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1 **Evolution in response to an abiotic stress shapes species**  
2 **coexistence**

3

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21

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23

## 24 **Abstract**

25 Adaptation to abiotic stresses is pervasive and generally relies on traits that are not  
26 independent from those affecting species interactions. Still, how such evolution affects  
27 species coexistence remains elusive. We addressed this using populations of two herbivorous  
28 spider mite species (*Tetranychus urticae* and *T. evansi*) evolving separately on tomato plants  
29 hyper-accumulating cadmium, a stressful environment for the mites, or on control plants with  
30 no-cadmium. Combinations of phenotypic analyses with structural stability theory predicted  
31 that adaptation of both species to cadmium allow them to coexist in that environment,  
32 whereas for cadmium-naïve mite populations the most likely outcome is competitive  
33 exclusion. The shift from exclusion to coexistence was due to an increase in structural niche  
34 differences caused by a simultaneous increase in intra and a decrease in interspecific  
35 competition. However, adaptation to cadmium did not affect species interactions and  
36 competitive outcomes in the cadmium-free environment, indicating that such evolutionary  
37 changes were environment-specific. Experimental outcomes of population dynamics with  
38 populations of the two species from each selection regime in each environment were fully  
39 compatible with model predictions. Therefore, evolution of single species in a new  
40 environment, even in absence of interspecific competitors, shapes species coexistence.  
41 Hence, population shifts to novel environments may have unforeseen evolutionary  
42 consequences for community composition and the maintenance of species diversity.

43

## 44 **Significance Statement**

45 The evolutionary consequences of strong selective pressures imposed by environmental  
46 changes on species interactions and their subsequent coexistence remain largely unknown. To  
47 fill this knowledge gap, we combined the power of experimental evolution and structural  
48 stability to analyze how evolution of two spider mite species on plants with or without  
49 cadmium affected their ability to coexist. We found that evolution in the high cadmium  
50 environment led to changes in growth rates, but also in the strength of intra- and interspecific  
51 competition, such that coexistence became possible, but only when the two species evolved  
52 in the new environment. Our study highlights that evolution under high pollutant  
53 concentrations, even in the absence of competitors, can shape long-term coexistence between  
54 species.

## 55 **Introduction**

56 Understanding how evolutionary dynamics shape and are shaped by long-term species  
57 persistence is key to predict community composition and biodiversity maintenance under  
58 global change. Character displacement in response to the presence of competitors is one of  
59 the classical examples of the role of natural selection in shaping trait evolution and species  
60 distribution[1–3]. In the last decades, the acknowledgment that ecology and evolution operate  
61 at similar timescales has led to the prediction that the presence of competitors selects for the  
62 evolution of competitive interactions (i.e., the negative per-capita effect of one species on  
63 another[4–6]), which in turn affects the ability of species to coexist[7–10]. In line with these  
64 predictions, empirical studies have shown that short term evolution in presence of  
65 competitors can modify competitive traits[11] and change coexistence patterns[6, 12–15].

66 Although the abovementioned studies have reinstated short-term evolution as an important  
67 force shaping ecological patterns, it may well be that we are still under-estimating the  
68 potential for evolution to impact species coexistence. An important yet overlooked possibility  
69 is that traits that affect species coexistence may be selected even in the absence of  
70 competitors. For example, species arriving in an environment before their interspecific  
71 competitors may adapt at a fast rate to that environment, which leads to an increased ability  
72 to monopolize it[16]. Likewise, prior adaptation to a given environment can lead to a lower  
73 relative growth rate of late arriving species[17]. In line with this, evidence that trait evolution  
74 affects species community composition has also been recently documented[18, 19]. However,  
75 to date no study has tested if and how trait evolution in response to an abiotic selection  
76 pressure modifies species coexistence through changes in both intra- and interspecific  
77 competition. Moreover, adaptation to one environment can lead to changes in competitive  
78 abilities in other environments[20] but the potential for this to translate into changes in  
79 coexistence patterns remains unclear. Hence, our knowledge of the role of evolution in  
80 response to abiotic stresses in shaping coexistence patterns is yet in its infancy.

81 The recent development of the complementary theoretical frameworks of modern  
82 coexistence theory and structural stability[21–23] provide clear mechanistic pathways to  
83 understand how competing species coexist in ecological time. Both theories agree that  
84 species can coexist whenever their niche differences, which arise when species specialize in  
85 different resources, overcome their differences in population growth in the presence of  
86 competitors[21, 24, 25], but structural stability, unlike modern coexistence theory, takes a  
87 probabilistic view of coexistence, which allows incorporating stochasticity and consider the

88 occurrence of both direct competition and other interactions such as mutualism[26]. This  
89 framework defines that species coexistence is possible when the opportunities for species to  
90 coexist, measured by the feasibility domain, can accommodate difference in intrinsic growth  
91 rates between species. Therefore, wider feasibility domains allow for the persistence of  
92 species combinations with more uneven intrinsic growth rates[22, 25]. To date, this tool has  
93 not been applied to address the role of evolution in shaping coexistence patterns.

94 Here, we assessed how evolution in response to an abiotic stress affects species  
95 coexistence by combining two powerful tools: experimental evolution and structural stability.  
96 We used a system composed of two closely-related spider-mite species, *Tetranychus urticae*  
97 and *T. evansi*, known to engage in competitive interactions when feeding on tomato plants  
98 (*Solanum lycopersicum*)[27, 28]. These plants can hyper-accumulate cadmium in their upper  
99 parts, which strongly reduces spider-mite fecundity and offspring survival, producing a  
100 strong selective pressure[29–31]. Each spider mite species evolved for 40 generations on  
101 plants with or without cadmium in absence of interspecific competitors (Figure S1). After this  
102 period, changes in intrinsic growth rates and in the strength of biotic interactions (intra- and  
103 interspecific competition) were assessed in both environments using a fully orthogonal  
104 experimental design: the evolved populations were exposed to a density gradient of  
105 intraspecific competitors (same species) that evolved in the same environment or of  
106 interspecific competitors (different species) that evolved in each environment (plants with or  
107 without cadmium; Figure S1). Subsequently, we combined structural stability theory with  
108 model parameterization to predict how evolution in response to an abiotic stress (cadmium)  
109 of each species, or both affected competitive outcomes. This allowed singling out the role of  
110 evolution of each species, as well as that of the environment where the interactions occurred.  
111 Finally, we empirically validated the short-term predictions of our models by conducting a  
112 population growth experiment with the same full orthogonal design.

113

## 114 **Results**

### 115 **Evolution in cadmium changes the strength of interspecific competition**

116 To verify that plants with cadmium represent a stress for these populations and thus pose a  
117 significant selection pressure, we first compared the intrinsic growth rate of naïve populations  
118 (evolving on plants without cadmium) on plants with cadmium. Populations of both mite  
119 species from the ‘no-cadmium’ selection regime had significantly lower growth rates in the

120 cadmium than in the no-cadmium environment (*Tetranychus urticae*:  $\chi^2_{1,7}= 71.985$ , P-  
121 value<0.001, *T. evansi*:  $\chi^2_{1,7}=117.15$ , P-value<0.001, Table S1), confirming our hypothesis.

122 After evolution for *circa* 40 generations, we estimated the offspring production of  
123 populations that had evolved on plants with or without cadmium when exposed to each of  
124 these environments, in presence or absence of intra- and interspecific competition. To this  
125 aim, we exposed mites from each species to a gradient of intra and interspecific competitors,  
126 then fitted the Ricker model [32] to estimate the intrinsic growth rate, intra and interspecific  
127 competition ability of each population in each environment. Using these estimated  
128 parameters, we predicted the number of females of each species in each environment. In the  
129 cadmium environment, the intrinsic growth rate of populations evolving in the cadmium  
130 selection regime was higher than that of populations evolving on plants without cadmium –  
131 the no-cadmium selection regime-, for both species (*T. urticae*:  $\chi^2_{1,6}=6.187$ , P-value=0.013,  
132 *T. evansi*:  $Z_{1,7}= 4.483$ , P-value=0.034, Fig 1, Fig. S2, Table S1). Associated with this  
133 increase, we also found an increase in the strength of intraspecific competition for *T. evansi*  
134 ( $\chi^2_{1,7} = 8.570$ , P-value=0.003, Fig S3A, Table S1), but not for *T. urticae* ( $\chi^2_{1,6} = 0.131$ , P-  
135 value=0.717, Fig S3B, Table S1). This resulted in a decreased predicted number of offspring  
136 produced by *T. evansi* in competition (relative to when growing alone) but only when *T.*  
137 *evansi* evolved in the cadmium selection regime (Fig. 1A,  $\lambda$  vs  $\lambda+\alpha_{ii}$  for the yellow and blue  
138 vs the green and red dot). Moreover, evolving in cadmium made *T. evansi* more sensitive to  
139 competition with *T. urticae* from the no-cadmium selection regime (Fig. S4A, Table S2A,  
140 S2B, contrasts between the *T. evansi* cadmium vs no-cadmium selection regime, when  
141 exposed to *T. urticae* from the no-cadmium selection regime: T ratio<sub>1,13</sub>= -0.053, P-  
142 value=0.003), reducing the predicted number of offspring produced after one generation of  
143 competition (Fig. 1A,  $\lambda+\alpha_{ii}+\alpha_{ij}$ , comparing yellow and red dots). Conversely, evolution in  
144 cadmium did not affect the impact of interspecific competition for *T. urticae* (Fig. S4B, Table  
145 S2A). Interestingly, we observe weak positive interactions within and between species in  
146 several replicates (i.e., negative alpha values, corresponding to facilitation) across selection  
147 regimes (Fig S3, S4), which reinforces the added value of using the structural stability  
148 framework.

