Evolution in abiotic environments shapes coexistence between two spider mite species

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Abstract

Adaptation to novel environments have been documented at the population, phenotype and genotype level. However, the ecological consequences of this process are often ignored. For example, recent evolutionary history in different environments is expected to lead to increased growth rates and competitive abilities. These traits have been identified as key ingredients underlying species coexistence, which suggests that adaptation to new environments may shape species coexistence patterns. However, this hypothesis remains untested.

To tackle this issue, we performed experimental evolution of two herbivorous spider mite species (*Tetranychus urticae* and *T. evansi*) feeding on tomato plants grown under high or low cadmium concentrations. We combined phenotypic analyses with structural stability theory to show that both the cadmium environment and evolution in it changed the coexistence patterns of the two species by increasing niche differences. In fact, the presence of cadmium reduced interspecific competition and led to facilitation between the two herbivores, entailing stable coexistence independently of the previous evolutionary history. Evolution in the cadmium environment also reduced interspecific competition in the ancestral environment, producing stable coexistence. These results show that evolution in a new environment, even in absence of interspecific competitors, affects long-term species coexistence. Importantly, it highlights that biotic interactions (within or between populations) should be accounted for when describing adaptation to novel environments.

Introduction

The recent development of theoretical frameworks such as modern coexistence theory or structural stability (*1–3*) has fostered our understanding of the mechanisms through which competing species coexist in ecological time. That is, species may coexist either through a reduction in niche overlap between species (i.e. low interspecific vs intraspecific competition) or via a reduction in fitness differences (i.e. the ability of species grow despite the presence of competitors)(*1, 4*).

Predictions on species coexistence are specific to a given environmental context. Indeed, the strength and signal of species interactions can be modified by the environment (*5, 6*), with implications for coexistence. For example, Matias *et al* (*7*) showed that extreme drought decreased fitness differences between plants species, but it also led to increased sensitivity to interspecific competition, reducing niche differences, thereby hampering coexistence (*7*). It is thus key to evaluate both niche and fitness differences (and their underlying traits) in order to accurately predict species coexistence.

Exposure to a given environment over some generations may also affect species coexistence due to evolution-driven changes in trait values. For example, competition between and within species is a strong selective agent (*8–11*). Theory predicts that the presence of competitors selects for the evolution of competitive ability(*12–14*). This, in turn, is predicted to affect species coexistence, through mechanisms such as character displacement (*15–17*), neighbour-dependent selection (*18*) or a trade-off between competitive ability and the rate of adaptation in a fluctuating environment (*19*). In line with these predictions, empirical, studies have shown that evolving with competitors can modify competitive traits (*20*) and change coexistence patterns (*21–24*).

An important, yet overlooked, potential role of evolution in species coexistence pertains to the fact that traits that affect coexistence may be selected even in the absence of competitors. For example, species that arrive in an environment before their interspecific competitors will spend more generations in that environment. As population growth rate is highly correlated with fitness, it is expected that this exposure will lead to an increase in the value of this trait. This may either lead to local habitat monopolization, as in ‘classical’ inhibitory priority effects (*25–27*) or foster coexistence, if the species arriving first is the weaker competitor (*28*). For example, adaptation to temperature in an archaeon species resulted in increased growth rate in that environment. This, in turn, has led to this species being more resistant to invasion by a species that typically dominates at high temperatures (*29*).

Evolution in environments without interspecific competitors may also change traits affecting coexistence outcomes other than the growth rate. Indeed, evolution in environments with stressors, different intraspecific densities or under low concentrations of some nutrients has led to changes in the intraspecific competitive ability (*30–32*). This, in turn, is expected to affect species coexistence (*33*). Curiously, although some studies have shown that these evolutionary changes affected community composition (*30*, *34*), none has evaluated how evolution in the absence of interspecific competitors affects the growth rate, intra- and interspecific competition in the novel environment, which is required to predict coexistence and understand its mechanistic basis.

To fill this gap, we performed experimental evolution with two spider-mite species, *Tetranychus urticae* and *T. evansi*, feeding on tomato plants (*Solanum lycopersicum*) grown with and without cadmium. Previous studies from our group have shown that tomato plants can hyperaccumulate cadmium in their leaves, which strongly affects the performance of both spider-mite species (*35*, *36*). In addition, it is known that, in plants without cadmium, *T. evansi* is the superior competitor, excluding *T. Urticae*, unless it arrives first (*28*). However, we don't know the effects that cadmium accumulation and subsequent evolution in this environment can have in the coexistence of these two species. Here, we estimated competitive ability and intrinsic growth rate of the two species in the ancestral and high cadmium environments. Combining these data with the structural stability framework, we predicted coexistence patterns between evolved and control populations of the two species in the two environments. Our initial hypothesis was that evolution in a new environment would increase the intrinsic growth rate of both species. If this change was larger in the inferior competitor (*T. urticae*) then we expected a reduction in fitness differences. The opposite pattern in fitness differences would happen if the growth rate of *T. evansi* increased more than *T. urticae*. At the same time, we also expected that adaptation would decrease intraspecific competition, which could potentially decrease niche differences and reduce the possibility for coexistence. Finally, we also postulated that, if the performance of *T. urticae* was higher than *T. evansi* in cadmium environments, we would also see a shift in the coexistence predictions, with increased likelihood in coexistence, as we saw in previous studies. The impact of evolution on coexistence of the two species would then be determined by the magnitude of changes in fitness and niche differences, with coexistence more likely if equalizing mechanisms were stronger than destabilizing mechanisms.

