052	-0,96	0,33729	
dispersal3	-0,15602	0,05197	-3,00	0,00268	**
dispersal4	-0,27490	0,05371	-5,12	3,09E-07	***

Table 8: Ecological Dynamics (competition treatment). Results for fixed effects form mixed linear models with the total number of adult females as response variable (Poisson error distributions were used).

Factor	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	
Generation 1					
(Intercept)	-1,3027	0,4784	-2,7230	0,0065	**
dispersal2	0,4855	0,4532	1,0710	0,2841	
dispersal3	-0,9808	0,6828	-1,4360	0,1509	
dispersal4	0,6286	0,4416	1,4240	0,1546	
Generation 2					
(Intercept)	-0,5747	0,4954	-1,1600	0,2460	
dispersal2	1,1331	0,1866	6,0730	0,0000	***
dispersal3	-0,5466	0,2680	-2,0390	0,0414	*
dispersal4	0,6931	0,1987	3,4880	0,0005	***
Generation 3					
(Intercept)	-1,2267	0,8221	-1,4920	0,136	
dispersal2	2,0655	0,2043	1,0109	< 2,00E-16	***
dispersal3	1,4491	0,2139	6,7750	1.24e-11	***
dispersal4	1,8222	0,2075	8,7840	< 2,00E-16	***
Generation 4					
(Intercept)	-0,8046	0,7142	-1,1270	0,259946	
dispersal2	2,2679	0,1532	1,4800	< 2,00E-16	***
dispersal3	1,2973	0,1646	7,8820	3,23E-15	***
dispersal4	0,6272	0,1807	3,4710	0,000518	***
Generation 5					
(Intercept)	-0,4255	0,5906	-0,7210	0,471	
dispersal2	0,9474	0,1561	6,0710	1,27E-09	***
dispersal3	0,9198	0,1567	5,8710	4,33E-09	***
dispersal4	-1,2098	0,2764	-4,3770	1,20E-05	***
Generation 6					
(Intercept)	-0,7956	0,5625	-1,4140	0,15728	
dispersal2	0,6539	0,242	2,7020	0,00689	**
dispersal3	0,9163	0,2323	3,9450	7,97E-05	***
Generation 7					
(Intercept)	0,3464	0,3058	1,1330	0,25732	
dispersal2	-0,6325	0,2125	-2,9770	0,00291	**
dispersal3	-0,4453	0,2003	-2,2230	0,02619	*

dispersal4	-2,2130	0,3986	-5,5520	2,82E-08	***
Generation 8					
(Intercept)	-1,3428	0,7407	-1,8130	0,0698	.
dispersal2	1,1750	0,2499	4,7020	2,58E-06	***
dispersal3	0,3567	0,2848	1,2520	0,2104	
dispersal4	-0,5596	0,3622	-1,5450	0,1224	
Generation 9					
(Intercept)	-2,4382	0,7511	-3,2460	0,00117	**
dispersal2	2,5819	0,3459	7,4640	8,40E-14	***
dispersal3	0,7472	0,4049	1,8450	0,064973	.
dispersal4	1,3581	0,3740	3,6320	0,000282	***
Generation 10					
(Intercept)	**-3,6697**	**1,1843**	**-3,0990**	**0,001944**	**
dispersal2	2,7408	0,5168	5,3030	1,14E-07	***
dispersal3	**1,9459**	**0,5355**	**3,6340**	**0,000279**	***
dispersal4	0,4055	0,6467	0,6270	0,530669	
Generation 11					
(Intercept)	**-1,6411**	**0,7475**	**-2,1950**	**0,028134**	*
dispersal2	1,4171	0,3960	3,5780	0,000346	***
dispersal3	**-2,0794**	**1,0658**	**-1,9510**	**0,051057**	.
dispersal4	-0,4700	0,5729	-0,8200	0,411961	

Table 9: Treatment. Results for fixed effects form mixed linear models with the total number of offspring as response variable (Poisson error distributions were used).