149 In the no-cadmium environment, having evolved in the cadmium selection regime did  
150 not lead to significant changes in the intrinsic growth rate (Fig. S5, *T. evansi*:  $\chi^2_{1,7}=2.628$ , P-  
151 value=0.105; *T. urticae*:  $\chi^2_{1,6}= 0.121$ , P-value=0.728, Table S1), intraspecific competition  
152 (Fig. S6, *T. evansi*:  $\chi^2_{1,7}= 1.445$ , P-value=0.229; *T. urticae*:  $\chi^2_{1,6}= 0.003$ , P-value=0.998,

153 Table S1) or interspecific competition (Fig. S7, Table S1, S3). Still, the predicted growth rate  
154 of *T. evansi* populations from the cadmium selection regime was lower than that of  
155 populations evolved in the no-cadmium selection regime (Fig 1A, right panel,  $\lambda$ , comparing  
156 green and red to blue and yellow dots), a reduction not observed in *T. urticae* (Fig. 1B, right  
157 panel,  $\lambda$ ). Weak intra- and interspecific facilitation was found for several replicates across  
158 selection regimes (Figs. S6, S7), similarly to what happened in the cadmium environment.

159

### 160 **Evolution of both competitors increases the probability of long-term coexistence in the** 161 **cadmium environment**

162 We predicted competitive outcomes, either coexistence or competitive exclusion, for each  
163 combination of selection regimes, by coupling structural stability with the population model  
164 that describes the temporal dynamics of interacting species (the Ricker model). This  
165 framework led to the prediction that, in the cadmium environment, coexistence was more  
166 likely when both species had evolved in that environment (Fig. 2). Indeed, evolution of both  
167 species in cadmium led to an increase in the size of the feasibility domain via an increased  
168 intraspecific competition, only for *T. evansi*, the better competitor, (Fig S3). It also led to  
169 increased intrinsic growth rate of both species, but with a smaller magnitude in *T. urticae*  
170 (Fig S2). Our prediction of coexistence under evolution in cadmium environments is robust  
171 because it holds even after taking uncertainty (95% CI) into account when estimating the  
172 feasibility domain (Fig 2, light blue region), and the differences of species intrinsic growth  
173 rates (Fig. 3, S8).

174 When only one species evolved in the cadmium selection regime, coexistence was not  
175 possible in the cadmium environment (Figs 2, 3). Contrary to our initial expectation that the  
176 species that evolved in cadmium would be best suited to the new environment and thus would  
177 exclude competitors from the no-cadmium selection regimes, we observe that the species that  
178 evolved in cadmium was predicted to be excluded (Figs. 2, 3, S8). When *T. evansi* was the  
179 species that evolved in cadmium, this can be explained by increased intraspecific competition  
180 (Fig S3) and increased sensitivity to competition from *T. urticae* of the no-cadmium selection  
181 regime (Fig S4). In the reverse case, *T. urticae* that evolved in cadmium was negatively  
182 affected by interspecific competition with *T. evansi* from the no-cadmium selection regime  
183 but did not affect it (Fig. S4), which led to a prediction of exclusion in the cadmium  
184 environment (Fig. 4). Again, predictions, in this case of competition exclusion, are robust to  
185 variation in parameter estimation when accounting for lower and upper 95% confidence  
186 intervals.

187           In the no-cadmium environment, the two species were generally predicted to coexist  
188 except when *T. urticae* from the cadmium selection regime competed with *T. evansi* from the  
189 no-cadmium selection regime, in which case *T. urticae* was predicted to be excluded by *T.*  
190 *evansi* (Fig. 2). However, the minimum distance to the edges of the feasibility domain was  
191 short in all cases (Fig. 3, S9), especially when considering the feasibility domains with lower  
192 confidence intervals, indicating that small perturbations may shift the prediction from  
193 coexistence to exclusion and vice versa. Importantly, there was high heterogeneity among  
194 replicates but little effect of the evolutionary history of both species (Fig. 3). Our results thus  
195 indicate that, unlike what we observed in the cadmium environment, evolution in cadmium  
196 did not affect the range of opportunities for species to coexist in the no-cadmium  
197 environment (Fig. 2, S8).

198

### 199 **Simulated competitive dynamics partially recover empirical patterns**

200 To validate our approach, we compared theoretical predictions of ecological short-term  
201 dynamics with a population dynamic experiment in which the two species, in all possible  
202 combinations of selection regimes, were maintained for two generations. (Fig. S1). We  
203 observed a close agreement between model predictions and experimental observations (Fig.  
204 4, slope pooled replicates: 0.707, P-value<0.001), despite some heterogeneity between  
205 replicate populations, especially in the no-cadmium environment (slope with replicates:  
206 0.631, P-value<0.001, Table S4). Interestingly, predictions for *T. urticae* evolved in the  
207 cadmium selection regime were the most accurate in the no-cadmium environment, but the  
208 least in the cadmium environment (Fig. 4).

209

## 210 **Discussion**

211 We used a combination of experimental evolution and structural stability theory to predict the  
212 impact of evolution in response to an abiotic selection pressure (cadmium) on coexistence  
213 patterns. We also tested how such evolution affected coexistence in an environment without  
214 cadmium. To obtain such theoretical predictions, we rigorously quantified the intrinsic  
215 growth rate of two spider-mite species and the strength of their intra- and interspecific  
216 competitive interactions across different environmental and selection scenarios. While  
217 evolutionary history had little effect on coexistence patterns in the environment with no-  
218 cadmium, the independent evolution of both species in response to cadmium led to a change  
219 from competitive exclusion to coexistence in that stressful environment. This was due to



220 differential changes in intrinsic growth rates, which equalized fitness between species,  
221 coupled with an increase in intraspecific competition in the superior, but not in the inferior  
222 competitor, that in turn, increase the potential range of fitness differences compatible with the  
223 persistence of both species. In sum, we here show for the first time that evolution in response  
224 to an abiotic selection pressure can change the interactions between and within populations  
225 and affect the probability of coexistence, even without a direct selection pressure posed by  
226 the presence of competitors.

227 We found that both species adapted to the cadmium environment after 40 generations of  
228 experimental evolution in that environment, as evidenced by an increase in the intrinsic  
229 growth rate of populations from the cadmium selection regime, compared to those from the  
230 no-cadmium regime. At the 33<sup>rd</sup> generation of evolution, these population of *T. evansi* had  
231 not shown signs of adaptation[31], hence the adaptation reported here occurred at a later time  
232 point. Moreover this previous study revealed lower performance of *T. evansi* populations  
233 from the cadmium selection regime on the environment without cadmium, compared to  
234 populations evolving in the no-cadmium selection regime [31]. We do not recover this result,  
235 suggesting that extending time for evolution to operate led to reduced costs of adaptation.  
236 This adaptation pattern is compatible with the existence of cryptic genetic variation that is  
237 released upon evolution in the cadmium environment[33]. This is also in line with the  
238 absence of genetic variation for traits associated to performance in the cadmium environment,  
239 found in the populations used to initiate the experimental evolution. Still, such adaptation  
240 may be too slow to enable the establishment of mites in cadmium-contaminated sites. Indeed,  
241 assuming equal generation time in the lab and in the field, one tomato growing season  
242 roughly corresponds to 15 generations in spider mites, which is not sufficient to lead to  
243 genetic changes allowing adaptation to cadmium.

244 Evolution of *T. evansi* in cadmium also led to stronger sensitivity to intraspecific  
245 competition in that environment, as compared to mites evolving on plants without cadmium.  
246 Recently, evidence that intraspecific competitive ability may evolve during adaptation to a  
247 novel abiotic environment has been accumulating[5, 20, 34]. There are many reasons to  
248 expect such evolution. For example, individuals may become more efficient at extracting  
249 resources when these are limiting[5], or higher population growth may lead to higher  
250 densities being reached earlier, thus increasing intraspecific competition. Measuring  
251 intraspecific competition should thus be mainstreamed in experimental evolution studies,  
252 which typically measure only individual life-history traits such as fecundity and survival[35].

