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Performance in a novel environment subject to ghost competition.

Running title: Ghost competition in novel environment

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ABSTRACT

A central tenet of evolutionary theory of communities is that both intra- and interspecific interactions impact evolutionary processes such as local adaptation. The precise nature of this impact is still an open question. Here, we studied the fitness effects of inter- and intraspecific competition using experimental evolution with spider mites as a model. We transferred *Tetranychus urticae* onto a novel host plant under presence or absence of a competing species, *T. ludeni*. We found that, with a competitor present, populations under higher densities of the competitor reached higher fecundity. In fact the populations with highest competitor densities evolved similar oviposition rates as the populations without a competitor present, suggesting that selection due to interspecific competition is of a similar magnitude as selection under intraspecific competition. Moreover, while the competitor, *T. ludeni*, already went extinct soon after the start of the experimental evolution, its effect on *T. urticae* lasted over at least 25 generations. Early experienced selection pressures, even from unsuccessful competitor species, can therefore exert a lasting evolutionary signal on species' performance in novel environments.

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INTRODUCTION

Species are facing a continuously changing world. If they are unable to track their favoured habitat or to cope with the novel environment through phenotypic plasticity, evolutionary rescue by genetic adaptation can eventually allow persistence if the necessary conditions are fulfilled (i.e. genetic variation in traits that are responsible for such adaptations, their heritability and the strength of the selection pressures) (Lindsey *et al.*, 2013). Intraspecific competition is an essential ingredient of selection and hence evolution, and can be expected to have a much larger impact on evolution than interspecific competition because niche overlap is larger within than among species (Bolnick, 2001; Svanbäck & Bolnick, 2007).

Interspecific competition is, however, also known to influence this adaptation process to the environment but the effect is still largely unpredictable (Rice & Knapp, 2008; Alzate *et al.*, 2017; Zhao *et al.*, 2018). First, heterospecific competitors might modify the selection pressure exerted by the abiotic environment, thereby enhancing or limiting genetic adaptation to the novel environment (Osmond & de Mazancourt, 2013). Classical examples of enhanced genetic adaptation are seen in adaptive radiations of three-spined sticklebacks or fast character displacements in Darwin finches or Myzomelid honeyeaters (Diamond *et al.*, 1989; Schluter, 1994; Reznick & Ghalambor, 2001). In previous work we found that additional selection pressure exerted by a congeneric species, facilitated adaptation of the focal species to a novel environment under high dispersal from a maladapted mainland population (Alzate *et al.*, 2017). Hence interspecific competition counteracted the effects of genetic load. Adaptation to the novel environment can also be reduced by interspecific competition when a population adapts more towards the competing species than to the novel environment (Siepielski *et al.*, 2016). Secondly, new niches can be constructed with the introduction of interspecific competition such as the use of waste products from coexisting individuals (Lawrence *et al.*,

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2012) or, in the case of arthropod herbivores, by modification of plant defences (Sarmento *et al.*, 2011). The new niches will subsequently open new avenues for adaptive shifts to novel environmental conditions. Third, interspecific competition can obviously hinder the process of local adaptation by restricting resource availability, and hence decrease effective population size. The resulting increased probabilities of genetic drift will then decrease the evolutionary potential and hence the chance of local adaptation (Lawrence *et al.*, 2012; Osmond & de Mazancourt, 2013; Zhao *et al.*, 2018).

While inferior competitors are expected to eventually become extinct, they may coexist with the superior competitor for many generations (Holmes & Wilson, 1998; Lankau, 2011). These early and non-persisting interactions may generate a strong signature on the future community dynamics (Law & Daniel Morton, 1996; Miller, terHorst, & Burns, 2009; Mallon *et al.*, 2018) because they have the possibility to induce strong habitat modifications or evolutionary changes in the extant species. Historical contingency in terms of limitations imposed by so-called ghost species (Hawkes & Keitt, 2015), may thus have a strong impact on the ecological and evolutionary trajectories of populations and communities, in the same way as successful species do (Fukami, 2015). Research investigating the role of competition intensity of an inferior species prior to its extinction on persisting species is largely unknown and remains to be discovered.