Material and methods

Plant and spider-mite maintenance

Populations were maintained and experiments were performed using tomato plants (*Solanum lycopersicum*, *var* MoneyMaker) maintained in a climatic room (25:20 ºC, 65% of humidity, light:dark = 16:8). To maintain the original outbred populations, we used 5-week-old plants, having at least five fully expanded leaves, watered thrice per week. Plants used in the experimental evolution (see below) were watered twice a week with 100 mL of tap water for a duration of two weeks, then transplanted to new pots and watered each week with 100mL tap water and another time with either 100mL of distilled water or 100mL of 2mM cadmium chloride solution during another three weeks. This cadmium concentration of 2mM is highly detrimental to both spider-mite species (*35*).

Experimental evolution

Outbred populations, formed via controlled, one-on-one crosses of 200 individuals of 3 and 4 field populations of *T. urticae* and *T. evansi* spider mites (see details in (*37*)) were used to create experimental evolution populations and were maintained in boxes with detached leaves with stems inside a small pot containing water. Twice a week, old leaves were removed, and water and new tomato leaves were added.

Experimental evolution populations were created by transferring 220 adult females from the outbred populations to a box with four tomato leaves, again with their stems in a small pot (2 pots per box), which was replenished every week. Each box contained leaves 2, 3, 4 and 5, each from a different plant. We created 5 populations for each of two selection regimes: cadmium and control, corresponding to mites exposed to leaves from plants watered with a 2mM cadmium) solution or only with water (see above). Every two weeks (corresponding to a mite generation), 220 adult females were transferred by aspiration to a new box containing four new tomato leaves. The remaining mites were kept to form generation T-1. These mites were used as a back-up when less than 220 females were found in the box. If still this did not reach 220 mites, females from the base population were added until 220 adult females were reached (see protocol details in (*37*)). Populations were thus maintained in discrete generations, in two selection regimes (mites exposed to plants with or without cadmium), each replicated 5 times.

Prior to experiments, individuals from all regimes were placed in a common garden of cadmium-free tomato leaves during two generations. For that, 100 females from each

population were transferred to a new box with two tomato leaves. Two weeks later, a new leaf was added. After three weeks, six cohorts of 50 adult females were transferred to petri dishes with cotton soaked in water and two tomato leaflets. Females were left to oviposit for 4 days, and then killed. An additional leaflet and water were added three days later. Adult females for the experiment were collected after one week.

Estimation of competitive ability and intrinsic growth rate

Replicate 2 of *T. urticae* evolving on leaves with cadmium did not produce enough individuals and was thus not used in trait measurements.

To test if evolution on plants with or without cadmium affected the probability of coexistence between *T. urticae* and *T. evansi* in each of these environments we estimated competitive ability and the intrinsic rate of increase for each experimental regime (control and evolved) in the water and cadmium environments, in order to estimate parameters to be used in the theoretical analyses (cf. below).

To estimate the intrinsic growth rate, the intra- and interspecific competitive abilities, we followed the methodology described in Hart *et al* (*38*). For that, we cut leaf disks (18mm diameter) from tomato plants grown with or without cadmium and placed one focal female with 1, 3 or 9 females of either the same or species or the competitor species. Leaf discs were placed in a square petri dish on water saturated cotton, with each box containing one disc of each treatment (4 densities and 4 selection regimes, amounting to 16 treatments). Females were left to oviposit for four days and then were removed. After two weeks, the number of adult females per patch was counted. 10 replicates per intra- or intraspecific treatment were done for each of the five experimental populations. The experiment was done in six blocks, the first three with replicates one to three and the last three with replicate populations four and five.

Theoretical estimation of competition and growth parameters

Data collected in the competitive ability experiment was used to parameterize a model, from which we can quantify niche and fitness differences and predict the outcome of competition between the two spider mite species. We assume that the population dynamics in our experiment can be described by Ricker's competition model (*39*). This model accounts for positive interactions, unlike the often-used Beverton-Holt model (*40*), and initial data scrutiny suggested these to occur in our system. In addition, this model has also been used in a previous study with spider mites (*41*). Ricker's model is described by the following equation (equation 1):

$$(1)\ \frac{N_{i,t+1}}{N_{i,t}} = \lambda_i e^{-\alpha_{ii}N_{i,t}-\alpha_{ij}N_{j,t}}$$

Where $N_{i,t+1}$ is the number of individuals of species *i* in the next generation, λ_i the intrinsic growth rate of species *i* in absence of competitors, α_{ii} is the intraspecific competitive ability describing the per-capita effect of species *i* on itself, α_{ij} is the interspecific competitive ability describing the per-capita effect of species *j* on species *i*, and $N_{i,t}$, $N_{j,t}$ are the number of individuals of species *i* and *j*, respectively, in the current generation,. To fit this model, we used the cxr package (*42*) in R to estimate λ, α_{ii} and α_{ij}. We used the function cxr_pm_multifit to obtain the estimation of parameters for all selection regimes per replicate population at the same time Initial parameters were set at $\lambda_i = 1$, $\alpha_{ii}=0.1$ and $\alpha_{ij}=0.1$ for all replicates and confidence intervals were estimated using 200 bootstrap samples.

To predict the outcomes of species interactions in our system, we used the structural stability approach (*2*, *43*, *44*). This approach generates a feasibility domain representing the range of species interactions (including competition and facilitation) that allow for coexistence, based on their intrinsic growth rate.

