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Research

The role of preadaptation, propagule pressure and competition in the colonization of new habitats

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To successfully colonize new habitats, organisms not only need to gain access to it, they also need to cope with the selective pressures imposed by the local biotic and abiotic conditions. The number of immigrants, the preadaptation to the local habitat and the presence of competitors are important factors determining the success of colonization. Here, using two experimental set-ups, we studied the effect of interspecific competition in combination with propagule pressure and preadaptation on the colonization success of new habitats. Our model system consisted of tomato plants (the novel habitat), the two-spotted spider mite *Tetranychus urticae* as our focal species and the red spider mite *Tetranychus evansi* as a competitor. Our results show that propagule pressure and preadaptation positively affect colonization success. More successful populations reach larger final population sizes either by having higher per capita growth rates (due to preadaptation effects) or by starting a population with a larger number of individuals. Although populations are more successful colonizing non-competitive environments than competitive ones, propagule pressure and preadaptation counteract the negative effects of competition, promoting colonization success. Our study shows the importance of propagule pressure and preadaptation for successful colonization of new habitats by providing the ability to cope with both the exigencies of new environments and the community context.

Keywords: competition, per capita growth rate, population size, preadaptation, propagule pressure, spider mites

Introduction

New habitats provide novel ecological opportunities, potentially facilitating speciation and biological diversification (Simpson 1953, Carson and Templeton 1984, Onstein et al. 2014, Delaux et al. 2015). Colonization of new habitats, however, relies on the interplay between ecological (e.g. competition, dispersal) and evolutionary (e.g. adaptation) processes that results in complex eco-evolutionary dynamics. Although some of these processes (dispersal, adaptation and competition) have been studied at large spatial and temporal (evolutionary) scales (Donoghue 2008, Edwards and

Donoghue 2013, Onstein et al. 2014), an understanding of how these factors interact to affect colonization success of new habitats is still lacking.

For individuals to successfully colonize new habitats, firstly they need to physically access it (via dispersal). Secondly, they need to establish self-sustaining populations, eventually allowing range expansion (Lockwood et al. 2005). Consequently, the number of individuals arriving in a colonization event and the number of colonization events (as a whole referred to as propagule pressure) affects the probability of colonization success (Lockwood et al. 2005, Maron 2006, Simberloff 2009). A high propagule pressure increases the chance that some of the immigrants can establish in the new habitat, for instance by having the right genetic make-up. Also, it reduces the probability of extinction, which is more likely to occur in small population sizes due to Allee effects, founder effects, genetic (inbreeding, drift) and demographic stochasticity (Ellstrand and Elam 1993, Newman and Pilson 1997, Dressler et al. 2019). Third, in order to establish populations and further expand, individuals need to cope with the ecological context of the new habitat, i.e. the abiotic conditions (which might differ from the ones in the original environment), and the presence or absence of competitors, resulting in differences in the availability of unexploited resources ('empty niches') (Simpson 1953). Preadaptation to the new habitat, that is, genetic or phenotypic traits allow the organism to survive in the new habitat, either due to evolution of these traits or phenotypic plasticity, may increase the probability of colonization success (Dlugosch and Parker 2007, Hamilton et al. 2015, Vahsen et al. 2018). Furthermore, these preadaptations may also help individuals to overcome competition exerted by the receiving community. Preadaptation of herbivores to a new host plant may involve the development of new metabolic pathways to metabolize anti-herbivory components and increase resource acquisition leading to a more efficient exploitation of resources (Van Leeuwen and Dermauw 2016, Dermauw et al. 2018). As a consequence, adaptation to a type of habitat (e.g. a type of plant or a new host from a parasite perspective) may increase fitness in that particular habitat and thus population growth rates (Strauss 2014, Hendry 2019). In a competitive environment, an increase in population growth rate also implies an increase in competitive abilities. Therefore, preadaptation might positively affect colonization success by avoiding competitive exclusion. Even though these pre-requisites for colonization success are generally recognized, the relative importance of physical access to the habitat, preadaptation and competition to determine success in new habitats, remains unknown.