Factor	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	
Experiment 2 Day 7 (generation 8)					
(Intercept)	2.2606	0.3159	7.155	8.37e-13	***
PlantSptomato	-0.4456	0.4283	-1.041	0.298104	
TreatmentnC	-0.2286	0.3251	-0.703	0.481842	
TreatmentST	0.1532	0.3588	0.427	0.669459	
PlantSptomato:TreatmentnC	-0.8013	0.4628	-1.731	0.083377	.
PlantSptomato:TreatmentST	-2.0007	0.5520	-3.625	0.000289	***
Experiment 2 Day 10 (generation 8)					
(Intercept)	2.6281	0.2378	11.053	< 2e-16	***
PlantSptomato	-0.2893	0.3253	-0.889	0.373770	
TreatmentnC	0.2122	0.2354	0.901	0.367330	
TreatmentST	0.8899	0.2697	3.300	0.000967	***
PlantSptomato:TreatmentnC	-0.3049	0.3409	-0.894	0.371143	
PlantSptomato:TreatmentST	-1.6812	0.3931	-4.277	1.9e-05	***
Experiment 2 Day 15 (generation 8)					
(Intercept)	3.44599	0.40877	8.430	< 2e-16	***
FemaleLong	0.06992	0.02738	2.554	0.010654	*
PlantSptomato	-1.56944	0.47105	-3.332	0.000863	***
TreatmentnC	-0.71472	0.23795	-3.004	0.002667	**
TreatmentST	-1.74332	0.35629	-4.893	9.93e-07	***
PlantSptomato:TreatmentnC	0.86679	0.46534	1.863	0.062504	.
PlantSptomato:TreatmentST	-0.86608	0.55647	-1.556	0.119615	
Experiment 3 Day 7 (generation 9)					

(Intercept)	1.9634	0.1055	18.616	< 2e-16	***
PlantSptomato	-4.4587	0.7166	-6.222	4.9e-10	***
Experiment 3 Day 10 (generation 9)					
(Intercept)	2.55525	0.23989	10.652	< 2e-16	***
FemaleLong	0.06592	0.01708	3.859	0.000114	***
PlantSptomato	-3.00977	0.51418	-5.853	4.81e-09	***
TreatmentnC	-0.18834	0.18342	-1.027	0.304519	
TreatmentST	-0.03915	0.18521	-0.211	0.832570	
PlantSptomato:TreatmentnC	1.54622	0.53828	2.873	0.004072	**
PlantSptomato:TreatmentST	0.49582	0.57458	0.863	0.388179	
Experiment 3 Day 15 (generation 9)					
(Intercept)	1.68280	0.58091	2.897	0.00377	**
FemaleLong	0.09850	0.03551	2.774	0.00553	**
PlantSptomato	-4.60936	0.94755	-4.864	1.15e-06	***
TreatmentnC	0.24378	0.47666	0.511	0.60904	
TreatmentST	0.94040	0.49698	1.892	0.05846	.
FemaleLong:PlantSptomato	0.20056	0.06372	3.147	0.00165	**
PlantSptomato:TreatmentnC	2.02266	0.49560	4.081	4.48e-05	***
PlantSptomato:TreatmentST	0.27537	0.45969	0.599	0.54915	

Table 10: Treatment. Results for fixed effects form mixed linear models with the female longevity as response variable (Poisson error distributions were used).

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
Experiment 2 (generation 8)					
(Intercept)	2.4361	0.0559	43.58	<2e-16	***
PlantSptomato	-0.1555	0.0870	-1.79	0.0739	.
Experiment 3 (generation 9)					
(Intercept)	2.18380	0.07883	27.7	<2e-16	***

Table 11: Dispersal. Results for fixed effects form mixed linear models with the total number of offspring as response variable (Poisson error distributions were used).