Here we present results from experimental evolution with an herbivore arthropod, *Tetranychus urticae* Koch, that was confronted with a congeneric competitor, *T. ludeni* Zacher, during adaptation to a novel host. The competitor was chosen to be competitively similar to the focal species, but the experiment demonstrated its inferiority: it coexisted temporarily with the focal species, but eventually went extinct. Because population dynamics

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varied among replicates and, hence the variation in competitive strength at the initial stages of the experiment, we investigated the effect of ghost competition. More precisely, we wanted to investigate whether we could find long-term evolutionary effects (measured with fecundity as a proxy of fitness) due to differences in initial selection pressures caused by an unsuccessful species or ghost species. For a better interpretation of the magnitude of this adaptation, we compared these results with a treatment without the competing species. This treatment with intraspecific competition only started with the same total initial density.

We found a positive correlation between higher densities of the competitor during the initial stages of the experiment and reproductive performance. This correlation was independent of time, indicating that ghost species are important for the long-term performance of initially coexisting species. We could not prove adaptation of the populations under interspecific competition to the novel host as no significant differences with the control population were found on the novel environment, we did find this difference with the control under the intraspecific competition treatment. However, no significant differences were found between the higher density of the competitor and the intraspecific treatment, suggesting that stronger interspecific competition can lead to similar local adaptation as purely intraspecific competition. We conclude that ghost competition is an underestimated process for adaptation and may lead to differences in long-term local adaptation.

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MATERIALS AND METHODS

Study species: *Tetranychus urticae* and *T. ludeni*

Our focal species was the two-spotted spider mite, *Tetranychus urticae* Koch, which was exposed to competition from the red-legged spider mite, *Tetranychus ludeni* Zacher. Both species are members of the family Tetranychidae (Acari, Arachnida). These herbivorous mite species are well suitable for experimental evolution due to their small body sizes (± 0.4 mm), which makes it possible to maintain large populations in the lab, and due to their short generation time of about 1-2 weeks depending on the temperature and the host plant (Zhang, 2003). Both species are haplodiploid (Zhang, 2003; Clemente *et al.*, 2018). Fast responses to selection are known to occur after just 10 generations (Belliure, Montserrat, & Magalhaes, 2010). The high standing genetic variation in established populations is suitable for local adaptation and around fifteen generations are sufficient to detect local adaptation (Gould, 1979; Fry, 1989; Magalhães *et al.*, 2007, 2009; Bonte *et al.*, 2010).

Experimental set-up

For this study, 13 isofemale lines of *T. urticae* were used (Bitume *et al.*, 2013). The initial population for these isofemale lines was the LS-VL line that was maintained on bean plants *Phaseolus vulgaris* Prelude and initiated from about 5000 spider mites from roses in October 2000 (Ghent, Belgium). We chose to further subject these isofemale lines to inbreeding by mother-son mating for one more generation prior to the experiments. It may sound counterintuitive to use inbred populations for an evolutionary experiment that mainly uses standing genetic variation because novel genetic variation through immigration could not arise (no spider mites were added during our experiment). We did this, however, to generate genetically similar replicates and hence starting conditions for the experiment to control for putative initial drift effects by differences in starting genetic variation, which we deemed

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more important than potential inbreeding effects, because no effects of inbreeding on genetic trait variation was found in these and other lines (Van Petegem *et al.*, 2018; Bonte unpub. results). We additionally created six isofemale lines for the competitor, *T. ludeni*; we wanted to create 13 lines for this species as well, but were unsuccessful due to low fertility or early mortality. Both species were initially maintained on two weeks' old bean plants, *Phaseolus vulgaris* 'Prelude'. At the beginning of the actual experiment, the isofemale lines were placed on novel host islands (four three-weeks-cucumber plants, *Cucumis sativus* 'Tanja', per island) with only conspecifics or with heterospecifics. A control population of *T. urticae* on bean plants was created from the same isofemale lines to investigate potential adaptation to the novel host.