Using the above-mentioned parameters, we estimated the structural niche differences (Ω), defined as the normalized solid angle of the cone that represents the feasibility domain of a system (Saavedra 2017):

$$(2)\ \Omega = \frac{2}{\pi} * arcsin\left(\frac{\alpha_{11}*\alpha_{22}-\alpha_{12}*\alpha_{21}}{\sqrt{\alpha_{11}^2+\alpha_{21}^2}}\right)$$

and structural fitness differences (θ), as the angle between the vector of intrinsic growth rates of the species (r) and the centroid of the feasibility cone (r_c):

$$(3)\ \theta = arcos\left(\frac{r*r_c}{\|r\|*\|r_c\|}\right)$$

For a system to be feasible (that is, for coexistence to occur) the angle has to be lower than 45º. This corresponds to individuals of each species affecting more conspecifics than heterospecifics and fitness differences being smaller than niche differences. Note that these are also the conditions for coexistence to occur in MCT.

To measure each species' vulnerability to exclusion, we tested how coexistence is resistant to perturbations. Following an approach from (*43*, *45*), we estimated the minimal distance between the vector of intrinsic growth rates (r= [λ_I, λ_j]) and the edges of the feasibility cone (vectors corresponding to either [0, $\frac{\alpha_{22}}{\alpha_{12}}$] or[0, $\frac{\alpha_{21}}{\alpha_{11}}$]) as a proxy for how strong a perturbation should be to change the coexistence outcome in each system. To calculate the distance between the vector of intrinsic growth rates and the edges of the cone of feasibility, we applied the following formula:

(4) $dist_i = \cos^{-1} \begin{bmatrix} \lambda_i \\ \lambda_j \end{bmatrix} . \begin{bmatrix} \alpha_{21} \\ \alpha_{11} \end{bmatrix}$

Data analyses

Environmental and evolutionary effects on competition

To test the impact of cadmium and of evolution in this environment on the competitive abilities and intrinsic growth rates, we performed the following linear models per species:

(5) Y_F= Environment + Focal Selection Regime + ε

(6) Y_F= Environment + (Focal Selection Regime * Competitor Selection Regime) + ε

Where Y_F corresponds to either intrinsic growth rate and intraspecific competitive ability (equation 5) or interspecific competitive ability (equation 6) of *T. urticae* or *T. evansi*, Environment to a fixed factor with two levels (cadmium and water) and Focal Selection Regime to a fixed factor with two levels (control, evolved) corresponding to the selection regime of the focal species, Competitor Selection Regime to a fixed factor with two levels (control, evolved) corresponding to the selection regime of the competitor species and ε to the residual error. Models were initially tested including the interaction between Environment and all other factors, but the interaction was not significant in any model, and was thus excluded (data not shown). To compare how evolution in cadmium affected the response to competitors a posteriori contrasts were done between selection regimes of each species using the testInteractions function from the phia package (*46*).

To test if evolution in cadmium changed the competitive ability or intrinsic growth rate in that environment, a linear model similar to equations 5 and 6 was performed. These models included only the cadmium environment; thus, the Environment factor was removed.

All analyses were done using R (*47*), statistical analysis were done using the package “lme4” (*48*) and graphical representation was done using “ggplot2” (*49*).

Results

All populations (had reduced intrinsic growth rate on plants with cadmium, as compared to on plants with water only (Figure 1, Table S1). This was also observed in the interspecific competitive ability, with an overall decrease in competition for all selection regimes (Figure 2, Table S2). In fact, competition with heterospecifics in the ancestral environment switches to no competition (overlap with 0) or even facilitation (negative values) for almost all regimes in the environment with cadmium (Figure 2). This is not the case of intraspecific competition, which is not affected by the presence of cadmium (Figure 3, Table S3).

Evolution in the environment with cadmium did not change the intrinsic growth rate of *T. urticae* ($F_{1,6}$ = 1.583, P-value=0.255) or *T. evansi* ‘s ($F_{1,6}$ = 1.5, P-value=0.267), nor interspecific competition values for most of the evolved populations (Figure 2, Table S4), in cadmium. However, there was a decrease in interspecific competition for *T. urticae* in the ancestral environment when both species evolved in cadmium, although it is only marginally significant (Fig. 2, Focal $_{Control}$ vs Focal $_{Evolved}$: $F_{1,1}$ = 3,698, P-value=0.064). Interestingly, evolution in cadmium led to an increase in intraspecific competition for *T. evansi* populations environment ($F_{1,6}$ = 6.839, P-value=0.039). This was not the case for *T. urticae* ($F_{1,6}$ = 0.686, P-value=0.439).

,. This was (Fig 2).Long-term predictions of coexistence patterns for both ancestral regimes (Figure 4, upper left panel) showed a clear shift from exclusion of *T. urticae* in two of the replicates in the water environment, to coexistence of both species in cadmium, mostly due to changes in structural niche differences. This is in accordance with the observed reduction of interspecific competition in the cadmium environment (Fig 4). This shift was also observed for the combination of *T. urticae* ancestral and *T. evansi* evolved regimes (Figure 4, upper right panel), and T. *urticae* evolved regime with *T. evansi* control regime (Figure 4, lower left panel). However, for both evolved regimes, coexistence was possible both in water and cadmium environments, with strong facilitation in the latter environment (Figure 4, lower right panel, structural niche differences above 1 indicate facilitation). In presence of, irrespective of past evolutionary history of the vector of intrinsic growth rates fact, the vectors of intrinsic growth rates were always inside of the feasibility cone in the cadmium environment (Figure S1), which does not happen in the water environment, except when both species evolved in cadmium. The

increased stability of coexistence in the cadmium environment is also inferred from an increase in the minimal distance between the vector of intrinsic growth rates and the edges of the feasibility domain (Figure S2), with higher values indicating more stable coexistence. In the water environment, even when coexistence is predicted, the short distance to the edges of the cone suggest that small perturbations could change the dynamics of the system, except when both species evolved in cadmium.