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
Experiment 1 Day 7 (generation 7)					
(Intercept)	0.8859	0.5036	1.759	0.0785	.
Dispersal1	0.9946	0.5248	1.895	0.0580	.
Dispersal2	0.7924	0.5258	1.507	0.1318	
Dispersal3	0.6705	0.5312	1.262	0.2069	
Dispersal4	1.0869	0.5245	2.072	0.0382	*
PlantSptomato	-4.8771	0.5839	-8.353	<2e-16	***
Experiment 1 Day 10 (generation 7)					
(Intercept)	1.70580	0.37132	4.594	4.32e-06	***
Dispersal1	0.68312	0.36113	1.892	0.058541	.
Dispersal2	0.74034	0.36144	2.048	0.040529	*
Dispersal3	0.74554	0.36228	2.058	0.039599	*
Dispersal4	0.88386	0.36027	2.453	0.014154	*
FemaleLong	0.05029	0.01219	4.125	3.70e-05	***
PlantSptomato	-1.73709	0.62595	-2.775	0.005518	**

Dispersal1:PlantSptomato	-2.48539	0.69222	-3.590	0.000330	***
Dispersal2:PlantSptomato	-2.58857	0.70535	-3.670	0.000243	***
Dispersal3:PlantSptomato	-2.76040	0.70559	-3.912	9.15e-05	***
Dispersal4:PlantSptomato	-1.22938	0.65566	-1.875	0.060790	.
FemaleLong:PlantSptomato	0.10704	0.03470	3.085	0.002036	**
Experiment 1 Day 15 (generation 7)					
(Intercept)	1.49877	0.37886	3.956	7.62e-05	***
Dispersal1	0.52366	0.36918	1.418	0.156067	
Dispersal2	0.76636	0.37019	2.070	0.038434	*
Dispersal3	0.67586	0.37077	1.823	0.068328	.
Dispersal4	0.82866	0.36879	2.247	0.024641	*
FemaleLong	0.10164	0.01214	8.374	< 2e-16	***
PlantSptomato	-2.26847	0.69241	-3.276	0.001052	**
Dispersal1:PlantSptomato	-1.41413	0.73210	-1.932	0.053408	.
Dispersal2:PlantSptomato	-2.30545	0.75985	-3.034	0.002413	**
Dispersal3:PlantSptomato	-1.36652	0.75049	-1.821	0.068632	.
Dispersal4:PlantSptomato	-2.23865	0.76257	-2.936	0.003328	**
FemaleLong:PlantSptomato	0.12973	0.03907	3.320	0.000899	***
Experiment 2 Day 7 (generation 8)					
(Intercept)	2.80254	0.17481	16.032	< 2e-16	***
Dispersal1	-0.25665	0.15721	-1.633	0.10257	
Dispersal2	-0.32662	0.15291	-2.136	0.03268	*
Dispersal3	-0.13374	0.15896	-0.841	0.40017	
Dispersal4	-0.43225	0.16339	-2.645	0.00816	**
FemaleLong	-0.03222	0.01161	-2.776	0.00551	**
PlantSptomato	-2.44295	0.32221	-7.582	3.4e-14	***
Dispersal1:PlantSptomato	1.04953	0.36820	2.850	0.00437	**
Dispersal2:PlantSptomato	1.18273	0.36501	3.240	0.00119	**
Dispersal3:PlantSptomato	0.78105	0.40392	1.934	0.05315	.
Dispersal4:PlantSptomato	0.74378	0.39180	1.898	0.05765	.
Experiment 2 Day 10 (generation 8)					
(Intercept)	3.083082	0.125152	24.635	< 2e-16	***
Dispersal1	-0.425786	0.112289	-3.792	0.000150	***
Dispersal2	-0.562165	0.110243	-5.099	3.41e-07	***
Dispersal3	-0.668972	0.119654	-5.591	2.26e-08	***
Dispersal4	-0.429217	0.115540	-3.715	0.000203	***
FemaleLong	0.038348	0.007723	4.966	6.85e-07	***
PlantSptomato	-1.714777	0.172175	-9.959	< 2e-16	***
Dispersal1:PlantSptomato	1.017477	0.198209	5.133	2.85e-07	***
Dispersal2:PlantSptomato	1.131467	0.195171	5.797	6.74e-09	***
Dispersal3:PlantSptomato	0.933953	0.225361	4.144	3.41e-05	***
Dispersal4:PlantSptomato	0.893661	0.202558	4.412	1.02e-05	***
Experiment 2 Day 15 (generation 8)					