Here, using two microcosms experiments we tested the importance of interspecific competition in combination with 1) propagule pressure, and 2) preadaptation on colonization success in novel environments. In this study we defined propagule pressure as the number of immigrants in a single dispersal event (also referred to as propagule size in the strictest sense). Our study system included tomato plants as the novel environment, a Solanaceae specialist, the red spider mite *Tetranychus evansi*, as the competitor and a generalist

herbivore, the two-spotted spider mite *Tetranychus urticae*, as the colonizer. Both spider mites are known to co-occur both in natural and in agricultural habitats (Ferragut et al. 2013). *Tetranychus urticae* individuals from different populations were introduced to the novel host plant (tomato), to which some of the populations were preadapted and others were not. Competitive environments were created by including competitive mites (*Tetranychus evansi*) in the novel environment. Propagule pressure was examined by varying the initial number of immigrants to the new habitat. After one generation in the novel environment, *T. urticae*' population size (number of adult female mites) and per capita growth rate was used as a proxy of colonization success. We specifically tested three hypotheses: (H1) higher propagule pressures will positively affect population sizes but not per capita growth rate, (H2) preadapted individuals will attain higher per capita growth rates (because more adapted individuals evolve higher fecundity) and thus higher population sizes in new habitats than less adapted individuals; and (H3) interspecific competition will reduce population sizes and population' per capita growth rate, but the extent of this reduction will depend on propagule pressure and preadaptation.

Methods

Study species

The two-spotted spider mite *Tetranychus urticae* (Acari, Tetranychidae) is a generalist herbivore that feeds on a wide variety of host plants (Gotoh et al. 1993). Because of its small body size (female size about 0.4 mm length), high fecundity (1–12 eggs day⁻¹) and short developmental time (11–28 days; Nacimiento de Vasconcelos et al. 2008), *T. urticae* is an ideal model organism for microcosm experiments on adaptation (Gould 1979, Egas and Sabelis 2001, Magalhães et al. 2007, Kant et al. 2008, Bonte et al. 2010, Alzate et al. 2017, 2019). Moreover, its biology has been thoroughly described and its genomics are well-known (Grbić et al. 2011). All populations used in this study were derived from the London strain, originally collected from the Vineland region in Ontario, Canada (Grbić et al. 2011). We used three populations of *T. urticae* that differ in their level of adaptation to tomato (the novel environment used in this study): non-adapted, medium adapted and highly adapted. The non-adapted population was reared on bean plants *Phaseolus vulgaris* (variety prelude) for more than six years. Both the medium adapted and the highly adapted populations were derived from the non-adapted population, but medium adapted populations were reared on tomato plants *Solanum lycopersicum* (variety 'moneymaker') for about 20 generations (populations receiving two female mites per week in Alzate et al. 2017), and the highly adapted population was reared on tomato plants for more than 100 generations, prior our experiment. These populations differed in their fitness, measured as fecundity (number of eggs as a proxy of fitness) on tomato plants, suggesting differences in their adaptation to the tomato host plant (Alzate et al. 2017).

As a competitor, we used the red spider mite *Tetranychus evansi* (Acari, Tetranychidae), which is a specialist herbivore of (mainly) Solanaceae (incl. tomato). Adult females are easily distinguishable from *T. urticae* as they show a characteristic red coloration and are slightly larger (0.5–0.6 mm length). Fecundity ranges from 10 to 14 eggs per day (Navajas et al. 2013) and development time can vary from 6.3 to 13.5 days, depending on the environmental temperature and host (Bonato 1999).

Experiments

Using two experiments, we examined how total population abundance and per capita growth rate was affected by inter-specific competition and either propagule pressure or pre-adaptation. Before each experiment we minimized epigenetic effects (juvenile and maternal effects) by collecting individual females from each population (non-adapted, medium adapted and highly adapted) and rearing them separately in a common garden for two generations (Magalhães et al. 2011). The common garden consisted of a 5 cm diameter bean leaf disk (per female) on cotton wool soaked in distilled water. All individuals derived from a single female are therefore considered an iso-female line and each line was used as a replicate for the experiments performed in this study.

Propagule pressure and competition

In the first experiment we used the highly adapted population to study the effect of propagule pressure and competition on colonization success (H1, H3). We tested three levels of propagule pressure (3, 5, 10 individual adult female mites), and the presence or absence of competition with *T. evansi* (three individuals). Per iso-female line, we placed adult female mites (3, 5 or 10) on either a complete (four weeks old) tomato plant with or without competition. In total we tested six treatment combinations with eight replicates (eight iso-female lines) for treatments with propagule pressure of three individuals and five replicates (five iso-female lines) for treatments with propagule pressure of 5 and 10 individuals (Supplementary material Appendix 1 Fig. A1).