Discussion

Here, we used structural stability theory to predict the impact of the environment (tomato plants with or without cadmium) and evolution in coexistence patterns between two closely-related mite species. We found that coexistence was possible in presence of cadmium, irrespective of the evolutionary history of populations. In contrast, on plants without cadmium, coexistence was only possible when the two species had evolved on plants with cadmium.

We find that coexistence is more likely in the presence of cadmium. In fact, feeding in plants that accumulate cadmium entails a major reduction in interspecific competition (irrespective of evolutionary history), leading to a large increase in niche differences in this environment, hence to an increase in the feasibility domain. Interestingly, this reduction in interspecific competition then leads to facilitation between species. Facilitation has been understudied mechanism involved in species persistence (*50*) and can be particularly important in harsh environments (*50–52*). Possibly the ability of *T. evansi* and *T. urticae* to suppress plant defences (*53–56*) facilitates growth in cadmium environments. However, this ability was shown not to interact with the ability to cope with metal-based defences on plants with cadmium (*35*). Still, it is possible that this facilitation has a stronger effect on interspecific competition in cadmium-accumulating plants in comparison to plants without cadmium. We also see a clear reduction in intrinsic growth rates for both species in the cadmium environment, which is in accordance with a previous study using this system (*36*). Changes in the growth rate and interspecific competition were also found in other studies that used modern coexistence theory (*7*, *57*, *58*) and/or structural stability frameworks (*59*, *60*) to predict coexistence in novel environments. In general, it seems that more stressful environments foster coexistence by equalizing fitness differences and/or reducing interspecific competition.

One of our initial expectations was that evolution in the cadmium environment enhanced population performance. However, intrinsic growth rate did not change in evolved populations

of both species., which is in line with a previous study on life-history traits that underlie the growth rate (*61*). We did, however, observe an increase of intraspecific competition in the *T. evansi* populations that evolved in cadmium when in this environment, as compared to populations that evolved in water. This finding is puzzling, as an increase in intraspecific competition is maladaptive, reducing the overall population growth. However, it suggests that resource uptake when together with conspecifics has increased during evolution, despite the fact that there were no changes in intrinsic (individual) growth rate. Zhang *et al* (*62*) also observed an increased intraspecific competitive ability in introduced populations of *Alternanthera philoxeroides*, without changes in growth rate. The authors suggest that this could happen in invasive genotypes due to reduced herbivory pressure, allowing for the plant to invest resources and become more competitive (following the theory of a trade-off between competition and defense in plants, (*63*)). One possible explanation for the results observed in our study is that the suppression of plant defences by *T. evansi* requires a certain number of individuals in order to be effective. In fact, most studies quantifying suppression of defences in spider mites use between 5 (*55*) and 45 (*64*) females, suggesting that plant defence suppression might be only seen in larger cohort of individuals. This highlights that studies addressing evolution in new environment (via experimental evolution) should consider measuring traits that are expressed in presence of conspecifics, and not only individual traits such as fecundity and survival when alone (*65*).

Most studies addressing the impact of evolution on coexistence compare populations that have evolved with or without an interspecific competitor (*20*, *24*). While this is clearly of great relevance, it is also important to note that competition is generally an indirect interaction, hence how the interaction between organisms with their resources evolves is bound to affect the outcome of competitive interactions as well. However, little is known about this. In our study, we observe no changes in the interspecific competition in the evolved regimes in the new environment. However, we see a marginal reduction in interspecific competition for *T. urticae's* evolved regime, when competing in the ancestral environment with the evolved competitor. This suggests that this trait is correlated to others that have been selected in the novel environment. In fact, theory has considered the possibility of a trade-off between growth and resistance to interspecific competition, with important consequences for coexistence (*66*). Other empirical studies have shown that evolution of a single species in a new environment can change interspecific competitive ability (*32*, *34*, *67*) . However, most of them do not predict the impact of changes in interspecific competition in coexistence of species. In our study, we find that evolving in cadmium favours coexistence in its absence, due to an increase in niche

differences in the ancestral environment. This may be due to a slight reduction (marginal significance) in interspecific competitive ability for the inferior competitor (*T. urticae*) after evolution in cadmium and a slight increase (non-significant) in the superior competitor in the ancestral environment. Despite the small magnitude of these changes, their combined effect has an important impact on species coexistence. While the mechanisms through which this shift occurs are unclear, this type of pattern has been observed previously in the same system. Indeed, niche preemption by the inferior competitor (*T. urticae*) can shift the outcome of competitive interactions between the two species, from extinction to stable coexistence (*28*). Thus, several mechanisms (ecological and evolutionary) may affect coexistence between species. Specifically, it will be important to incorporate trait changes in response to selective pressures and how this affects interactions between species, when predicting coexistence, both in empirical (*21–24*) and theoretical studies (*3*, *19*).