(Intercept)	2.70286	0.17482	15.461	< 2e-16	***
Dispersal1	-0.23345	0.16324	-1.430	0.152694	
Dispersal2	-0.06497	0.15756	-0.412	0.680100	
Dispersal3	-0.12506	0.16536	-0.756	0.449475	
Dispersal4	-0.38915	0.16334	-2.383	0.017195	*
FemaleLong	0.06645	0.00940	7.069	1.56e-12	***
PlantSptomato	-2.20922	0.27988	-7.894	2.94e-15	***
Dispersal1:PlantSptomato	1.26395	0.25548	4.947	7.52e-07	***
Dispersal2:PlantSptomato	1.00516	0.25848	3.889	0.000101	***
Dispersal3:PlantSptomato	1.08987	0.27015	4.034	5.48e-05	***
Dispersal4:PlantSptomato	1.16598	0.26504	4.399	1.09e-05	***
FemaleLong:PlantSptomato	0.03794	0.01576	2.407	0.016088	*
Experiment 3 Day 7 (generation 9)					
(Intercept)	1.8313	0.1436	12.755	<2e-16	***
Dispersal1	0.3538	0.1788	1.979	0.0479	*
Dispersal2	0.2791	0.1777	1.571	0.1162	
Dispersal3	0.2815	0.1753	1.606	0.1083	
Dispersal4	0.2050	0.1867	1.098	0.2723	
PlantSptomato	-19.1555	1926.1785	-0.010	0.9921	
Dispersal1:PlantSptomato	16.2577	1926.1786	0.008	0.9933	
Dispersal2:PlantSptomato	15.4213	1926.1787	0.008	0.9936	
Dispersal3:PlantSptomato	17.4205	1926.1786	0.009	0.9928	
Dispersal4:PlantSptomato	17.1926	1926.1786	0.009	0.9929	
Experiment 3 Day 10 (generation 9)					
(Intercept)	2.73548	0.12942	21.137	< 2e-16	***
Dispersal1	0.02722	0.11704	0.233	0.816074	
Dispersal2	-0.06601	0.11422	-0.578	0.563320	
Dispersal3	-0.08987	0.11784	-0.763	0.445642	
Dispersal4	-0.01958	0.12379	-0.158	0.874328	
FemaleLong	0.04789	0.00901	5.316	1.06e-07	***
PlantSptomato	-2.53077	0.25494	-9.927	< 2e-16	***
Dispersal1:PlantSptomato	0.95114	0.29210	3.256	0.001129	**
Dispersal2:PlantSptomato	1.07002	0.29981	3.569	0.000358	***
Dispersal3:PlantSptomato	1.48954	0.27623	5.392	6.95e-08	***
Dispersal4:PlantSptomato	0.75707	0.30563	2.477	0.013247	*
Experiment 3 Day 15 (generation 9)					
(Intercept)	2.89250	0.20880	13.853	< 2e-16	***
Dispersal1	-0.62094	0.16658	-3.728	0.000193	***
Dispersal2	-0.68645	0.16666	-4.119	3.81e-05	***
Dispersal3	-0.43600	0.16764	-2.601	0.009298	**
Dispersal4	-0.57964	0.17369	-3.337	0.000846	***
FemaleLong	0.09820	0.01132	8.675	< 2e-16	***
PlantSptomato	-2.77398	0.29087	-9.537	< 2e-16	***
Dispersal1:PlantSptomato	1.33358	0.26458	5.040	4.65e-07	***

Dispersal2:PlantSptomato	1.83186	0.29820	6.143	8.10e-10	***
Dispersal3:PlantSptomato	1.12637	0.26070	4.321	1.56e-05	***
Dispersal4:PlantSptomato	1.30793	0.26973	4.849	1.24e-06	***
FemaleLong:PlantSptomato	0.03360	0.01913	1.756	0.079123	.

Table 12: Dispersal. Results for fixed effects form mixed linear models with the female longevity as response variable (Poisson error distributions were used).

	Estimate	Std. Error	z value	Pr(>|z|)	
Experiment 1 (generation 7)					
(Intercept)	2.40734	0.03363	71.58	<2e-16	***
Experiment 2 (generation 8)					
(Intercept)	2.37413	0.04450	53.36	< 2e-16	***
PlantSptomato	-0.19275	0.05759	-3.35	0.000816	***
Experiment 3 (generation 9)					
(Intercept)	2.27860	0.05660	40.26	<2e-16	***
PlantSptomato	-0.12189	0.06558	-1.86	0.0631	.