Preadaptation and competition

In the second experiment we evaluated the effect of pre-adaptation and competition on colonization success to new environments (H2, H3). We placed three adult females from each adaptation treatment (and iso-female line) either on a complete (four weeks old) tomato plant without cohabitants (no competition treatment) or on a complete tomato plant together with three females of *T. evansi* (competition treatment). We tested three pre-adaptation and two competition levels, for a total of six treatment combinations. We used eight replicates (iso-female lines) for treatments with non-adapted and highly adapted populations and 12 replicates for the treatment with medium adapted populations. Medium adapted populations have more replicates because we collected females from four independent populations, whereas for the non-adapted and highly adapted treatments, females came from a single population (Supplementary material Appendix 1 Fig. A2).

For both experiments, plants were maintained in a climate regulated room at $25 \pm 0.5^\circ\text{C}$ with a 16/8 h light/dark regime for 15 days. Because fecundity varies with female age (Sabelis and van der Meer 1986) we chose adult female mites of similar age (1–2 days after emerging from the last quiescent stage) to be placed on tomato plants. In the competitive environments, we ensured that females of *T. urticae* were placed on the same leaves as females of *T. evansi* for competition to be effective. Population sizes of *T. evansi* and *T. urticae*, and growth rate of *T. urticae* were recorded after 15 days (one generation). To estimate population sizes, we counted all adult female mites present on each complete tomato plant. Juveniles and males were not included in the counting because their small size made their detection with the naked eye difficult. Complete population sizes are therefore larger than the ones presented in this study, when accounting for juveniles and males (S2 in De Roissart et al. 2015). Per capita growth rate was calculated by first subtracting the initial number of females from the final number of females after one generation, then dividing this by the initial number of females.

In addition to the competition experiments using *T. evansi* and *T. urticae* populations with different propagule pressures and pre-adaptations, we simultaneously studied five populations of *T. evansi* without competition, in which three adult females of *T. evansi* were placed on tomato plants.

Statistical analyses

Propagule pressure and competition

We tested the effect of propagule pressure and competition on per capita growth after one generation of population growth on the novel environment, using a general linear mixed model. The effect of propagule pressure and competition on population size was tested using generalized linear mixed models with Poisson error distribution. For both models, we used propagule pressure (with three levels: 3, 5 and 10 female mites) and competition (with two levels: competition with *T. evansi* and no-competition) as fixed categorical factors. Because females coming from the same iso-female line (Supplementary material Appendix 1 Fig. A1) might respond similarly to a treatment than females that are not related, we used iso-female line as a random factor. We used per capita growth rate and final population size (number of adult females after one generation) as response variables. Per capita growth rate was log-transformed to meet the assumption of normal distribution of model residuals. To correct for the initial differences in population sizes on final population sizes, we subtracted the initial number of immigrants (3, 5 or 10 female mites) from the final population size. Model selection (for both the random and fixed part) was performed using a stepwise removal of non-significant effects based on log-likelihood ratio test until only significant effects remained. Post hoc tests were performed to test for differences between the least square means of treatments using the `diffsmeans` function from the package `lmerTest` and p-values were adjusted for multiple comparisons using a Tukey HSD test (Kuznetsova et al. 2017).

Preadaptation and competition

To test the effect of preadaptation and competition on per capita growth rate and final population size, we used the same statistical procedure as described above, but including preadaptation (three levels: no adapted, medium adapted and highly adapted) and competition (two levels: competition and no competition) as fixed factors. Model selection and post hoc test was performed similarly as described above.

Effects of *T. urticae*' propagule pressure and preadaptation on *T. evansi*' population size and on *T. urticae*' competitive ability

To test the effect of competition with populations with different propagule pressures and preadaptation levels on *T. evansi* population sizes, we performed a generalized linear mixed model with Poisson error distribution. We used a combined factor of competition and preadaptation/propagule pressure as fixed categorical factor (4 levels for propagule pressure experiments: Single, Competition with propagule pressure of 3 individuals, Competition with propagule pressure of 5 individuals and, Competition with propagule pressure of 10 individuals; and 4 levels for preadaptation experiments: Single, Competition with non-adapted population, Competition with medium-adapted population and Competition with highly-adapted population) and iso-female line as a random factor (this only applied to the preadaptation experiment).

Competitive ability of *T. urticae* was calculated as the fraction of individuals of *T. urticae* among the total number of individuals (*T. urticae* + *T. evansi*). To test the effect of propagule pressure and preadaptation on *T. urticae*' competitive abilities we performed a general linear model with preadaptation as a fixed categorical factor. Model selection and post hoc tests for both analyses were performed as described above.

All analyses were performed in R ver. 3.5.3 (<www.r-project.org>) with the R packages lme4 (Bates et al. 2015), lsmeans (Lenth 2016), lmerTest (Kuznetsova et al. 2017) and multcomp (Hothorn et al. 2008).