Our study highlights that it is important to combine experimental evolution with ecological theory to be able to fully predict species persistence and to understand the mechanisms through which species adapt to a new environment. On one side, there has been an increase in the attention to how species interactions evolve in response to a new environment (*8*, *30–32*, *34*). However, these studies generally quantify evolution by measuring life-history traits of individuals when alone (*65*, *68*) and this may not reflect the conditions in which populations evolve (*69*), masking the mechanisms involved in adaptation. On the other side, ecological studies have also to gain when incorporating past evolutionary history to understand how species interact and coexist (*25*, *27*, *33*, *66*). Currently, it is well established that quick evolution can operate in ecological times (*70*) and that ecological interactions can shape evolutionary trajectories (*71*), the next step is to merge theoretical frameworks from both fields to predict how eco-evolutionary interactions affects persistence of communities and design well informed empirical studies to test them.

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Figures

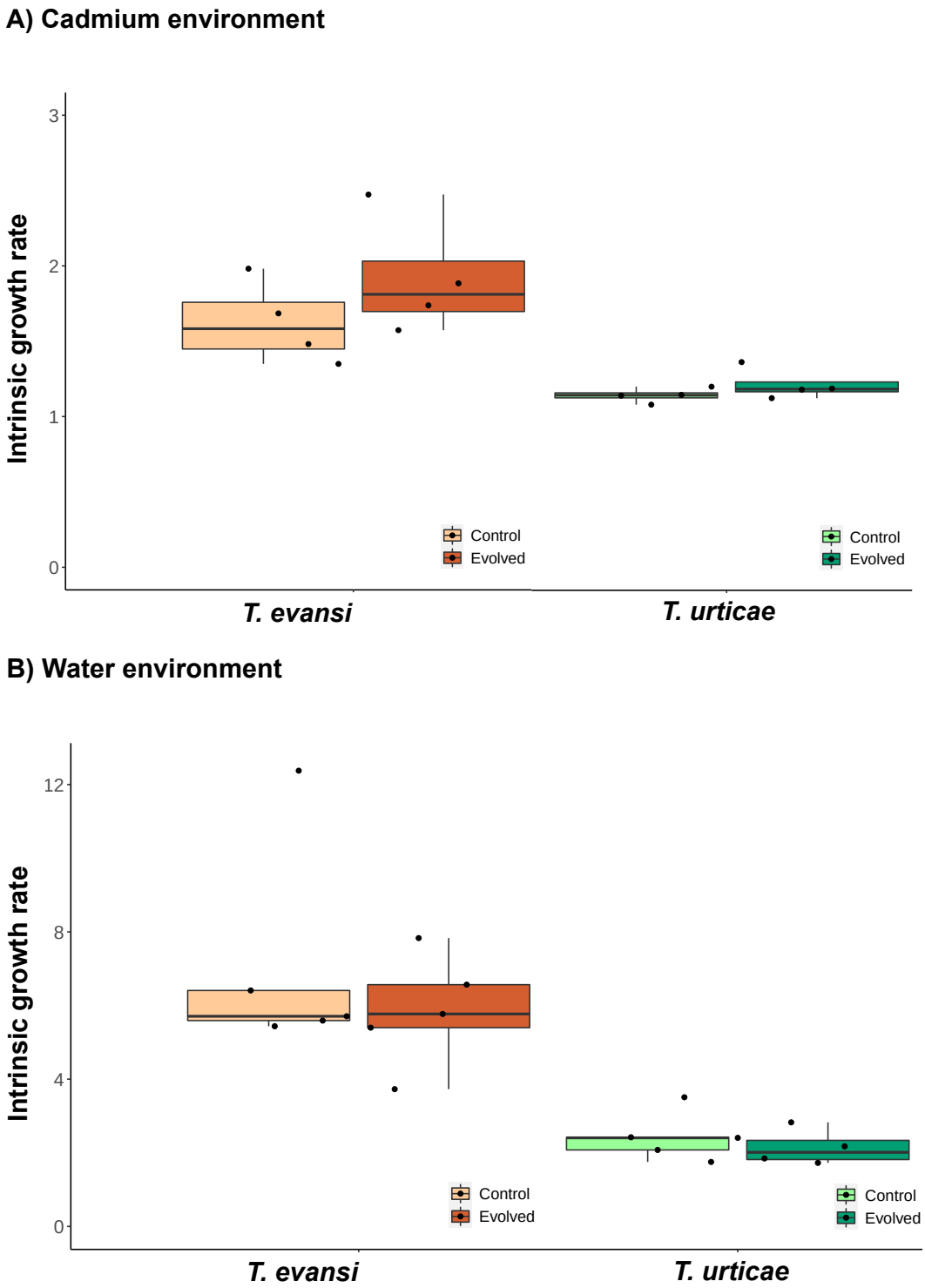


Figure 1 – Intrinsic growth rate in cadmium (A) and water (B) for control and evolved regimes of the two species. *T. evansi* regimes are represented in light (control) or dark (evolved) orange and *T. urticae* regimes are represented in light (control) or dark (evolved)

green. Boxplots represent variation across the five (or four in the case of *T. urticae* evolved regime) experimental replicates. Note that the scales are different between the two panels.