The novel host islands were placed in boxes with yellow sticky paper (Pherobank) at the bottom and Vaseline at the walls to avoid contamination between islands, this method is known to work from previous research (Alzate *et al.*, 2017; Alzate, Etienne, & Dries Bonte, 2018). Eight islands received both *T. urticae* and *T. ludeni*. Eight islands received only *T. urticae* and another eight islands received only *T. ludeni*. These single-species islands represented the control for our test of the effect of interspecific competition. Each island started with the same total population size and as similar as possible gene pool for the focal species. The group with interspecific competition received 26 adult females of *T. urticae* (two from each of the isofemale lines) and 26 adult females of *T. ludeni*. Twelve *T. ludeni* females per island came from the six isofemale lines and were supplemented with 14 mites from its stock population, because of the lack of success for creating more isofemale lines. The use of the outbred stock population of *T. ludeni* led to larger initial variation in the gene pool among replicates and thus an unforeseen benefit for differences in initial selection pressures on the focal species. The group with intraspecific competition of *T. urticae* received four adult

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females from each of the thirteen isofemale lines (resulting in 52 adult females). The last group with only the competitor species, *T. ludeni*, received four adult females from the six isofemale lines and was supplemented with 28 females from its stock population. We started with this population size, because natural populations usually colonise a plant at small population sizes.

Depending on the level of deterioration, which was censored every week, the islands were refreshed. This was done by replacing the two oldest plants with two new three-weeks-old cucumber plants. In this way, sufficient time was provided for a generation of spider mites to develop on the plants, while allowing the entire population to move toward the fresh leaves. Hence, while the removed old plants may have contained mites, their number was low because most mites would have left the deteriorated plant in favour of the fresh plants. The islands were kept in a climate controlled room (25-30°C and 16:8 LD). The total experiment lasted for ten months, which is about 25 generations and long enough to detect local adaptation (Gould, 1979; Fry, 1989; Magalhães *et al.*, 2007, 2009; Bonte *et al.*, 2010). For logistical reasons the experiment was performed in two blocks with one month difference, each block consisted of four islands with intraspecific competition and four islands with interspecific competition.

<u>Measurements</u>

Every two weeks, the density of the spider mites on the experimental cucumber populations was measured by counting adult females on a square of 1 x 1 cm. The location of the square was right next to the stalk of the highest, fully grown leaf of the two newest plants of the island; the abaxial as well as the adaxial side were measured and summed for a total overview. The location on the leaf was chosen to standardise the measurements in time and make them comparable. We assessed the density because this gives a better idea about

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competition than the total population size (which would have been labour intensive to measure).

The congeneric competitor *T. ludeni* went extinct after about two months. To have an impression about its competitive pressure on the focal species and to explore possible drift effects due to putative differences in the initial population densities of the focal species, we calculated the initial density, which we defined as the mean density of the first two measurements in the first month.

Fecundity tests on *T. urticae* females from the control bean and experimental cucumber populations were performed every two months to determine the level of adaptation. Five two-spotted spider mite females were sampled from each island and separately placed on a bean leaf disc for two generations; bean is a very suitable host plant and will not cause a change in allele frequencies of the evolved lines (Magalhães *et al.*, 2011). These 17 x 27 mm^2 leaf discs were placed in a petri dish on wet cotton wool and surrounded with paper strip borders. The common garden conditions of two generations was necessary to exclude juvenile and maternal effects (Magalhães *et al.*, 2011; Kawecki *et al.*, 2012). Then, the fecundity of two quiescent deutonymph females that originated from the same common-garden replicate was tested; one female was put on a bean leaf and one on a cucumber leaf (same set-up as for common garden) in a climate cabinet of 30°C. Fecundity (number of eggs laid during six days) was measured based on daily pictures taken. Females that drowned in the cotton before the sixth day were excluded from the analysis.

<u>Statistical analysis</u>

We used general linear mixed models (GLMMs) with Negative Binomial distribution with log link to account for overdispersion of the data. The variance was determined as $\mu * (1 + \mu/k)$ in which μ is the mean and k is the overdispersion parameter (standard negative binomial

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parametrisation). Fecundity (eggs laid during six days, tested after two, four, six, eight and ten months) represented the performance and was the dependent variable of our models.

We first performed an analysis to investigate the impact of the ghost competitor on the populations under interspecific competition. Because the performances on both plants differed significantly (higher fecundity on bean compared to cucumber; $Z = 5.48$, $p = 4.26e\text{-}08$) and no significant interaction effects were observed, we subsequently performed separate analyses for performance on bean and cucumber. Fixed explanatory effects in the full model were initial density of the competitor (continuous variable) through time (months; categorical variable). We chose a categorical variable instead of a continuous one because differences in quality of leaves at the different measurements are not unlikely. The islands were treated as random effects and were nested within the two experimental blocks for the assessment on bean. We did not use random effects for the cucumber assessment as the random effect variance was estimated as zero which resulted in convergence errors (Magnusson *et al.*, 2018). Model selection was based on the lowest AICc.