253 An overlooked logical follow-up of the fact that adaptation to abiotic selection pressures  
254 may affect intraspecific interactions is that it may affect interspecific interactions as well.  
255 Indeed, the latter are also based on (the relative values of) traits that may be modified by  
256 adaptation in absence of competitors. Here, we shed light on this poorly studied issue by  
257 documenting that evolving in a stressful environment without heterospecific competitors  
258 affects competitive interactions between species in that environment. Specifically, when  
259 spider mites evolved in cadmium, they affected their competitors as much or less than mites  
260 that evolved on plants with no-cadmium. This counter-intuitive result may be due to a  
261 growth-competition trade-off, given that both species also increased their growth rate on  
262 plants with cadmium upon evolution in that environment. Such trade-off has been an  
263 assumption of theoretical models[36], and experimentally demonstrated in *Brassica nigra*[37,  
264 38]. Also, Limberger and Fussmann[20] report that algae adapt more rapidly to abiotic  
265 selection pressures when they evolve alone vs when in presence of competitors, which is  
266 compatible with the existence of such trade-off. In sum, we show that interspecific  
267 competitive ability evolves in absence of competitors, a result similar to when competing  
268 species coevolve[6, 11, 12, 18]. The fact that we recover such patterns even in the absence of  
269 a competitor in the environment implies both that causality needs to be scrutinized in eco-  
270 evolutionary studies and that evolution has consequences for community structure that are  
271 much more far reaching than initially thought.

272 Many empirical studies have shown that adaptation to an abiotic selection pressure can  
273 change species interactions[18, 20, 39] but none have addressed how it affects species  
274 coexistence. In fact, the only studies applying coexistence theory to evolutionary data  
275 concern adaptation to the presence of a competitor[11, 12, 15]. In our study, we found that, in  
276 the cadmium environment, species are only predicted to coexist when both competitors  
277 evolved separately in the presence of cadmium. Such change from competitive exclusion to  
278 coexistence was not due to the large change of a specific parameter but rather a small but full  
279 reorganization of how species grow and interact with each other. Namely, coexistence was  
280 due to a combination of an increase in the intrinsic growth rate of both species as they adapt  
281 to the cadmium environment, with stronger intraspecific competition of the superior  
282 competitor, coupled with a reduced impact of interspecific competition. Although the  
283 ultimate mechanisms of these changes are unclear, we speculate that evolution improved the  
284 ability of spider-mites to feed on tomato plants that accumulated cadmium, likely by  
285 increasing resource uptake, which in turn decreased resources available to others (thus  
286 increasing intraspecific competition). This positive covariance between an increase in fitness

287 and an increase in self-limitation is congruent with theoretical predictions[40], which have  
288 been previously reported in other systems (e.g. [41]). Additionally, the observed reduction in  
289 interspecific competition (leading often to reciprocal facilitation) for the two species could be  
290 due to the increased benefits from plant defence suppression, which was found in both  
291 populations used [27]. Curiously, studies addressing how evolution in the presence of a  
292 competitor affected species coexistence have not found such a radical effect of changing from  
293 exclusion to coexistence. Instead, they found that coexistence is maintained when species  
294 coevolve, albeit by mechanisms different than those operating in the absence of such  
295 evolution[11, 12, 15]. We thus find that adaptation to an abiotic selection pressure may affect  
296 community composition to a higher degree than direct adaptation to the presence of  
297 competitors.

298 We also provide a test for the accuracy of the theoretical predictions, by comparing  
299 relative abundance of both species obtained by model predictions based on parameters  
300 estimated from competition experiments with a short-term population dynamics experiment.  
301 We found a high overlap between predicted and observed relative abundances of the two  
302 species. Some mismatch was found when only one of the populations evolved in the  
303 cadmium environment. This is probably due to stochasticity, as the experiment started with a  
304 small number of individuals (six females of each species). Still, the strong correlation  
305 between observed and predicted values suggests that our model parameterization is robust to  
306 changes in the number of individuals, resource and space availability, indicating that the  
307 combination of theoretical modelling and experimental estimation of competitive interactions  
308 has a high predictive power.

309 Another strength of our study is that, unlike previous studies, we applied a full factorial  
310 design, in which we explore how different combinations of evolutionary histories of both  
311 competitors affect the probability of coexistence. We find that coexistence in an environment  
312 with cadmium is only possible when both species evolved in that environment. Hence,  
313 evolution does not follow a linear path, being contingent on the evolutionary history of the  
314 two species. This suggests that asynchronies in the arrival to cadmium-contaminated sites  
315 may lead to species exclusion, due to evolution of the species first colonizing that  
316 environment. Coexistence is only possible when the two species are both adapted, which can  
317 be achieved either if they arrive simultaneously to a site with cadmium, then adapt at a  
318 similar pace, or if they are already adapted upon arrival. Hence, as previously shown for  
319 short-term differences in arrival time[27], we here show that historical contingencies affect  
320 species coexistence also via their effect on evolution.

321 We also explored how evolution in response to cadmium affects coexistence outcomes in  
322 an environment without cadmium. As reported in other studies with no evolution, we found  
323 that interactions are specific to a given environment[42–45]. In general, our results align well  
324 with previous work showing that stable coexistence is fostered in stressful environments via a  
325 reduction in growth rate that equalize fitness differences, and by a shift from interspecific to  
326 intraspecific competition, which increases the range of coexistence opportunities (i.e. increases  
327 the size of the feasibility domain)[42–46], and stabilize the population dynamics of  
328 interacting species. However, our study tempers this statement by the finding that this is only  
329 true when both species have evolved in that stressful environment and that such stabilization  
330 only occurs in the environment where they evolved. Moreover, the use of the structural  
331 stability framework allows incorporating sensitivity to changes in environmental conditions  
332 in these coexistence predictions[47–49]. In the environment without cadmium, we found a  
333 small distance to the edge (i.e., low robustness) across all selection regimes, suggesting that  
334 changes in competitive outcomes are likely to occur due to stochastic events. Instead, in the  
335 cadmium environment, the distance to the edge was higher in all cases, suggesting that  
336 communities in that environment are more long-lasting. Thus, our results suggest that  
337 communities in cadmium-free environments will be modulated by small environmental  
338 changes, whereas those in environments with cadmium will be more shaped by evolution.

339 Our study highlights the added value of combining experimental evolution and  
340 controlled experiments with ecological theory, by providing novel insights of how species  
341 adaptation to an abiotic stressor affects their ability to coexist. This work provides significant  
342 advances in both evolutionary and ecological fields. On the one hand, it shows that traits such  
343 as the strength of intra- and interspecific competition should be incorporated in the  
344 characterization of species adaptation to novel environments. This is particularly true in  
345 experimental evolution studies, which generally quantify evolution by measuring classical  
346 life-history traits such as fecundity or offspring juvenile survival of single individuals[35,  
347 50], which may not reflect the conditions in which populations evolve[51]. On the other  
348 hand, ecological studies benefit from incorporating past evolutionary history, as such  
349 approach has the capacity to refine our understanding of how species interact and coexist[36,  
350 52–54]. All in all, our work provides novel arguments for the need to combine ecological and  
351 evolutionary perspectives and methodologies to understand community composition.

352

## 353 **Material and methods**

## 354 **Overview of the experimental system and maintenance conditions**

355 We used a system composed of *Tetranychus urticae*, a generalist spider mite species that  
356 feeds on several economically important crops[55], *T. evansi*, a solanaceous specialist that  
357 has recently invaded Europe[56], and tomato plants (*Solanum lycopersicum*, var  
358 MoneyMaker). Population maintenance and experiments were performed in a climatic room  
359 under controlled conditions (25:20 °C, 65% of humidity, light:dark = 16:8). Outbred  
360 populations of each species were maintained using 5-week-old plants, having at least five  
361 fully expanded leaves. Plants used in all experiments (including in the experimental  
362 evolution) were watered twice a week with 100 mL of tap water for a duration of two weeks,  
363 then transplanted to new pots and watered each week once with 100mL tap water and another  
364 two times with either 100mL of distilled water or 100mL of 2mM cadmium chloride solution  
365 during another three weeks. This cadmium concentration is highly detrimental to both spider-  
366 mite species, resulting in at least a 50% reduction in fecundity as compared to mites on  
367 metal-free plants[29, 30].

368

## 369 **Experimental evolution**

370 Outbred populations, formed via controlled, one-on-one crosses of 400 individuals (200  
371 females and 200 males of each population) of three and four field populations of *T. urticae*  
372 and *T. evansi* spider mites, respectively[57] were used to initiate experimental evolution  
373 populations. The latter were created by transferring 220 adult females of each species from  
374 the outbred populations to an experimental box (size: 26 x 18 x 13.5 cm) covered with a lid  
375 with a gauze-covered opening to allow air circulation. The box contained four tomato leaves  
376 with their stems in a small pot with water (two leaves per pot, two pots per box), replenished  
377 every week. To minimize differences among plants and leaves, each box contained the  
378 second, third, fourth and fifth leaves to develop (starting from the cotyledons), taken from a  
379 different plant. We established five populations for each of four selection regimes: *T. urticae*  
380 or *T. evansi*, exposed to leaves from plants watered either with a 2mM cadmium solution (the  
381 cadmium selection regime) or with water only (the no-cadmium selection regime). Every two  
382 weeks (corresponding to a mite generation), 220 adult females were transferred by aspiration  
383 to a new experimental box containing four new tomato leaves (i.e., populations were  
384 maintained in discrete generations). The remaining mites were transferred to a new box with  
385 two tomato leaves to create a T-1 box. These mites were used as a back-up when less than  
386 220 females were found in the experimental box. If still this did not reach 220 mites, females

387 from the base population were added until 220 adult females were reached (cf. [57] for  
388 details).