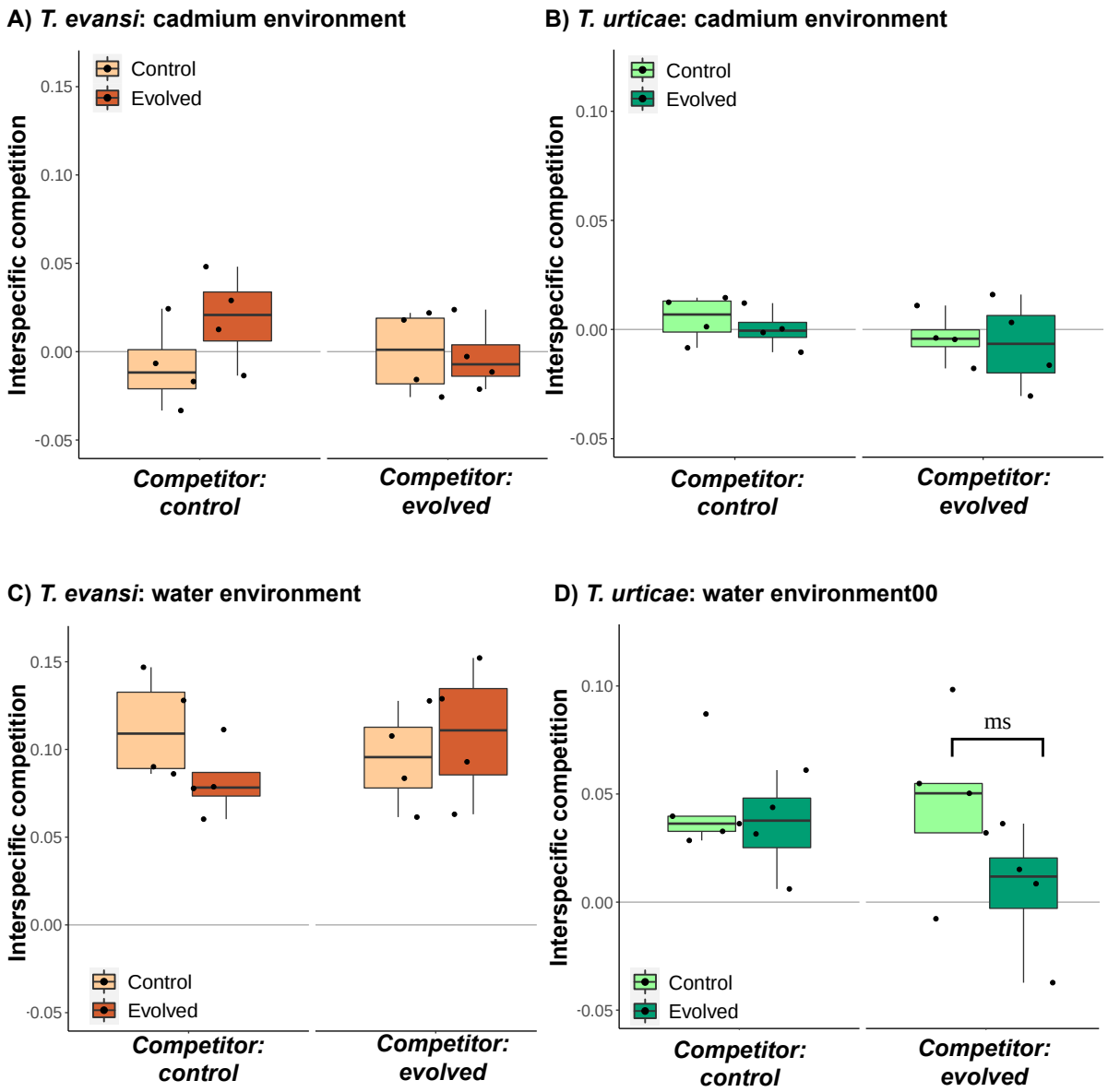
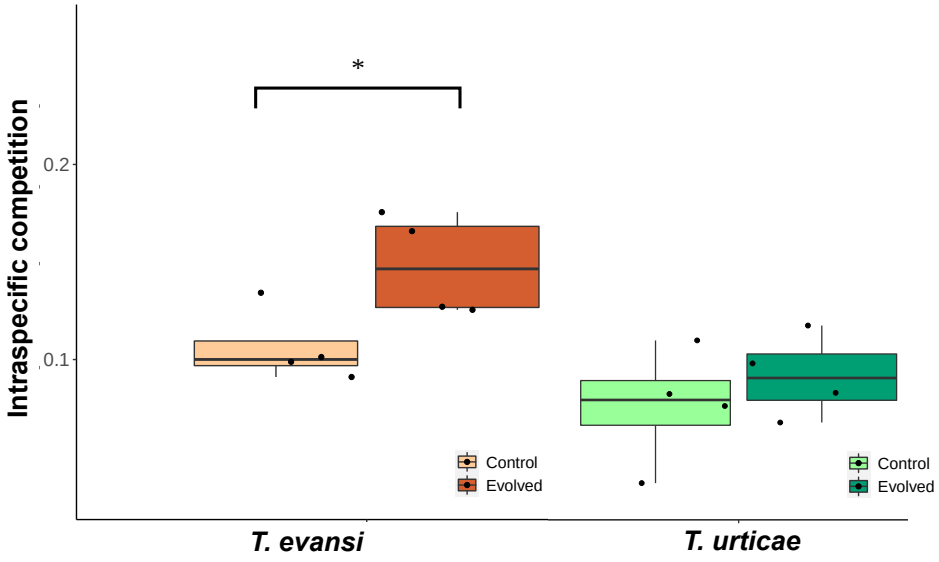


Figure 2 – Interspecific competitive ability for *T. urticae* and *T. evansi* depending on focal and competitor selection regime, in cadmium (A, B) and water (C, D) environments. Boxplots represent variation across the five (or four in case of *T. urticae* evolved regime) experimental replicates. Note that the scales are different between the two panels.