Results

Propagule pressure and competition

Final population size (number of adult female mites) was best explained by the additive effects of propagule pressure and competition (Table 1, see Supplementary material Appendix 1 Table A1 for model selection). While propagule pressure positively affected population size of *Tetranychus urticae*, both with and without competition, competition always exerted a negative effect on population size irrespective of propagule pressure (Fig. 1A). Populations receiving a higher number of propagules (10 females) attained larger

Table 1. Summary of final statistical models testing 1) the effects of propagule pressure and competition and 2) the effects of preadaptation and competition on population size and per capita growth rate of *Tetranychus urticae* when colonizing a novel habitat. Marginal (fixed effects only) and conditional (fixed and random effects) coefficients of determination for the final models are shown (R^2_m , R^2_c respectively). Estimates for models testing preadaptation and competition are log-transformed.

Test	Response variable	Effect	Estimate	SE	z	p	
Propagule pressure and Competition	Population size	No competition – 3 females	4.11	0.12	34.68	0.000	
		Competition	-1.74	0.12	-14.87	0.000	
		5 females	0.49	0.09	4.67	0.000	
		10 females	0.77	0.08	9.64	0.000	
		$R^2_m = 0.89$; $R^2_c = 0.98$	Competition × 5 females	0.34	0.17	2.02	0.040
			Competition × 10 females	0.71	0.14	5.05	0.000
		Response variable	Effect	Estimate	SE	t	p
	Per capita growth rate		No competition – 3 females	23.53	2.16	10.88	0.000
			Competition	-18.78	2.42	-7.75	0.000
			5 females	-5.34	2.92	-1.83	0.081
10 females			-9.55	2.83	-3.37	0.003	
$R^2_m = 0.65$; $R^2_c = 0.77$			Competition × 5 females	6.33	3.85	1.64	0.118
		Competition × 10 females	10.80	3.70	2.92	0.009	
Preadaptation and Competition	Population size	No competition – no Adapted	0.27	0.37	0.74	0.460	
		Competition	-1.41	0.09	-14.99	0.000	
		Medium adapted	1.97	0.41	4.76	0.000	
		Highly adapted	3.77	0.43	8.72	0.000	
		Response variable	Effect	Estimate	SE	t	p
	Per capita growth rate		No competition – no Adapted	0.34	0.18	1.87	0.067
			Competition	-0.19	0.24	-0.80	0.430
			Medium adapted	0.98	0.23	4.26	0.000
			Highly adapted	2.81	0.27	10.27	0.000
			$R^2_m = 0.76$; $R^2_c = 0.78$	Competition × Medium adapted	-0.52	0.31	-1.66
		Competition × Highly adapted	-1.29	0.36	-3.62	0.001	

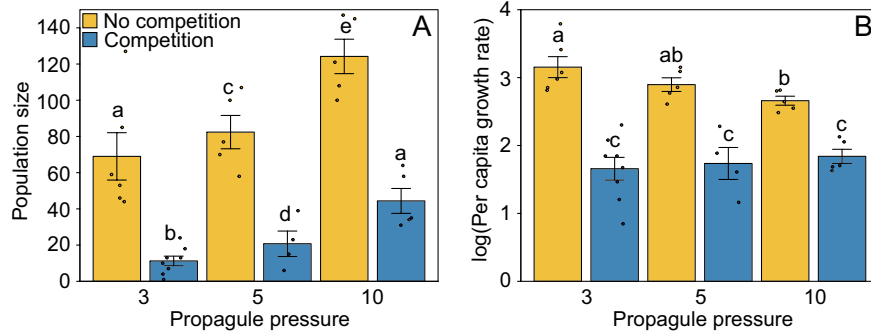


Figure 1. Effect of propagule pressure (number of *Tetranychus urticae* colonizers) on population size measured as the total number of adult females (A) and per capita growth rate (log transformed) (B) of *T. urticae*. Bars show the mean population size or per capita growth rate and standard errors for the raw data. The underlying raw data is shown as points for each treatment combination. Letters show significant differences between treatments (GLMM (A)–LMM (B), Tukey HSD, $p < 0.05$).

population sizes after one generation than populations receiving fewer propagules (3 females).

Per capita growth rate was best explained by both the additive and interaction effects of propagule pressure and competition (Table 1, Supplementary material Appendix 1 Table A1 for model selection). While competition always affected growth rate negatively, the effect of propagule pressure depended on the competitive environment (Table 1). In a non-competitive environment, propagule pressure exerted a negative effect on per capita growth rate, whereas in a competitive environment propagule pressure did not have an effect (Fig. 1B).