389 Prior to the experiments, individuals from all regimes were placed in a common garden of  
390 cadmium-free tomato leaves for two generations. For that, 200 females from each population  
391 were transferred to new boxes (100 per box) with two tomato leaves, except for replicate 2 of  
392 *T. urticae* evolving on leaves with cadmium, which did not produce enough individuals and  
393 was thus not used in subsequent experiments. After three weeks, six cohorts of 50 adult  
394 females were transferred to petri dishes with cotton soaked in water and two tomato leaflets.  
395 Females were left to oviposit for four days, and then killed. Two weeks later, the adult female  
396 offspring was collected for the experiment. Experiments were performed at generation 40  
397 (empirical estimation of competitive ability and intrinsic growth rate) and 42 (estimation of  
398 the growth rate of populations in cages with interspecific competitors).

399

#### 400 **Empirical estimation of competitive abilities and intrinsic growth rate**

401 To test if evolution on plants with or without cadmium affected the probability of coexistence  
402 between *T. urticae* and *T. evansi* in environments with or without cadmium, we estimated the  
403 intrinsic growth rates and the strength of intra- and interspecific interactions of mites from  
404 each selection regime in each environment (Fig. S1). The data generated was then used to  
405 estimate parameters of a population model that describes the dynamics of interacting species  
406 (cf. below).

407 To quantify changes in growth rate with different competition scenarios and estimate the  
408 parameters to predict coexistence outcomes, we followed the methodology described in [58].  
409 For that, we cut leaf discs (18mm diameter) from tomato plants grown with or without  
410 cadmium and placed one female alone or with 1, 3 or 9 females (i.e., competitors). To  
411 estimate intraspecific competition, the competitor females were from the same species,  
412 selection regime (cadmium or no-cadmium) and replicate population as the focal female. To  
413 estimate interspecific competition, the focal females were exposed to females from different  
414 species, either from the same or a different selection regime (full factorial design) with  
415 matching population replicates (replicate 1 of *T. urticae* was exposed to replicate 1 of *T.*  
416 *evansi*, etc). The intrinsic growth rate was estimated from leaf discs with single females.

417 Leaf discs were placed on water-saturated cotton inside a square petri dish (size: 12.6 x  
418 12.6 x 1.6 cm, with a gauze covered top to allow for ventilation), with 16 or 12 discs (for  
419 intra and interspecific assays, respectively). Each petri dish corresponded to one environment  
420 (leaf discs from plants exposed to cadmium or not) and one treatment (a combination of the



421 selection regimes of the focal female and of the competitors – in the case of intraspecific  
422 competition these are the same), with each density of competitors being allocated to one row  
423 within the petri dish (i.e., each petri dish had four replicates of all densities). Females were  
424 left to oviposit for three days and then killed. Two weeks later, the number of adult females  
425 per patch was counted. Ten replicates per intra- or intraspecific treatment were done for each  
426 of the five experimental populations. The experiment was done in six blocks, the first three  
427 with replicate populations one to three and the last with replicate populations four and five.

428

#### 429 **Empirical estimation of population growth rate in presence of interspecific competitors**

430 To test if evolution on plants with or without cadmium affected the population growth rate  
431 under competition, we placed six females of the two species from different selection regimes  
432 on plants with or without cadmium (full factorial design, *T. urticae* cadmium / no-cadmium \*  
433 *T. evansi* cadmium / no-cadmium \* plants with / without cadmium, i.e., eight experimental  
434 conditions) and measured the number of adult females produced after two generations. For  
435 that, we placed two leaves from plants with or without cadmium in plastic boxes (size: 16.5 x  
436 16.5 x 12 cm) covered with a lid with a gauze-covered opening to allow air circulation. The  
437 petiole of the leaves was in a small pot with water. After one mite generation (two weeks),  
438 another two leaves were added to the box. By the end of the second generation, we counted  
439 the number of adult females from each species in each box. Ten experimental replicates were  
440 tested per experimental condition. The experiment was done in five blocks, each including  
441 one replicate population of each selection regime. This data was then compared with model  
442 predictions based on parameters estimated from the intrinsic growth rate and competitive  
443 abilities (cf. Model validation section below).

444

#### 445 **Theoretical estimation of competition and growth parameters**

446 Data collected in the intrinsic growth rate and competitive ability experiment was used to  
447 parameterize a model, from which we quantified niche and fitness differences to predict the  
448 outcome of competition between the two spider mite species. We assume that the population  
449 dynamics in our experiment can be described by Ricker's competition model[32], which has  
450 been used in a previous study with spider mites[59]. Unlike the often-used Beverton-Holt  
451 model[60], this model allows incorporating positive interactions (i.e., facilitation), which  
452 based on initial data scrutiny, were likely to occur in our system. The Ricker model is  
453 described by the following equation (equation 1):

454

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

455

456 where  $N_{i,t+1}$  is the number of individuals of species  $i$  in the next generation,  $\lambda_i$  the intrinsic  
457 growth rate of species  $i$  in absence of competitors,  $\alpha_{ii}$  corresponds to the strength of  
458 intraspecific competition, which describes the per-capita effect of species  $i$  on itself,  $\alpha_{ij}$  is the  
459 strength of interspecific competition, which describes the per-capita effect of species  $j$  on  
460 species  $i$ , and  $N_{i,t}$ ,  $N_{j,t}$  are the number of competitors of species  $i$  and  $j$ , respectively, in the  
461 current generation. To fit the Ricker model, we used the function `cxr_pm_fit` from the “`cxr`”  
462 package[61] in R to estimate  $\lambda_i$ ,  $\alpha_{ii}$  and  $\alpha_{ij}$  for all selection regimes. The parameters were  
463 estimated for each replicate population separately. To ensure enough statistical power (as  
464 survival in the cadmium environment was low), we also pooled the data of all replicates  
465 associated with each selection regime. As most females (across replicate populations) did not  
466 produce offspring in the cadmium environment, and the `cxr` package does not allow the  
467 inclusion of zeros, we transformed our data by summing one to each of our datapoints (since  
468 the logarithm of one is zero, we can this way include the filtering effect of cadmium in our  
469 data). Initial parameters were set at  $\lambda_i=1$ ,  $\alpha_{ii}=\alpha_{ij}=0.1$  and confidence intervals were estimated  
470 using 1000 bootstrap samples. Visual inspection of the model fitting was done for each  
471 combination of parameters, selection regimes and environments by plotting predicted vs.  
472 observed values (figures available in the git repository). To test if the `cxr` package produced  
473 the best fit to our data, we compared the euclidean distance between predicted and observed  
474 estimates for 5 different fitting algorithms (Fig. S9), all using the Ricker model (details are  
475 available in the git repository). To estimate the relative impact of intra- and interspecific  
476 competition in the offspring production of the two spider mite species, we simulated the  
477 number of offspring produced after one generation using the estimated parameters and the  
478 Ricker model. We used as a starting condition 10 individuals of each species and simulated  
479 one generation assuming population growth following only the intrinsic growth rate, joint  
480 effects of intrinsic growth rate and of intraspecific competition and joint effects of the  
481 intrinsic growth rate and both intra- and interspecific competition. Confidence intervals for  
482 the predictions were calculated using the lower and upper estimates of the intrinsic growth  
483 rate and intra and interspecific competition indexes obtained from the `cxr` package [61].

484

485 **Structural stability approach to predict coexistence**



486 Estimates obtained from the Ricker model (Fig. S4, S5, S7, S8) showed widespread weak  
487 positive interspecific interactions (i.e., facilitation) across selection regimes and replicate  
488 populations. Since Modern Coexistence Theory does not incorporate facilitation between  
489 species, we used the structural stability framework[22, 47, 62] to predict the outcomes of  
490 species interactions in our system. Based on the strength and sign of species interactions  
491 (including competition and facilitation), this approach calculates the feasibility domain. The  
492 size of this domain measures the range of species intrinsic growth rates compatible with  
493 species coexistence (bounded by the vectors  $[0, \frac{\alpha_{22}}{\alpha_{12}}]$  and  $[0, \frac{\alpha_{21}}{\alpha_{11}}]$  when considering only  
494 positive growth rates). The main prediction from structural stability is that if the vector  
495 containing differences between species in their intrinsic growth rate falls within the feasibility  
496 domain, coexistence is possible, otherwise there is exclusion. In principle, the feasibility  
497 domain can include both negative and positive intrinsic growth rates, however, we restricted  
498 our coexistence predictions only to positive values, as our experimental design would not  
499 allow for negative growth rates. Finally, to account for uncertainty in the estimation of model  
500 parameters, we also estimated the feasibility domain bound by the upper (lower) 95% of the  
501 vector  $[0, \frac{\alpha_{22}}{\alpha_{12}}]$  and the lower (upper) boundaries of the  $[0, \frac{\alpha_{21}}{\alpha_{11}}]$  to obtain the widest  
502 (narrowest) conditions under which species are able to coexist.