As we were interested in the magnitude of the differences in performance, we did a further analysis including also the control population and the intraspecific competition treatment, and dividing the interspecific competition treatment in a low density and high density treatment, because we observed that interspecific competition caused lower performance under low densities than under high densities in the cucumber assessment (this division was at a density of 2.5 adult females of *T. ludeni* per cm^2). Fixed explanatory effects included in the full model were the time in months (categorical variable), the treatment (control, intraspecific competition, low density and high density interspecific competition) and their interactions. The islands were treated as random effects and were nested within the two experimental

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blocks for bean, and not nested in blocks for cucumber (same reason as explained above). Model selection was based on the lowest AICc and the pairwise comparisons of the least square means were adjusted for multiple comparisons based on Tukey's method.

The estimates provided in the tables are the raw and untransformed estimates for the fixed effects of the final models (negative binomial distribution).

All analyses were performed in R (version 3.5.1) with glmmTMB version 0.2.2.0 (Brooks *et al.*, 2017), MuMIn version 1.42.1 (Barton, 2018), ggplot2 version 3.0.0 (Wickham, 2016), ggpubr version 0.1.8 (Kassambara, 2018).

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RESULTS

In absence of a competing species both species survived, although the focal species *T. urticae* reached higher densities than *T. ludeni* (Fig. 1). In mixed populations, *T. ludeni* went extinct after about two months and hence we will refer to it as the ghost competitor. Nevertheless, the ghost competitor left a strong signature on the reproductive performance of the focal species in the novel environment. A significant positive correlation was found between the initial density of the competitor and the fecundity of spider mites measured on cucumber (Z = 2.33 and p = 0.0199) (Fig. 2b). This effect emerged from the start of the experiment and remained stable. Performance on the initial host plant, bean, was not related to initial ghost competitor density. (Table 1 and S1).

As absolute performance does not provide insights on the level of adaptation, an additional analysis was performed in which we quantified the differences among treatments in time on the novel and the original host. Here, the interspecific competition treatment was divided in a low density treatment and a high density treatment (depending on the density of the ghost competitor). We observed that performance of *T. urticae* on bean in the last month was significantly lower than in the previous months (Fig. 2a; Table 1 and S1). Populations under intraspecific competition on cucumber had a higher fecundity on cucumber than the control population of *T. urticae* that had been kept on bean (and fecundity was assessed on cucumber; Z = 3.235 and p = 0.0067). This indicates local adaptation to the novel host plant. Our experimental design is not strictly suitable to assess adaptation in the interspecific competition treatment, as we did not keep a control mixed population on bean, but we did find that the high density interspecific competition treatment did not significantly differ from the intraspecific competition treatment (Z = 1.212 and p = 0.6193, whereas the low density treatment had a significantly lower fecundity than the intraspecific competition treatment (2 = 2.876 and p = 0.0210) (Fig 2b; Table 1 and S1).

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DISCUSSION

The process of genetic adaptation to novel environmental conditions is typically studied and understood from the perspective of the available genetic variation and selection pressures as imposed by the environment. Because competing species are an intrinsic part of novel experienced environmental conditions, they are known to mediate sometimes complex evolutionary processes. Here, we have shown that temporarily coexisting, competing species that eventually go extinct, can have a long lasting effect on the performance in a novel environment.

We have shown that *T. urticae* populations under purely intraspecific competition reached higher oviposition rates on the novel host plant than the control population maintained on the initial host plant, implying local adaptation to the novel host (Fig. 2b). This difference in fecundity with the control population was not found for the interspecific competition treatment as a whole or for those replicates with low initial densities of the interspecific competitor, but we did find that *T. urticae* populations that experienced a higher density of the interspecific competitor during population build-up showed similar oviposition rates as the intraspecific treatment (Fig. 2b). A likely explanation for the lack of evidence for adaptation in the interspecific competition treatment (at low initial densities) is initial differences in population size and subsequent drift effects, while the replicates where *T. ludeni* successfully reached higher densities during the first month, its selection pressure was stronger eventually leading to an increase in fecundity of the focal species (Fig. 2b). Our last time point showed a significant drop in fecundity on the ancestral host plant, bean (Fig. 2a). We attribute this change to a temporal drop in resource quality rather than to genetic mechanisms as for instance inbreeding load, because the same decline was observed in the control population, but not in the performance on cucumber.