Table 13: Experiments. Results for fixed effects form mixed linear models with the total number of offspring as response variable (Poisson error distributions were used).

	Estimate	Std. Error	z value	Pr(>|z|)	
Day 7					
(Intercept)	1.95927	0.06245	31.373	<2E-16	***
Experiment2	0.23480	0.06580	3.569	0.000359	***
Experiment3	0.15802	0.07000	2.258	0.023975	*
PlantSptomato	-4.87104	0.58008	-8.397	<2E-16	***
Experiment2:PlantSptomato	3.47297	0.58837	5.903	3.58e-09	***
Experiment3:PlantSptomato	2.66040	0.59807	4.448	8.66e-06	***
Day 10					
(Intercept)	2.59030	0.08951	28.939	<2E-16	***
Dispersal2	0.04544	0.07771	0.585	0.558687	
Dispersal3	0.11472	0.08123	1.412	0.157854	
Dispersal4	0.20225	0.07396	2.735	0.006243	**
Experiment2	0.09353	0.07385	1.267	0.205321	
Experiment3	0.29645	0.07805	3.798	0.000146	***
FemaleLong	0.03827	0.00514	7.445	9.69e-14	***
PlantSptomato	-2.64747	0.16620	-15.929	<2E-16	***
Dispersal2:Experiment2	-0.12571	0.10058	-1.250	0.211335	
Dispersal3:Experiment2	-0.38014	0.11358	-3.347	0.000817	***
Dispersal4:Experiment2	-0.19266	0.10004	-1.926	0.054118	.
Dispersal2:Experiment3	-0.18711	0.10892	-1.718	0.085825	.
Dispersal3:Experiment3	-0.09388	0.10803	-0.869	0.384875	
Dispersal4:Experiment3	-0.17497	0.11048	-1.584	0.113234	
Experiment2:PlantSptomato	1.70795	0.11495	14.859	<2E-16	***
Experiment3:PlantSptomato	0.98909	0.12143	8.145	3.78e-16	***
FemaleLong:PlantSptomato	0.02478	0.01095	2.263	0.023653	*
Day 15					
(Intercept)	2.347547	0.085152	27.569	<2E-16	***

Dispersal2	0.118965	0.068513	1.736	0.082496	.
Dispersal3	0.247071	0.071398	3.460	0.000539	***
Dispersal4	0.278429	0.065748	4.235	2.29e-05	***
Experiment2	-0.121288	0.070405	-1.723	0.084940	.
Experiment3	0.155938	0.076061	2.050	0.040348	*
FemaleLong	0.087406	0.004798	18.216	<2E-16	***
PlantSptomato	-2.666622	0.162529	-16.407	<2E-16	***
Dispersal2:Experiment2	0.081355	0.093656	0.869	0.385032	
Dispersal3:Experiment2	-0.138923	0.106419	-1.305	0.191746	
Dispersal4:Experiment2	-0.331572	0.097412	-3.404	0.000665	***
Dispersal2:Experiment3	-0.153954	0.106645	-1.444	0.148849	
Dispersal3:Experiment3	-0.141126	0.105223	-1.341	0.179851	
Dispersal4:Experiment3	-0.075609	0.103653	-0.729	0.465728	
Dispersal2:PlantSptomato	-0.273048	0.099685	-2.739	0.006161	**
Dispersal3:PlantSptomato	-0.202568	0.096407	-2.101	0.035625	*
Dispersal4:PlantSptomato	-0.222897	0.099157	-2.248	0.024582	*
Experiment2:PlantSptomato	1.788694	0.103592	17.267	<2E-16	***
Experiment3:PlantSptomato	1.277351	0.110754	11.533	<2E-16	***
FemaleLong:PlantSptomato	0.040418	0.009828	4.113	3.91-05	***