Preadaptation and competition

Population size (number of adult female mites) was best explained by the additive and interaction effects of preadaptation and competition (Table 1, see Supplementary material Appendix 1 Table A1 for model selection). Populations that co-occurred with *T. evansi* were significantly smaller than populations without the competitor for populations with medium and high preadaptation (Fig. 2A). Populations with no preadaptation had the lowest population size in both competitive and non-competitive environments, and populations

with high preadaptation in non-competitive environments had the largest population sizes (Fig. 2A).

Per capita growth rate was best explained by the additive and interaction effects of preadaptation and competition. Preadaptation affected growth rate positively, whereas competition affected growth rate negatively (Fig. 2B). Populations without any preadaptation showed the lowest growth rate, both in competitive and non-competitive environments, whereas populations with high preadaptation in non-competitive environments showed the highest growth rate (Fig. 2B).

Effects of *T. urticae*' propagule pressure and preadaptation on *T. evansi*' population size and on *T. urticae*' competitive ability

Tetranychus urticae' propagule pressure negatively affected *T. evansi*' population sizes ($R^2 = 0.85$; Fig. 3A). *Tetranychus evansi* populations showed a reduction of 33 and 24 individuals on average when in competition with populations that started with low (3 individuals) (estimate = -0.37 , SE = 0.06, $Z = -6.22$, $p < 0.0001$) and medium (5 individuals) (estimate = -0.25 , SE = 0.07, $Z = -3.87$, $p = 0.0001$) propagule pressure, respectively, but a reduction of 57 individuals on average when in competition with the populations that

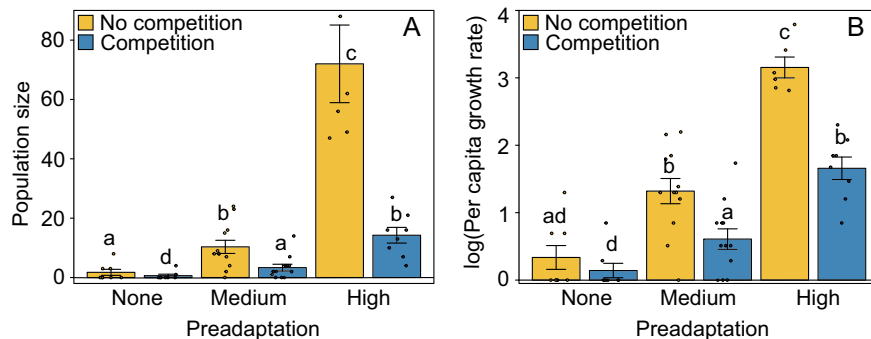


Figure 2. Effect of preadaptation and competition on population size measured as the total number of adult females (A) and per capita growth rate (log transformed) (B) of *Tetranychus urticae* after one generation on a novel environment. Bars show the mean population size or per capita growth rate and standard errors for the raw data. The underlying raw data is shown as points for each treatment combination. Letters show significant differences between treatments (GLMM (A)–LMM (B), Tukey HSD, $p < 0.05$).

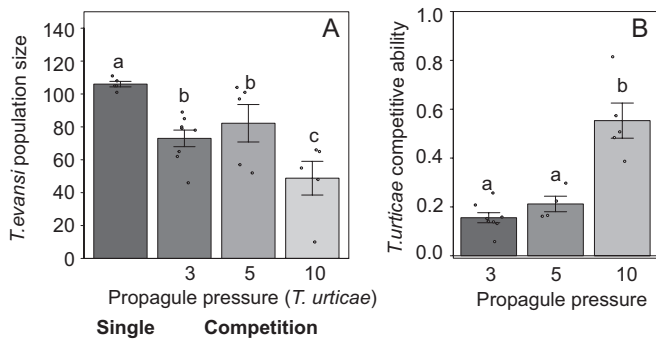


Figure 3. Effect of *Tetranychus urticae* propagule pressure on (A) *T. evansi* population size (number of adult females) and on (B) the overall competitive ability of *T. urticae*. Overall competitive ability was calculated as the fraction of individuals of *T. urticae* among the total number of individuals (*T. urticae* + *T. evansi*). Bars show the mean population size or mean competitive ability and standard errors for the raw data. The underlying raw data is shown as points for each treatment combination. Letters show significant differences between treatments (GLMM (A)–LM (B), Tukey HSD, $p < 0.05$).

started with high (10 individuals) propagule pressure (estimate = -0.77 , SE = 0.08 , $Z = -10.03$, $p < 0.0001$).