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It is known that the competitor, *T. ludeni*, can down-regulate plant defences (Godinho et al. 2016), but this cannot explain the correlation between its higher density and the increased fecundity of the focal species under interspecific competition (Fig. 2b). The presence of the ghost competitor was only temporary, so the down-regulation could not persist during the experiment as plants were refreshed weekly.

The history of species in a community can have an impact on interspecific interactions (Fukami, 2015). The magnitudes of such historical contingencies do, however, strongly differ among species and environments (Vannette & Fukami, 2014). Differences in historical contingency have been put forward as an explanation for the fact that some populations can experience radiations, whereas others from the same clade are not capable to achieve this under seemingly similar conditions (Seehausen, 2007). Our results experimentally confirm this perspective and suggest that increased interspecific competition led to higher selection pressures and thus improved performance. Our results coincide in this respect with other empirical work demonstrating that increased competition with heterospecifics increased local adaptation in bunchgrasses (Rice & Knapp, 2008). Similarly, intraguild predation between lizard species increased the selection pressure and led to strong divergence in morphological adaptation as associated with niche specialisation (Stuart *et al.*, 2014).

The higher densities of competing species exert a higher selection pressure that leads to comparable level of adaptation as under intraspecific competition. Intraspecific competition is known to push towards ecological specialisation (Silvertown, 2004). As seen in the ecological dynamics, initially higher densities of *T. urticae* were found in the intraspecific competition treatment compared to the treatment containing both species (Fig. 1), which could exert

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stronger intraspecific competition. Intraspecific effects are found to be particularly strong in those cases where communities are affected by indirect interactions such as cascading effects (Des Roches *et al.*, 2018). Given that we are working in a system with entire plants, direct and indirect interactions between the spider mites and their host plants are very likely. Many examples are found where indirect interactions are induced after a herbivore attack (e.g. the release of volatiles to attract natural enemies, activation or production of toxins or defensive structures; Zhang *et al.*, 2009; Kant *et al.*, 2015). We do note that the observed high densities may be an artefact of the experiment, where refreshing plants might have kept the population densities higher than in natural populations and thus might have promoted intraspecific competition.

In conclusion, the initial strength of interspecific competition has a significant impact on the long-term performance of species in novel environments. Even when one species becomes extinct, the competition signature continues to affect the adaptation process of the successful species. We thus provide experimental evidence on the impact of ghost species on the long term performance of populations reaching new environments.

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AUTHOR CONTRIBUTIONS

The idea and the design of the study was developed by K.B., D.B. and R.S.E. The data was collected by K.B. and F.M. and the statistical analyses were performed by K.B. K.B. wrote the draft of the manuscript and all authors contributed to revisions and discussions.

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FIGURES

Figure 1: Overview of the population density for the different treatments. Population density of *T. urticae* (green dots) and *T. ludeni* (red dots) measured as the sum of the abaxial and adaxial density (number of adult females/cm^2) per island through time. The lighter colours correspond to the populations in absence of the competing species and the darker to the interspecific competition treatment. The grey zone shows the 95% confidence interval.

Figure 2: Fecundity (number of eggs during six days) of *T. urticae* assessed on: **(a) bean,** fecundity through time, and **(b) cucumber**, fecundity significantly affected by the initial density of *T. ludeni* within the inter- and intraspecific competition treatment ($R^2 = 0.05$). The upper panel shows the significant difference between intraspecific competition on the one hand and the control and the population under low interspecific competition on the other hand. The split between low and high interspecific competition in the inter- and intraspecific competition treatment is illustrated with the vertical black line.

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TABLES

Table 1: **Summary of the final GLMM explaining reproductive performance**. (A) Investigation of the variation in density of the ghost competitor through time. The final model for female mites assessed on bean did not include fixed effects; female mites measured on cucumber showed a significant correlation between reproductive performance and the initial density of the competitor was found. (B) Investigation of the magnitude of adaptation. On bean, only a time effect was found in which the last month performed worse for all populations, including control. On cucumber, the treatments were the only explaining variable.