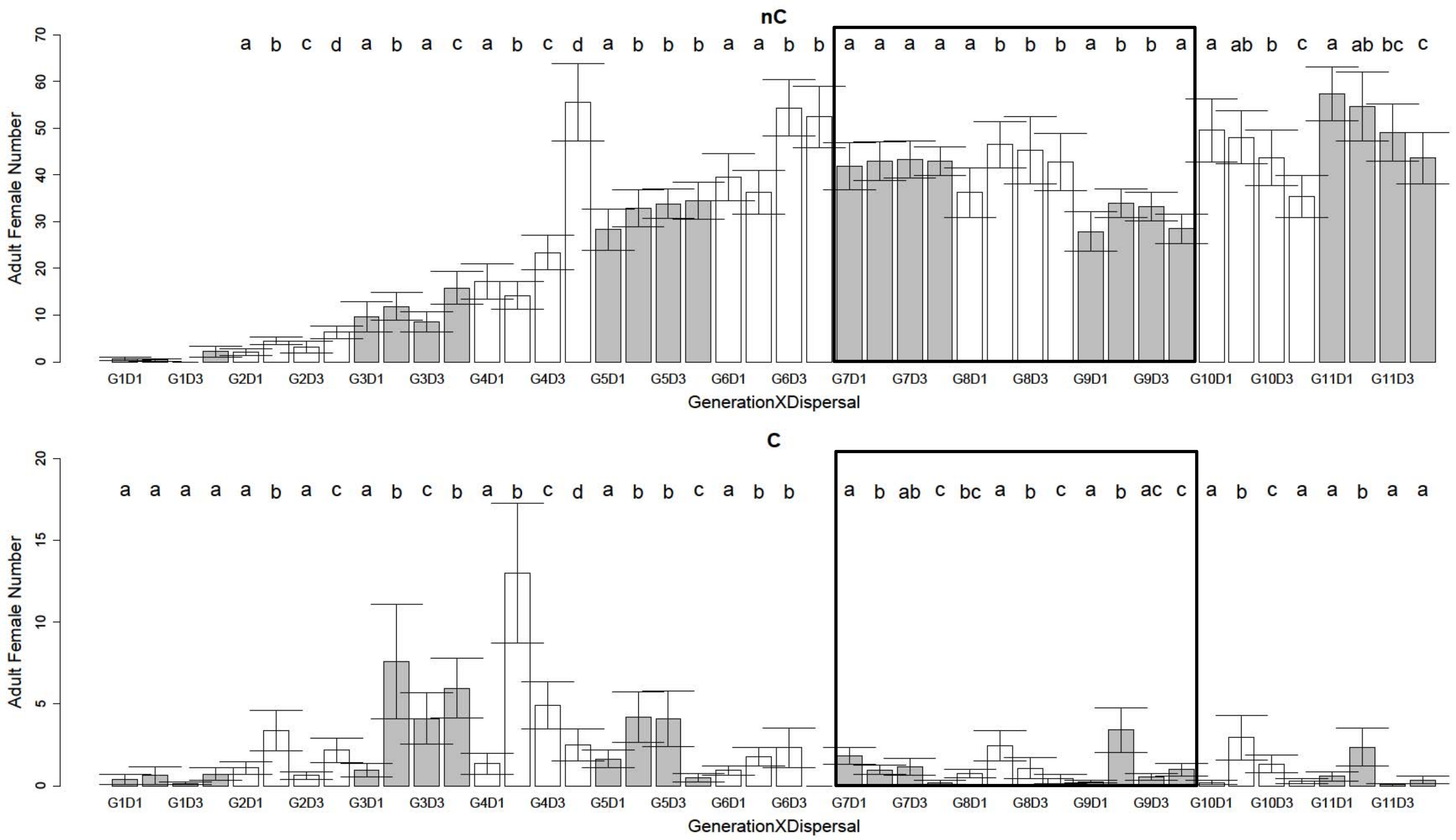

Figure 36: averages of the number of adult females of *T. urticae* (corrected for the input of the number of immigrants) for each generation (G: 1 – 11) are plotted, the upper graph presents the situation without competition and the lower graph under competition. Four different levels of dispersal are considered (D1: 2 mites/week; D2: 3 mites/week; D3: 5 mites/week; D4: 10 mites/week). The letter code on top indicates the differences between the dispersal levels within each generation. The mites for the different fitness experiments are taken from generation 7, 8 and 9, indicated with the rectangle. The figure is made with the observed data.