503 To measure each species' vulnerability to exclusion, we tested how resistant coexistence is  
504 to perturbations. Following a recently-developed approach[47, 63], we estimated the species  
505 exclusion distance, which corresponds to the minimal distance between the vector of intrinsic  
506 growth rates ( $r = [\lambda_i, \lambda_j]$ ) and the edges of the feasibility domain (vectors corresponding to  
507 either  $[0, \frac{\alpha_{22}}{\alpha_{12}}]$  or  $[0, \frac{\alpha_{21}}{\alpha_{11}}]$ ) as a proxy for how strong a perturbation must be to change the  
508 coexistence outcome in each system. To calculate the distance between the vector of intrinsic  
509 growth rates and the edges of the feasibility domain, we applied the following formula[47]:

$$510 \quad (2) \text{ dist}_i = \cos^{-1} \begin{bmatrix} \lambda_i \\ \lambda_j \end{bmatrix} \cdot \begin{bmatrix} \alpha_{21} \\ \alpha_{11} \end{bmatrix}$$

511

## 512 **Model validation**

513 We validated our approach by comparing model predictions with the empirical results from  
514 the population growth experiment. For that, we used the Ricker model to predict the relative  
515 abundance of each species after two generations in each treatment, starting with the initial  
516 conditions of the experiment. Then, we performed a general linear regression with a binomial  
517 error distribution to estimate the correlation between the mean observed proportions of each

518 competitor (using the cbind function to join the number of *T. evansi* and *T. urticae* females)  
519 in all replicates of all treatments with the model proportion estimates (Number of *T. evansi*  
520 females/Number of *T. urticae* females) obtained for each replicate.

521

## 522 **Statistical analyses**

523 To test the impact of the cadmium environment on the intrinsic growth rate of *T. urticae* and  
524 *T. evansi* populations that were naïve to this selection pressure, we applied, for each species,  
525 a linear model using as dependent variables the estimates of the intrinsic growth rate  
526 (estimated from the cxr, see above) of the five experimental replicates of the no-cadmium  
527 selection regimes and environment as fixed factor (with two levels, cadmium and no-  
528 cadmium)

529 To test how evolution on plants with cadmium affected population growth and  
530 competition in the cadmium environment, we used general linear models with a gamma  
531 distribution for the intrinsic growth rate, and with a normal distribution for the coefficients  
532 for intra- and interspecific competition. All models were applied separately for both species,  
533 and normality and dispersion of the residuals was inspected for all models tested. For all  
534 models, we included the parameters estimated with the cxr package for each replicate as a  
535 dependent variable and Selection Regime as fixed factor (with two levels corresponding to  
536 selection regimes evolving in cadmium or no-cadmium environment). For the strength of  
537 interspecific competition, the model included the selection regime of the focal and of the  
538 competitor species, as well as their interaction as fixed factors. Whenever the interaction term  
539 was significant, we applied contrasts to compare estimates for all combinations of focal and  
540 competitor selection regimes. Similar models were applied to test the impact of evolution in  
541 cadmium on the performance in the no-cadmium environment. Finally, we applied a  
542 bootstrap technique to estimate the likelihood of finding differences between  
543 environments/selection regimes randomly. For that, we randomized (with replacement) the  
544 parameter estimates within environments/selection regimes (depending on the model) and  
545 applied the same models as described above. Then, we estimated the probability of randomly  
546 obtaining a significant p-value (below or equal to 0.05) with our data set by computing the  
547 number of times a significant result was obtained. For each model we performed 1000  
548 samples.

549 All analyses were done using R 4.2.1 version[64], statistical analyses were done using the  
550 package “glmmTMB”[65], contrasts were performed using the “emmeans” package[66],  
551 analyses of residuals were done for each model using the DHARMA package[67], and

552 graphical representation was done using “ggplot2”[68]. All data scripts and data used for the  
553 analyses are available in the git repository  
554 [https://github.com/irfragata/evolution\\_cadmium\\_coexistence](https://github.com/irfragata/evolution_cadmium_coexistence).

555

556

### 557 **Authorship Statement**

558 IF, OG and SM conceived the original idea. IF, DG, OG and SM designed the experiments.  
559 IF, DG, LRR and MC performed the experiments and collected the data. IF performed the  
560 modelling work and analysed data, with advice from FZ and OG. IF produced the figures,  
561 with help from LRR. IF, SM and OG wrote the first draft of the manuscript, and all authors  
562 contributed substantially to revisions. SM supervised DG, IF, LRR and MC, FZ supervised  
563 MC, OG supervised IF. SM provided the financial support for the experiments, SM and OG  
564 for the meetings to analyze the data and write the paper.

565

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581

582 **Competing interests:** Authors declare no competing interests.

583

### 584 **Bibliography**

- 585 1. Brown WL, Wilson EO (1956) Character displacement. *Syst Zool* 5:46–94.  
586 <https://doi.org/10.2307/2411924>
- 587 2. Lack D (1947) *Darwin's Finches*, 2nd ed. Cambridge University Press, Cambridge
- 588 3. Slatkin M (1980) Ecological character displacement. *Ecology* 61:163–177.  
589 <https://doi.org/10.2307/1937166>
- 590 4. Abrams PA, Matsuda H (1994) The evolution of traits that determine ability in  
591 competitive contests. *Evol Ecol* 8:667–686. <https://doi.org/10.1007/BF01237849>
- 592 5. Bernhardt JR, Kratina P, Pereira AL, et al (2020) The evolution of competitive ability  
593 for essential resources. *Philosophical Transactions of the Royal Society B: Biological*  
594 *Sciences* 375:20190247. <https://doi.org/10.1098/rstb.2019.0247>
- 595 6. Sakarchi J, Germain RM (2023) The Evolution of Competitive Ability. *American*  
596 *Naturalist* 201:1–15. <https://doi.org/10.1086/722234>
- 597 7. Edwards KF, Kremer CT, Miller ET, et al (2018) Evolutionarily stable communities: a  
598 framework for understanding the role of trait evolution in the maintenance of diversity.  
599 *Ecol Lett* 21:1853–1868. <https://doi.org/10.1111/ele.13142>
- 600 8. Germain RM, Williams JL, Schluter D, Angert AL (2018) Moving Character  
601 Displacement beyond Characters Using Contemporary Coexistence Theory. *Trends*  
602 *Ecol Evol* 33:74–84. <https://doi.org/10.1016/j.tree.2017.11.002>
- 603 9. Vasseur DA, Amarasekare P, Rudolf VHW, Levine JM (2011) Eco-evolutionary  
604 dynamics enable coexistence via neighbor-dependent selection. *Am Nat* 178:96–109.  
605 <https://doi.org/10.1086/662161>
- 606 10. Yamamichi M, Letten AD (2021) Rapid evolution promotes fluctuation-dependent  
607 species coexistence. *Ecol Lett* 24:812–818. <https://doi.org/10.1111/ele.13707>
- 608 11. Hart SP, Turcotte MM, Levine JM (2019) Effects of rapid evolution on species  
609 coexistence. *Proc Natl Acad Sci* 116:2112–2117.  
610 <https://doi.org/10.1073/pnas.1816298116>
- 611 12. Germain RM, Srivastava D, Angert AL (2020) Evolution of an inferior competitor  
612 increases resistance to biological invasion. *Nat Ecol Evol* 4:419–425.  
613 <https://doi.org/10.1038/s41559-020-1105-x>
- 614 13. Hiltunen T, Kaitala V, Laakso J, Becks L (2017) Evolutionary contribution to  
615 coexistence of competitors in microbial food webs. *Proc Roy Soc B: Biol Sci* 284:7–9.  
616 <https://doi.org/10.1098/rspb.2017.0415>
- 617 14. Lankau R (2011) Rapid evolutionary change and the coexistence of species. *Annu Rev*  
618 *Ecol Evol Syst* 42:335–354. <https://doi.org/10.1146/annurev-ecolsys-102710-145100>
- 619 15. Zhao L, Zhang QG, Zhang DY (2016) Evolution alters ecological mechanisms of  
620 coexistence in experimental microcosms. *Funct Ecol* 30:1440–1446.  
621 <https://doi.org/10.1111/1365-2435.12611>
- 622 16. Nadeau CP, Farkas TE, Makkay AM, et al (2021) Adaptation reduces competitive  
623 dominance and alters community assembly. *Proc Roy Soc B: Biol Sci* 288:20203133.  
624 <https://doi.org/10.1098/rspb.2020.3133>
- 625 17. Low-Décarie E, Fussmann GF, Bell G (2011) The effect of elevated CO<sub>2</sub> on growth  
626 and competition in experimental phytoplankton communities. *Glob Chang Biol*  
627 17:2525–2535. <https://doi.org/10.1111/j.1365-2486.2011.02402.x>