A) Cadmium environment



B) Water environment

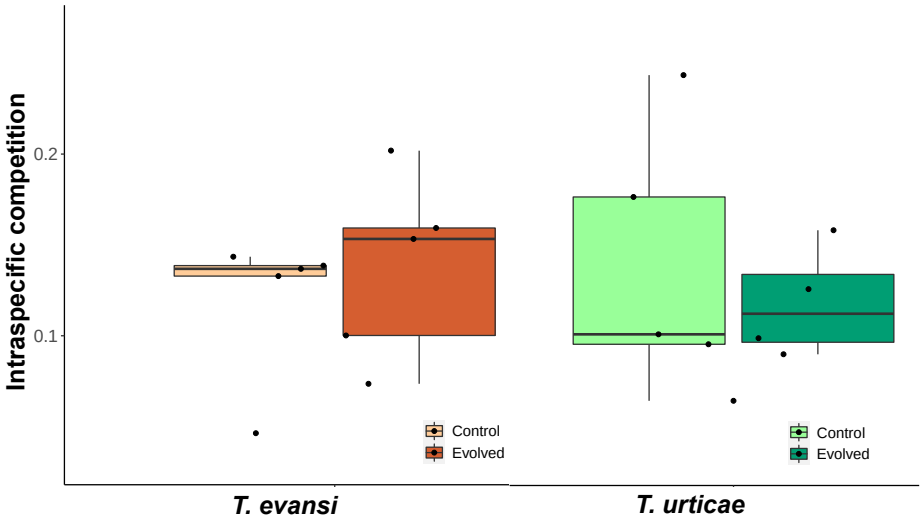


Figure 3 – Intraspecific competition in cadmium (A) and water (B) for control and evolved regimes of the two species. *T. evansi* regimes are represented in light (control) or dark (evolved) orange and *T. urticae* regimes are represented in light (control) or dark (evolved) green. Boxplots represent variation across the five (or four in the case of *T. urticae* evolved regime) experimental replicates. Note that the scales are different between the two panels.

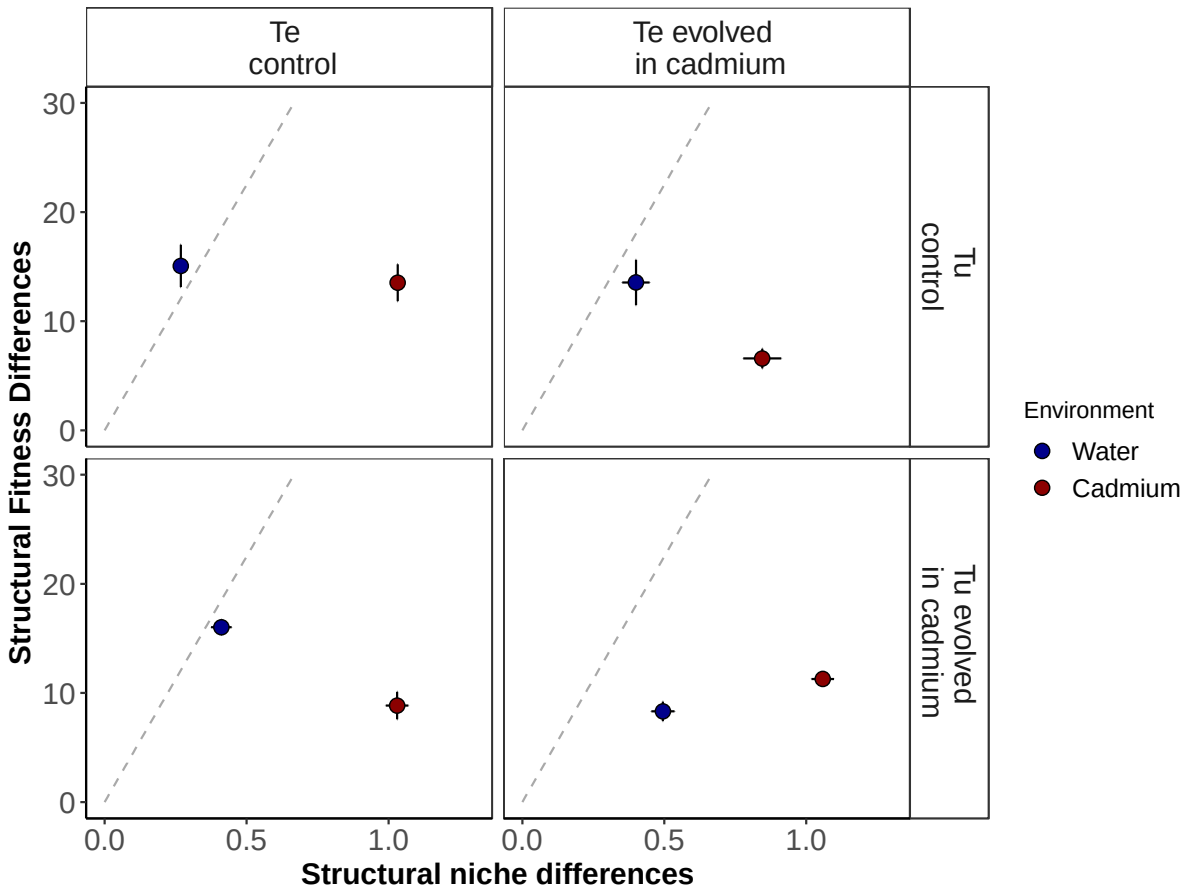


Figure 4 – Map of structural niche and fitness differences according to the focal and competitor selection regime, in water (blue shapes) and cadmium (red shapes) environment. Standard error represents the variation of the five population replicates (or four in the case of the T. urticae evolved regime). Smaller points represent the value from each experimental replicate.