Propagule pressure has a positive effect on *T. urticae* competitive abilities ($R^2 = 0.76$; Fig. 3B). Populations that started with 5 individuals only experience an increase 1.4 times higher than populations starting with 3 individuals (estimate = 0.05 , SE = 0.06 , $t = 0.92$, $p = 0.37$), whereas populations that started with 10 individuals experienced an increase in competitive ability 3.5 times higher with respect to populations that started with 3 individuals (estimate = 0.39 , SE = 0.06 , $t = 6.99$, $p < 0.0001$), respectively.

Population sizes of *T. evansi* were negatively affected by the preadaptation level of *T. urticae* ($R^2_m = 0.6$, $R^2_c = 0.69$; Fig. 4A). *Tetranychus evansi* populations showed a reduction of 2 individuals on average when in competition with the non-adapted populations (estimate = -0.02 , SE = 0.09 , $Z = -0.20$, $p = 0.84$), but a reduction of 15 and 33 individuals on average when in competition with the medium (estimate = -0.17 , SE = 0.08 , $Z = -01.97$, $p = 0.05$) and the highly adapted (estimate = -0.37 , SE = 0.10 , $Z = -3.71$, $p = 0.0002$) populations, respectively.

Populations of *T. urticae* show an increase in their competitive ability with an increase in preadaptation to tomato plants ($R^2 = 0.7$; Fig. 4B). Highly adapted populations experienced an increase in competitive ability 98 times higher with respect to the non-adapted populations (estimate = 0.15 , SE = 0.02 , $t = 6.99$, $p < 0.0001$), whereas the medium adapted populations showed only 21 times higher competitive ability (estimate = 0.03 , SE = 0.02 , $t = 1.53$, $p = 0.14$).

Discussion

We experimentally studied how colonization of novel environments is affected by interspecific competition and furthermore how the outcome of this interaction depends on

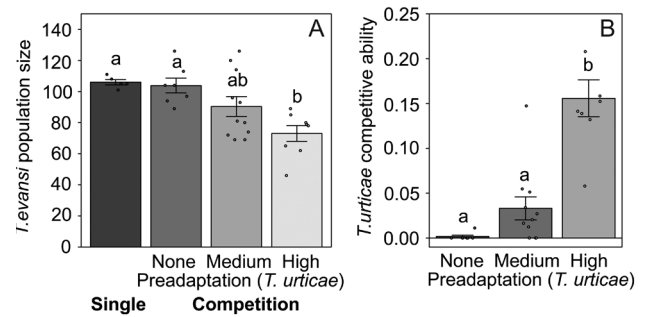


Figure 4. (A) Effect of *Tetranychus urticae* preadaptation on *T. evansi* population size (number of adult females). (B) effect of preadaptation on the overall competitive ability of *T. urticae*. Overall competitive ability was calculated as the fraction of individuals of *T. urticae* among the total number of individuals (*T. urticae* + *T. evansi*). Bars show the mean population size or mean competitive ability and standard errors for the raw data. The underlying raw data is shown as points for each treatment combination. Letters show significant differences between treatments (GLMM (A)–LM (B), Tukey HSD, $p < 0.05$).

preadaptation to the novel environment and the propagule pressure (number of colonizing individuals in a single dispersal event). We showed that populations are more likely to successfully colonize low competitive environments. However, in the presence of competition, preadaptation to the novel environment or a high propagule pressure can increase the chances of colonization success, counteracting the negative effects of interspecific competition. Our results show that preadaptation and propagule pressure benefit successful colonization differently. While preadaptation positively affects population sizes by increasing per capita growth rate, propagule pressure increases population sizes due to the additive effect of starting with a large population size. In either way both propagule pressure and preadaptation help the colonizing population to cope with competition in the new environment.

The population dynamics of the herbivorous two-spotted spider mite *Tetranychus urticae* are in general characterized by series of colonization events (by mated female mites), fast population growth that leads to food resource over-exploitation and subsequent dispersal to new host plants (Mitchell 1973, Helle and Sabelis 1985, Sabelis et al. 1991, Bancroft and Margolies 1999). Due to the nature of these dynamics, *T. urticae* are distributed patchily and on diverse host plants (to which they might be preadapted), resulting in plenty of opportunities to coincide in the same host plants with *T. evansi*. Nevertheless, it has been shown that coexistence of both species is relatively rare (Ferragut et al. 2013); *T. evansi* usually outcompetes *T. urticae* both in natural (Ferragut et al. 2013) and in laboratory conditions (Sarmiento et al. 2011a). Based on the effect of both species on tomato plant defenses, we might expect a positive indirect effect of *T. evansi* on *T. urticae* (*T. evansi* is known to down-regulate tomato plant defenses) and a negative indirect effect of *T. urticae* on *T. evansi* (*T. urticae* up-regulates tomato plant defenses) (Sarmiento et al. 2011b, Godihno et al. 2016).