- 628 18. Fukano Y, Tachiki Y, Kasada M, Uchida K (2022) Evolution of competitive traits  
629 changes species diversity in a natural field. *Proc Roy Soc B: Biol Sci* 289:20221376.  
630 <https://doi.org/10.1098/rspb.2022.1376>
- 631 19. Gallego I, Narwani A (2022) Ecology and evolution of competitive trait variation in  
632 natural phytoplankton communities under selection. *Ecol Lett* 25:2397–2409.  
633 <https://doi.org/10.1111/ele.14103>
- 634 20. Limberger R, Fussmann GF (2021) Adaptation and competition in deteriorating  
635 environments. *Proc Roy Soc B: Biol Sci* 288:20202967.  
636 <https://doi.org/10.1098/rspb.2020.2967>
- 637 21. Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol*  
638 *Syst* 31:343–366. <https://doi.org/10.1146/annurev.ecolsys.31.1.343>
- 639 22. Saavedra S, Rohr RP, Bascompte J, et al (2017) A structural approach for  
640 understanding multispecies coexistence. *Ecol Monogr* 87:470–486.  
641 <https://doi.org/10.1002/ecm.1263>
- 642 23. Yamamichi M, Gibbs T, Levine JM (2022) Integrating eco-evolutionary dynamics and  
643 modern coexistence theory. *Ecol Lett* 25:2091–2106. <https://doi.org/10.1111/ele.14078>
- 644 24. Barabás G, D’Andrea R, Stump SM (2018) Chesson’s coexistence theory. *Ecol*  
645 *Monogr* 88:277–303. <https://doi.org/10.1002/ecm.1302>
- 646 25. Godoy O, Bartomeus I, Rohr RP, Saavedra S (2018) Towards the Integration of Niche  
647 and Network Theories. *Trends Ecol Evol* 33:287–300
- 648 26. Rohr RP, Saavedra S, Bascompte J (2014) On the structural stability of mutualistic  
649 systems. *Science* (1979) 345:1253497. <https://doi.org/10.1126/science.1253497>
- 650 27. Fragata I, Costa-Pereira R, Kozak M, et al (2022) Specific sequence of arrival  
651 promotes coexistence via spatial niche pre-emption by the weak competitor. *Ecol Lett*  
652 25:1629–1639. <https://doi.org/10.1111/ele.14021>
- 653 28. Sarmiento RA, Lemos F, Dias CR, et al (2011) A herbivorous mite down-regulates  
654 plant defence and produces web to exclude competitors. *PLoS One* 6:e23757.  
655 <https://doi.org/10.1371/journal.pone.0023757>
- 656 29. Godinho DP, Serrano HC, Da Silva AB, et al (2018) Effect of cadmium accumulation  
657 on the performance of plants and of herbivores that cope differently with organic  
658 defenses. *Front Plant Sci* 871:1723. <https://doi.org/10.3389/fpls.2018.01723>
- 659 30. Godinho DP, Branquinho C, Magalhães S (2023) Intraspecific variability in herbivore  
660 response to elemental defences is caused by the metal itself. *J Pest Sci* (2004) 96:797–  
661 806. <https://doi.org/10.1007/s10340-022-01525-0>
- 662 31. Godinho DP, Fragata I, Majer A, et al (2024) Limits to the adaptation of herbivorous  
663 spider mites to metal accumulation in homogeneous and heterogeneous environments.  
664 *J Evol Biol* voae003:. <https://doi.org/10.1101/2023.03.15.532545>
- 665 32. Fowler CW (1981) Density dependence as related to life history strategy. *Ecology*  
666 62:602–610
- 667 33. Paaby AB, Rockman M V. (2014) Cryptic genetic variation: Evolution’s hidden  
668 substrate. *Nat Rev Genet* 15:247–258. <https://doi.org/10.1038/nrg3688>
- 669 34. Bono LM, Gensel CL, Pfennig DW, Burch CL (2015) Evolutionary rescue and the  
670 coexistence of generalist and specialist competitors: An experimental test. *Proc Roy*  
671 *Soc B: Biol Sci* 282:20151932. <https://doi.org/10.1098/rspb.2015.1932>

- 672 35. Kawecki TJ, Lenski RE, Ebert D, et al (2012) Experimental evolution. *Trends Ecol*  
673 *Evol* 27:547–560. <https://doi.org/10.1016/j.tree.2012.06.001>
- 674 36. Wittmann MJ, Fukami T (2018) Eco-Evolutionary Buffering  $\square$ : Rapid Evolution  
675 Facilitates Regional Species Coexistence despite Local Priority Effects. *Am Nat*  
676 191:171–184. <https://doi.org/10.1086/697187>
- 677 37. Lankau RA, Strauss SY (2007) Genetic and Species Diversity in a Plant Community.  
678 *Science* (1979) 317:1561–1563
- 679 38. Lankau R (2008) A Chemical Trait Creates a Genetic Trade-Off between Intra- and  
680 Interspecific Competitive Ability. *Ecology* 89:1181–1187
- 681 39. Bach LT, Lohbeck KT, Reusch TBH, Riebesell U (2018) Rapid evolution of highly  
682 variable competitive abilities in a key phytoplankton species. *Nat Ecol Evol* 2:611–  
683 613. <https://doi.org/10.1038/s41559-018-0474-x>
- 684 40. Carroll IT, Cardinale BJ, Nisbet RM (2011) Niche and fitness differences relate the  
685 maintenance of diversity to ecosystem function. *Ecology*, 92: 1157-1165.  
686 <https://doi.org/10.1890/10-0302.1>
- 687 41. Angert AL, Huxman TE, Chesson P, Lawrence Venable D (2009) Functional tradeoffs  
688 determine species coexistence via the storage effect. *Proc Nat Acad Sci*, 106(28),  
689 11641-11645. <https://doi.org/10.1073/pnas.0904512106>
- 690 42. Grainger TN, Letten AD, Gilbert B, Fukami T (2019) Applying modern coexistence  
691 theory to priority effects. *Proc Natl Acad Sci* 116:6205–6210.  
692 <https://doi.org/10.1073/pnas.1803122116>
- 693 43. Granjel RR, Allan E, Godoy O (2023) Nitrogen enrichment and foliar fungal  
694 pathogens affect the mechanisms of multispecies plant coexistence. *New Phyt*  
695 237:2332–2346
- 696 44. Matías L, Godoy O, Gómez-Aparicio L, Pérez-Ramos IM (2018) An experimental  
697 extreme drought reduces the likelihood of species to coexist despite increasing  
698 intransitivity in competitive networks. *J Ecol* 106:826–837.  
699 <https://doi.org/10.1111/1365-2745.12962>
- 700 45. Wainwright CE, HilleRisLambers J, Lai HR, et al (2019) Distinct responses of niche  
701 and fitness differences to water availability underlie variable coexistence outcomes in  
702 semi-arid annual plant communities. *J Ecol* 107:293–306.  
703 <https://doi.org/10.1111/1365-2745.13056>
- 704 46. Song C, Rohr RP, Vasseur D, Saavedra S (2020) Disentangling the effects of external  
705 perturbations on coexistence and priority effects. *J Ecol* 108:1677–1689.  
706 <https://doi.org/10.1111/1365-2745.13349>
- 707 47. Allen-Perkins A, García-Callejas D, Bartomeus I, Godoy O (2023) Structural  
708 asymmetry in biotic interactions as a tool to understand and predict ecological  
709 persistence. *Ecol Lett* 26:1647–1662. <https://doi.org/https://doi.org/10.1111/ele.14291>
- 710 48. Song C, Von Ahn S, Rohr RP, Saavedra S (2020) Towards a Probabilistic  
711 Understanding About the Context-Dependency of Species Interactions. *Trends Ecol*  
712 *Evol* 35:384–396. <https://doi.org/10.1016/j.tree.2019.12.011>
- 713 49. Tabi A, Pennekamp F, Altermatt F, et al (2020) Species multidimensional effects  
714 explain idiosyncratic responses of communities to environmental change. *Nat Ecol*  
715 *Evol* 4:1036–1043. <https://doi.org/10.1038/s41559-020-1206-6>