Supplementary Figures

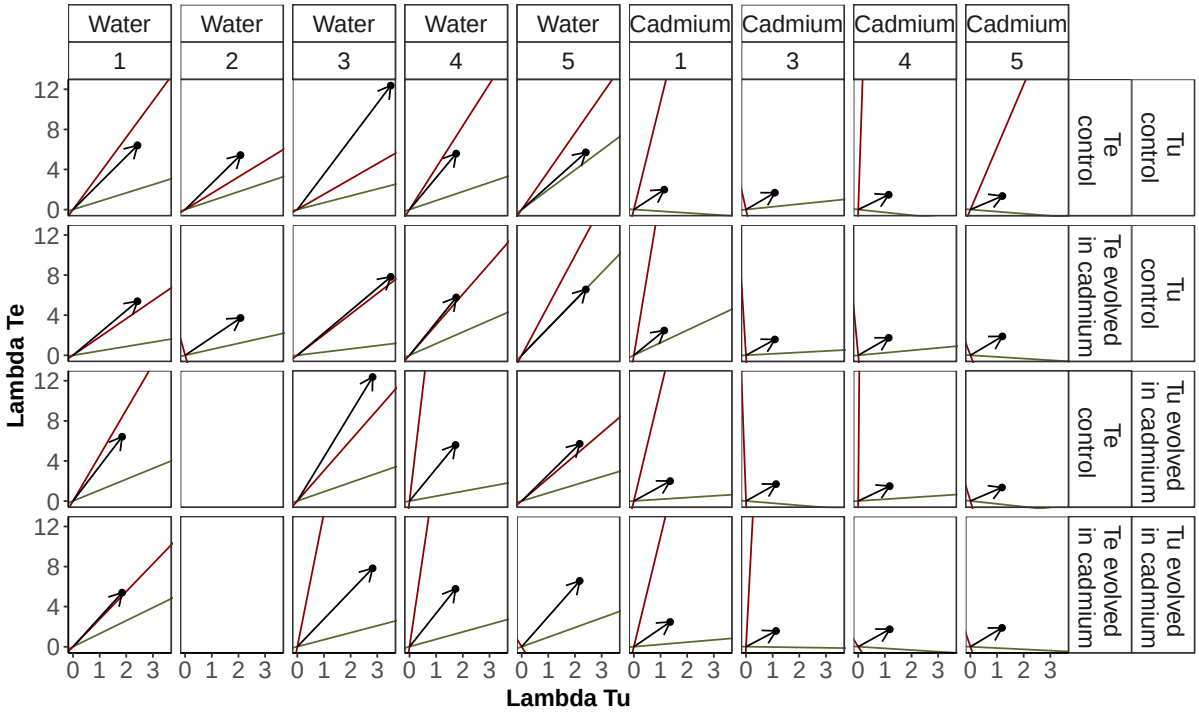


Figure S1 – Feasibility domain for the different combinations of evolved and control regimes of *T. urticae* (Tu) and *T. evansi* (Te). The arrow represents the vector of intrinsic growth for the two populations and the edges of the cone represent the area under which the isoclines cross at positive abundances. In order for coexistence to occur, the vector of intrinsic growth has to fall within the cone. Red isoclines correspond to *T. evansi* and green isoclines to *T. urticae*.

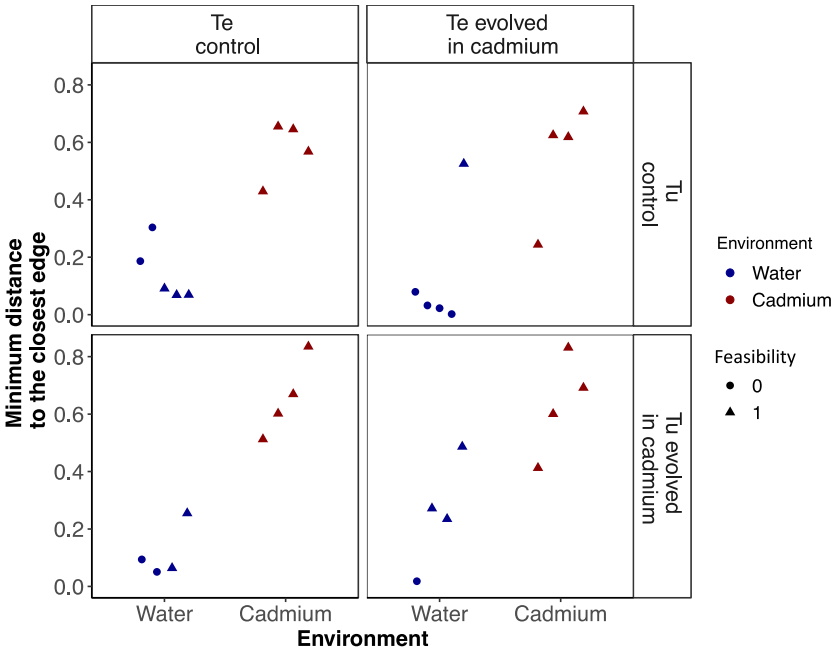


Figure S2 – Minimum distance between the vector of intrinsic growth rate and the edges of the feasibility domain for water (blue) and cadmium (red) environments. Triangle shape

points indicate systems with coexistence and round points indicate extinction of one of the species.