Nevertheless, resource competition, reproductive interference (Sato et al. 2014) or feeding interference by web production (Sarmiento et al. 2011a) likely have made *T. evansi* an overall stronger competitor. Consequently, it is more common to see resource partitioning and host separation for both species (Ferragut et al. 2013). Our results show that to avoid competitive exclusion by *T. evansi*, *T. urticae* needs to quickly reach large population sizes. Therefore, in nature there might be few possibilities for coexistence: either by starting a population with a large number of colonizers (high propagule pressure) or by being highly preadapted to the host plant. In either case colonization is more likely before *T. evansi* populations have reached a high population density. We have shown that when populations start with a low-medium propagule pressure (3 and 5 individuals), populations of both species reach similar sizes, but with a high propagule pressure (10 individuals) population sizes of *T. urticae* are on average 1.5 times higher than population sizes of *T. evansi* (Fig. 2A, 4A). Our results suggest that colonization is more likely before *T. evansi* populations have reached a high population size (in relative terms to the ones of *T. urticae*).

Propagule pressure has been widely studied using empirical, observational and experimental approaches mainly because of its relevance to invasion biology and its role on colonization success of invaders (Blackburn and Duncan 2001, Simberloff 2009, Lockwood et al. 2005, Cassey et al. 2018). In general, propagule pressure (here referred to as propagule size) has been shown to be positively correlated to colonization and establishment success (Maron 2006, reviewed by Cassey et al. 2018), and our results are in line with these findings. Moreover, our experiment is the first, to our knowledge, to explore how the effect of propagule pressure on colonization success is affected by the ecological context in which individuals arrived (environments with and without interspecific competition). Firstly, we have shown that competitive environments have a strong negative effect on *T. urticae*' population size, but propagule pressure counteracted this effect, positively affecting population size (Fig. 1A). Secondly, we have shown that in a competitor-free environment, propagule pressure negatively affected per capita growth rate, whereas it had no effect in a competitive environment (Fig. 1B). This strongly suggests that intraspecific competition increases with propagule pressure, which in turn hinders population growth. In a competitive environment, interspecific competition reduces population sizes to a degree that intraspecific competition may be of less importance. Siepielsky et al. (2016) showed that intraspecific competition driven by density dependence in damselflies increases when populations are more adapted to the local conditions. More adapted individuals might be more efficient in acquiring resources, which can decrease quickly and therefore reduce population sizes. For this experiment we used the highly adapted population of *T. urticae*, which are likely better in acquiring resources. Although this makes them more competitive than other populations (a higher competitive ability, Fig. 3), it can also increase intraspecific competition. Because

the outcome of the interaction between propagule pressure and competition might depend on the preadaptation level of the population, it is possible that density dependence is less strong in less adapted populations compared with highly adapted ones. Despite the negative effects of propagule pressure on population per capita growth rate, propagule pressure does have a positive effect on the total population size. Since larger populations are less affected by demographic stochasticity and therefore less likely to go extinct than smaller populations (Alzate et al. 2019), total population size may be a more relevant indicator for colonization success than per capita growth rate.