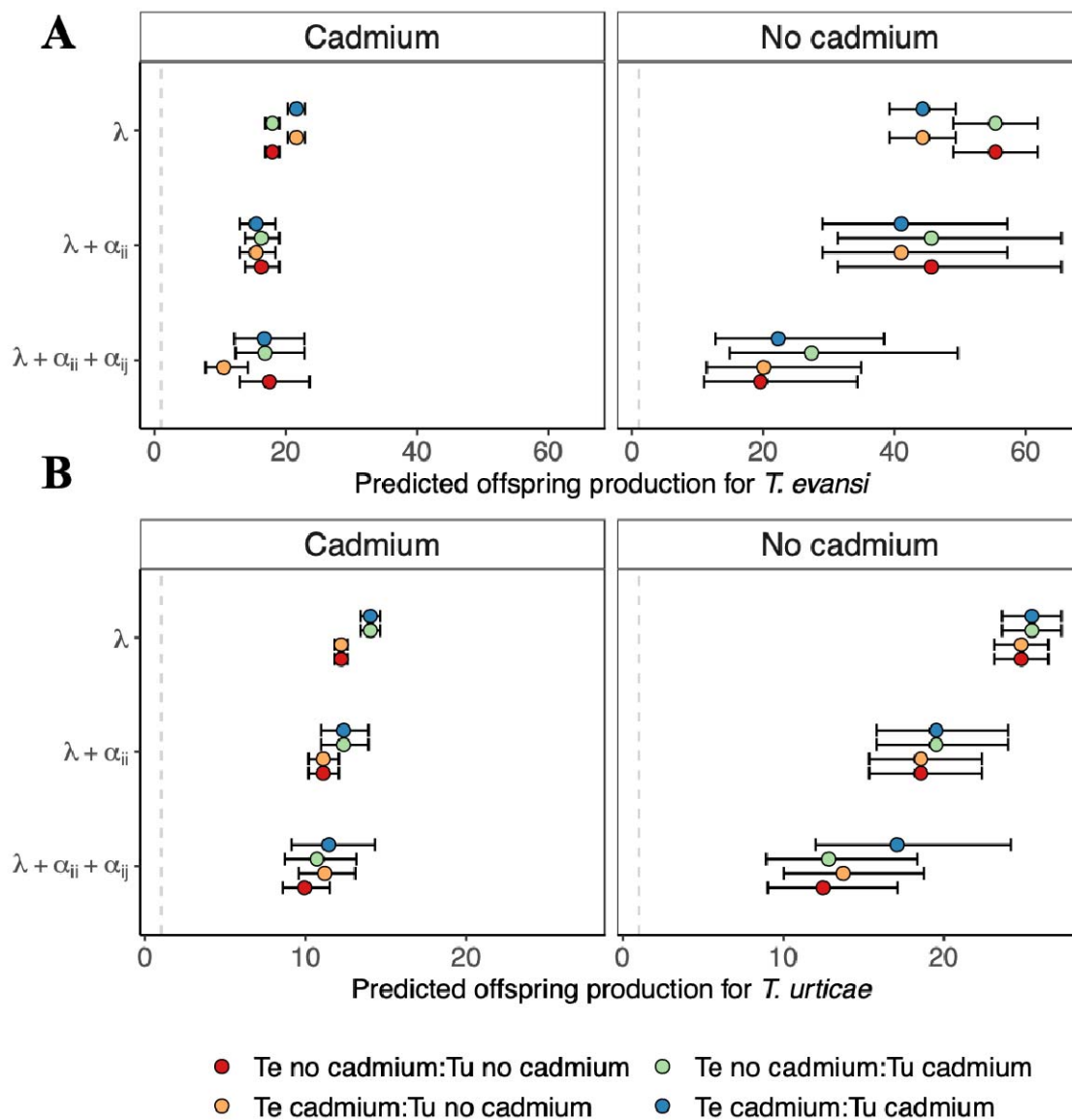
- 716 50. Garland TJR, Rose MR (2009) *Experimental Evolution: Concepts, Methods and*  
717 *Applications of Selection Experiments*. University of California Press, Berkeley, Los  
718 Angeles and London
- 719 51. Chippindale AK, Ngo AL, Rose MR (2003) The devil in the details of life-history  
720 evolution: instability and reversal of genetic correlations during selection on  
721 *Drosophila* development. *J Genet* 82:133–145. <https://doi.org/10.1007/BF02715814>
- 722 52. Leibold MA, Urban MC, De Meester L, et al (2019) Regional neutrality evolves  
723 through local adaptive niche evolution. *Proc Natl Acad Sci* 116:2612–2617.  
724 <https://doi.org/10.1073/pnas.1808615116>
- 725 53. Urban MC, De Meester L (2009) Community monopolization: Local adaptation  
726 enhances priority effects in an evolving metacommunity. *Proc Roy Soc B: Biol Sci*  
727 276:4129–4138. <https://doi.org/10.1098/rspb.2009.1382>
- 728 54. Yamamichi M, Kyogoku D, Iritani R, et al (2020) Intraspecific Adaptation Load: A  
729 Mechanism for Species Coexistence. *Trends Ecol Evol* 35:897–907.  
730 <https://doi.org/10.1016/j.tree.2020.05.011>
- 731 55. Sousa VC, Zélé F, Rodrigues LR, et al (2019) Rapid host-plant adaptation in the  
732 herbivorous spider mite *Tetranychus urticae* occurs at low cost. *Curr Opin Insect Sci*  
733 36:82–89. <https://doi.org/10.1016/j.cois.2019.08.006>
- 734 56. Boubou A, Migeon A, Roderick GK, et al (2012) Test of colonisation scenarios reveals  
735 complex invasion history of the red tomato spider mite *Tetranychus evansi*. *PLoS One*  
736 7:e35601. <https://doi.org/10.1371/journal.pone.0035601>
- 737 57. Godinho DP, Cruz MA, Charlery de la Masselière M, et al (2020) Creating outbred  
738 and inbred populations in haplodiploids to measure adaptive responses in the  
739 laboratory. *Ecol Evol* 10:7291–7305. <https://doi.org/10.1002/ece3.6454>
- 740 58. Hart SP, Freckleton RP, Levine JM (2018) How to quantify competitive ability. *J Ecol*  
741 106:1902–1909. <https://doi.org/10.1111/1365-2745.12954>
- 742 59. Bisschop K, Alzate A, Bonte D, Etienne RS (2022) The Demographic Consequences  
743 of Adaptation: Evidence from Experimental Evolution. *Am Nat* 199:729–742.  
744 <https://doi.org/10.1086/719183>
- 745 60. Beverton RJH, Holt SJ (1957) *On the dynamics of exploited fish populations*. Springer  
746 Science+Business Media Dordrecht , Great Britain
- 747 61. García-Callejas D, Godoy O, Bartomeus I (2020) cxr: A toolbox for modelling species  
748 coexistence in R. *Methods Ecol Evol* 11:1221–1226. [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.13443)  
749 [210X.13443](https://doi.org/10.1111/2041-210X.13443)
- 750 62. Saavedra S, Medeiros LP, AlAdwani M (2020) Structural forecasting of species  
751 persistence under changing environments. *Ecol Lett* 23:1511–1521.  
752 <https://doi.org/10.1111/ele.13582>
- 753 63. Medeiros LP, Boege K, Del-Val E, et al (2021) Observed ecological communities are  
754 formed by species combinations that are among the most likely to persist under  
755 changing environments. *Am Nat* 197:17–29. <https://doi.org/10.1086/711663>
- 756 64. R Core Team (2022) R: A language and environment for statistical computing.
- 757 65. Brooks ME, Kristensen K, van Benthem KJ, et al (2017) glmmTMB Balances Speed  
758 and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed  
759 Modeling. *R J* 9:378–400. <https://doi.org/10.32614/RJ-2017-066>

760 66. Lenth R (2019) Emmeans: estimated marginal means. Aka Least-Squares Means.  
761 67. Hartig F (2022) DHARMA: Residual Diagnostics for Hierarchical (Multi-Level /  
762 Mixed) Regression Models  
763 68. Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis  
764  
765  
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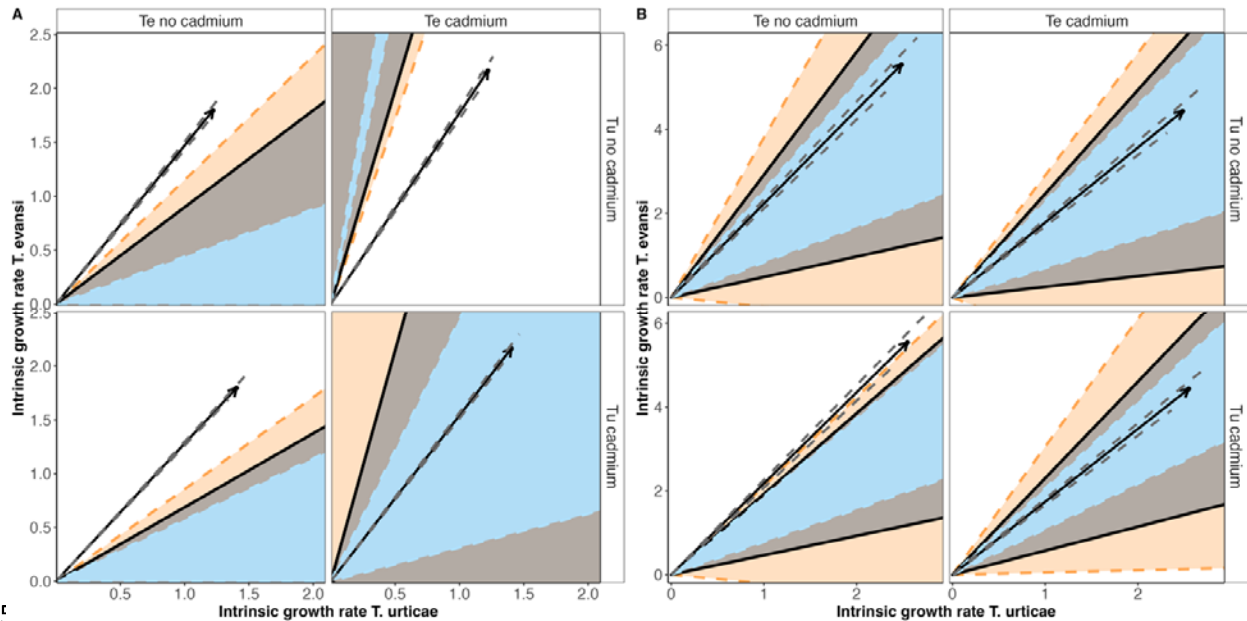
## Figures