		Estimate	Std. error	Z value	Pr (>|z|)	
Investigation of the variation in density of the ghost competitor through time						
Bean	(Intercept)	3.70979	0.08988	41.27	<2e-16	***
Cucumber	(Intercept)	3.22094	0.08831	36.47	<2e-16	***
	Comp. Dens.	0.06929	0.02977	2.33	0.0199	*
Investigation of the magnitude of the adaptation						
Bean	(Intercept)	3.777932	0.079304	47.64	< 2e-16	***
	4 months	0.021016	0.068052	0.31	0.757	
	6 months	0.029561	0.067775	0.44	0.663	
	8 months	0.001468	0.067359	0.02	0.983	
	10 months	-0.309824	0.071536	-4.33	1.48e-05	***
Cucumber	(Intercept)	3.52841	0.03516	100.36	< 2e-16	***
	High Dens.	-0.06953	0.05738	-1.21	0.22559	
	Low Dens.	-0.20141	0.07004	-2.88	0.00403	**
	Control	-0.16410	0.05072	-3.24	0.00121	**

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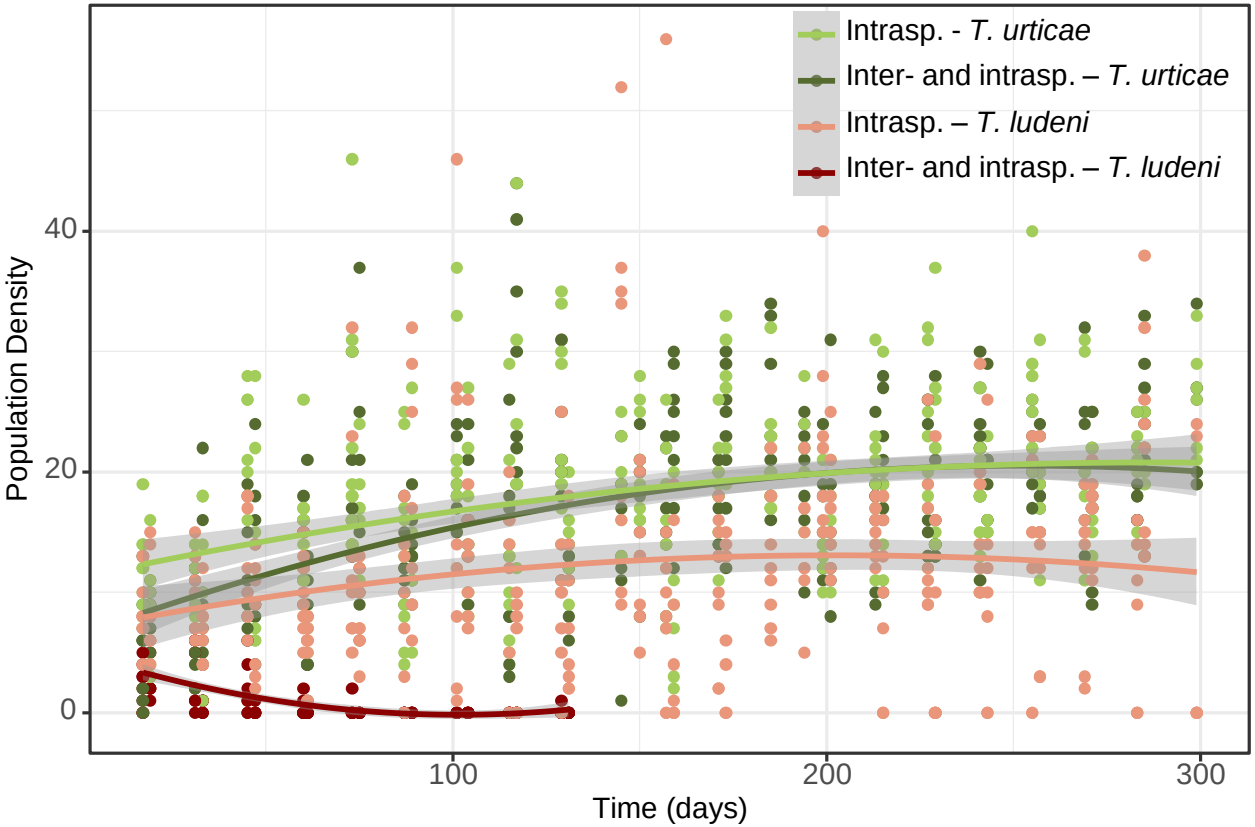
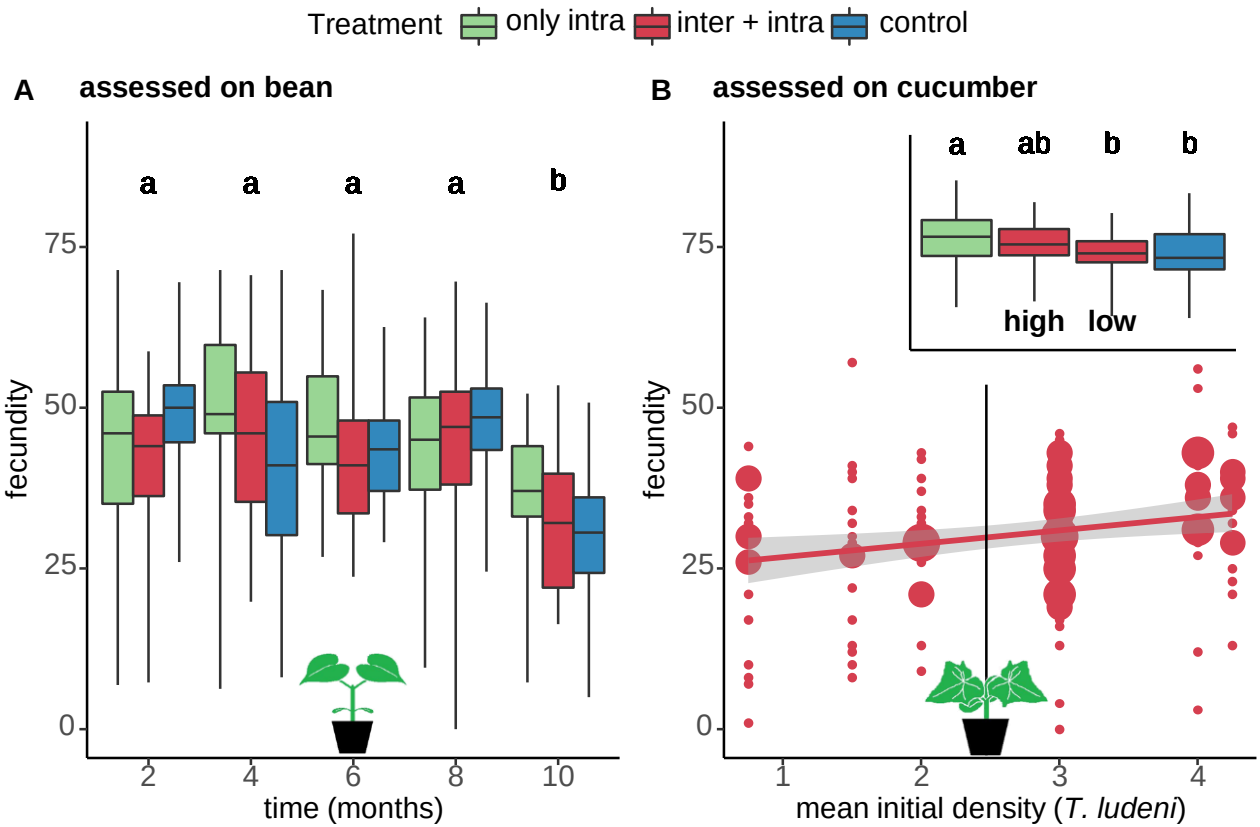

Intrasp. - T. urticae
Inter- and intrasp. – T. urticae
Intrasp. – T. ludeni
Inter- and intrasp. – T. ludeni
Population Density
0
20
40
100
200
300
Time (days)


Treatment
only intra
inter + intra
control
A
assessed on bean
a
a
a
a
b
fecundity
75
50
25
0
2
4
6
8
10
time (months)
B
assessed on cucumber
a
ab
b
b
high
low
fecundity
75
50
25
0
1
2
3
4
mean initial density (T. ludeni)