Besides the ecological context, the nature of the new habitat can determine the fate of the colonizing individuals. The outcome likely depends on the relative differences between the old and the new habitat, and the degree of niche-conservatism of arriving individuals. In other words, immigrants that come from a very different habitat might be less able to cope with the new conditions than individuals that come from a similar habitat, making them likely preadapted. Studies on invasion ecology suggest that preadaptation (or proxies such as phylogenetic relatedness to the local species) can increase the chance of successful colonization (Li et al. 2015). However, Maron (2006) shows that latitude (their surrogate for preadaptation) does not affect colonization success. Nevertheless, to truly assess the importance of preadaptation, it is important to evaluate the environmental conditions that may require adaptations and thus constrain survival and fitness of organisms based on their morphology, physiology and reproduction (Colautti and Barret 2013). In our study, mites were preadapted to a new host plant (tomato) on which survival and fecundity is much lower in absence of preadaptation (Alzate et al. 2017), probably due to herbivore-induced plant defenses that hamper feeding and reproduction (Kant et al. 2015, Godihno et al. 2016). We have shown that preadaptation to the new habitat is key for successful colonization, as it increases population growth rates and in consequence total population sizes (Fig. 2). Although preadapted populations are, in absolute terms, more affected by competition, possibly due to the combined effect of inter- and intraspecific competition, in relative terms preadapted populations are less affected than non-preadapted populations. The reduction in per capita growth rate due to competition is on average 5.13 times versus 21 times for highly and medium adapted populations, respectively (Fig. 2B). Therefore, preadapted populations have a higher per capita growth rate that allows them to attain larger population sizes, thus decreasing extinction risk. Furthermore, preadaptation helps individuals to cope with competition by increasing their competitive abilities (e.g. more efficient resource consumption). For example, in *Drosophila* species, it has been shown that adaptation to the abiotic environment is the most important component to increase competitive ability (Joshi and Thompson 1996). In our experiment, the most adapted populations had not only larger growth rates and larger final population sizes (Fig. 2), they also exerted a higher competitive effect on the

competitor species, *T. evansi* (Fig. 3A) and displayed a higher overall competitive ability (Fig. 3B), compared with less adapted populations. This effect is also present when increasing propagule pressure (Fig. 4B).

The context of our study for propagule pressure is relatively simple as we only examined the effect of the number of colonizers in a single dispersal event (propagule size in the strictest sense) and used populations that were already highly preadapted to the new host. Including propagule frequency might result in a more complex and context-dependent outcome, affecting not only ecological but also evolutionary processes (Wittmann et al. 2014, Koontz et al. 2018, Peniston et al. 2019). Moreover, outcomes of manipulating propagule frequency would likely depend on the source of immigrants (their level of preadaptation), the number of colonizers in a single dispersal event and the competitive context of the habitat (Vahsen et al. 2018). For instance, successful colonization is very unlikely for *T. urticae* populations that are not preadapted to the new habitat because of their small population sizes which increase extinction risk (Alzate et al. 2017, 2019). However, it has been shown that frequent colonization events (of non-preadapted individuals) allow non-preadapted populations of *T. urticae* to locally adapt to tomato plants, which ultimately allows successful colonization and establishment (Alzate et al. 2017, 2019). The number of colonizers has been shown to play an important role in adaptation: an increase in the number of immigrants helps populations to adapt to new habitats via genetic and demographic rescue (Alzate et al. 2019, Peniston et al. 2019), but a further increase has a detrimental effect due to genetic load (Alzate et al. 2017, Peniston et al. 2019). An increase in propagule frequency might benefit non-preadapted populations (but not too high as this leads to maladaptation, see Brady et al. 2019a, b for a review on causes and definitions of maladaptation), whereas, it might harm preadapted population (by turning them maladapted). If the immigrants are preadapted, an increase in propagule pressure might benefit non-preadapted populations. For a population to successfully colonize and establish in a novel habitat it is necessary to be adapted to it, either by starting a population with already preadapted individuals or by local adaptation, for which both components of propagule pressure are important (size and frequency). Thus, in a competitive environment, high propagule pressure is key to maintain large population sizes and avoid competitive exclusion, which might allow non-preadapted individuals to persist long enough to locally adapt.

Conclusion

Understanding the factors that determine species colonization success in novel habitats is of great importance given the biodiversity crisis we are currently facing. Habitat fragmentation, loss and transformation constantly challenge populations with novel habitats. Inability to successfully colonize or survive in those habitats may lead species to extinction as populations become more isolated attaining smaller population

sizes (Fahrig 1997, Wiegand et al. 2005). In this study, we experimentally tested how propagule pressure, preadaptation and competition affect colonization success in novel habitats. Our results confirm the intuitively evident hypothesis that propagule pressure and preadaptation positively affect colonization success. In competitive environments, however, colonization success is reduced, and to successfully colonize habitats that lack ‘empty niches’ (which is likely the most common scenario), it is important to be either preadapted or to start a population with a large number of colonizing individuals (higher propagule pressure). Our results show that large propagule pressures, preadaptation and low competition are pre-requisites for successful colonization of novel habitats.

Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.bg79cnp7m>> (Alzate et al. 2020).

This preprint of this article has been reviewed and recommended by Peer Community in Ecology (<<https://ecology.peercommunityin.org/public/rec?id=20>>).

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Supplementary material (available online as Appendix oik-06871 at <www.oikosjournal.org/appendix/oik-06871>). Appendix 1.