770

771 Figure 1 – Predicted number of female offspring after one generation for A) *T. evansi* (Te)  
 772 and B) *T. urticae* (Tu), to estimate the relative effect of competition on the growth rate of the  
 773 different populations. To represent the cumulative impact of each parameter on the offspring  
 774 production, predictions were done using only the intrinsic growth rate ( $\lambda$ ), the intrinsic  
 775 growth rate plus intraspecific competition ( $\lambda + \alpha_{ii}$ ) and the latter plus interspecific  
 776 competition ( $\lambda + \alpha_{ii} + \alpha_{ij}$ ) in an environment with or without cadmium (left and right  
 777 panels, respectively). Note that since two of the four treatments share the same focal selection  
 778 regime (e.g. for *T. urticae* the orange and red dots correspond to the focal control regime “Tu  
 779 no-cadmium”), two colours are duplicates for the metrics without interspecific competition

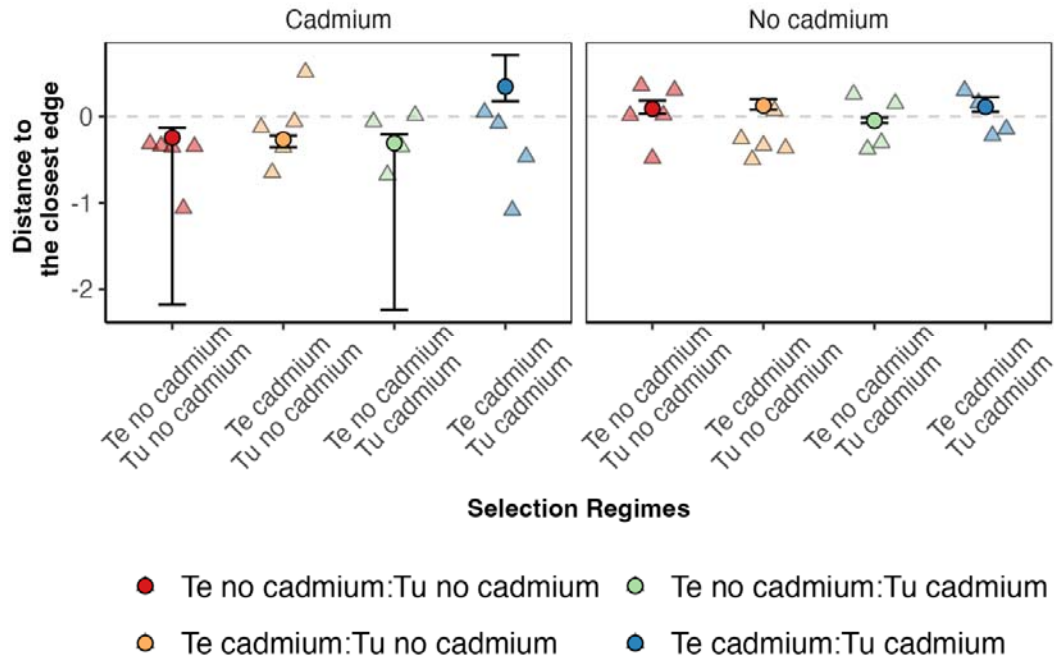
780 ( and ). Starting conditions for simulations: 10 individuals of each species.  
781 Treatments correspond to combinations of *T. evansi* (Te) and *T. urticae* (Tu) selection  
782 regimes (cf. colour code). Note the different scales on the X-axis between the two species (A  
783 vs B).  
784



785  
786 Figure 2 – Feasibility domain predicted for environments with (A) or without (B) cadmium  
787 for the different combinations of cadmium and no-cadmium selection regimes in which *T.*  
788 *urticae* (Tu) or *T. evansi* (Te) have evolved. The x and y axis correspond to the positive  
789 intrinsic growth rate for *T. urticae* and *T. evansi*, respectively. The arrow represents the  
790 vector of intrinsic growth for each of the two species and the edges of the cone delimiting the  
791 area under which the isoclines cross at positive abundances (i.e., the feasibility domain, in  
792 which coexistence is possible). Dashed lines surrounding the arrows represent the 95%  
793 confidence interval of the intrinsic growth rate. Arrows that fall outside of the cone indicate  
794 that Te excludes Tu, except in the upper-right panel of figure A (Te cadmium- Tu no-  
795 cadmium), in which Tu excludes Te. The dark grey region indicates the feasibility domain  
796 obtained from the ratio of intra and interspecific competitive abilities estimated with data  
797 from all replicates pooled (see methods). This region has been evaluated only under the  
798 conditions in which both species show positive intrinsic growth rates. The light blue and light  
799 orange regions delimitate the smallest and largest feasibility domains obtained from the lower  
800 and upper 95% confidence interval of the competitive ability parameters. White regions  
801 denote the unfeasibility domain (region for exclusion). Confidence intervals of the estimates

802 were obtained by performing 1000 bootstrap samples with replacement when estimating  
803 parameters from the data of all experimental replicates pooled.

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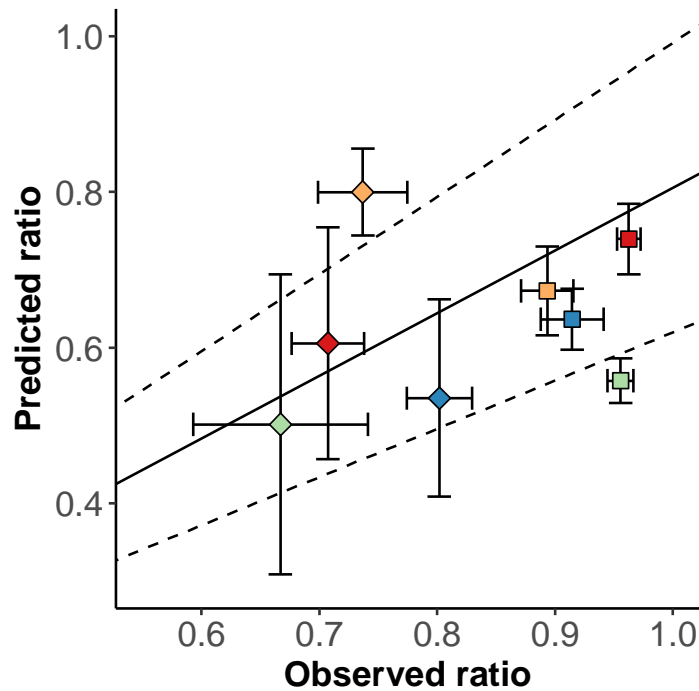
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806 Figure 3 – Distance between the vector of intrinsic growth rates and the closest edge of the  
807 feasibility domain in environments with (left panel) or without (right panel) cadmium for the  
808 different combinations of no-cadmium or cadmium selection regimes for *T. evansi* (Te) and  
809 for *T. urticae* (Tu) (cf. colour code). Positive distances indicate that the vector of growth rates  
810 is inside the feasibility domain (i.e., coexistence is possible), and negative distances indicate  
811 that the vector is outside the feasibility domain (i.e., exclusion is predicted). Circles  
812 correspond to the distance calculated with data from all replicates pooled and triangles to  
813 distances calculated per replicate. Error bars were obtained by performing 1000 bootstrap  
814 samples with replacement when estimating parameters and were obtained from the data of all  
815 experimental replicates pooled.

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820 ● Te no cadmium:Tu no cadmium    ● Te no cadmium:Tu cadmium  
821    ● Te cadmium:Tu no cadmium    ● Te cadmium:Tu cadmium

822

823 Figure 4 – Correlation between predicted and observed relative abundance of *T. evansi*  
824 (Number of *T. evansi* females/Number of females of both species) after 2 generations in an  
825 independent population growth experiment in which the two species are released at equal  
826 densities. Squares indicate data from the cadmium environment and diamonds data from the  
827 no-cadmium environment. Predicted error bars were calculated based on standard error  
828 obtained from 1000 bootstrap samples and observed error bars were obtained from replicate  
829 populations. The full line represents the slope obtained from a general linear model (see  
830 methods) and the dashed lines to the standard error obtained from the model. Treatments  
831 correspond to combinations of selection regimes to which *T. evansi* (Te) and *T. urticae* (Tu)  
were exposed (cf. colour code).

831