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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, λ 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_{1,13}= -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, λ , comparing
156 green and red to blue and yellow dots), a reduction not observed in *T. urticae* (Fig. 1B, right
157 panel, λ). 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 33rd 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, λ_i the intrinsic
457 growth rate of species i in absence of competitors, α_{ii} corresponds to the strength of
458 intraspecific competition, which describes the per-capita effect of species i on itself, α_{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 λ_i , α_{ii} and α_{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.

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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578 copyright licence has been applied by the authors to the present document and will be applied
579 to all subsequent versions up to the Author Accepted Manuscript arising from this
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581

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

583

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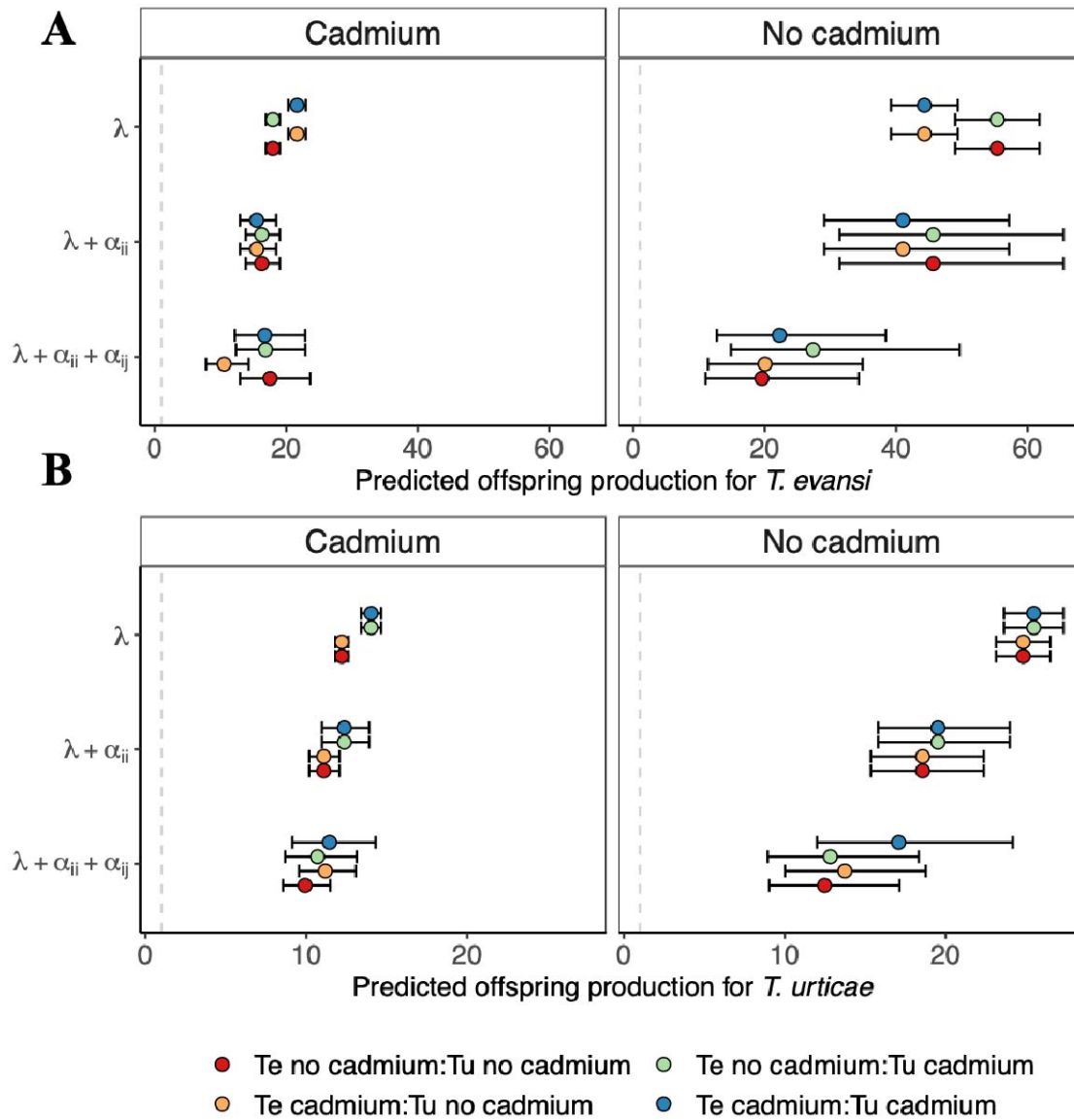
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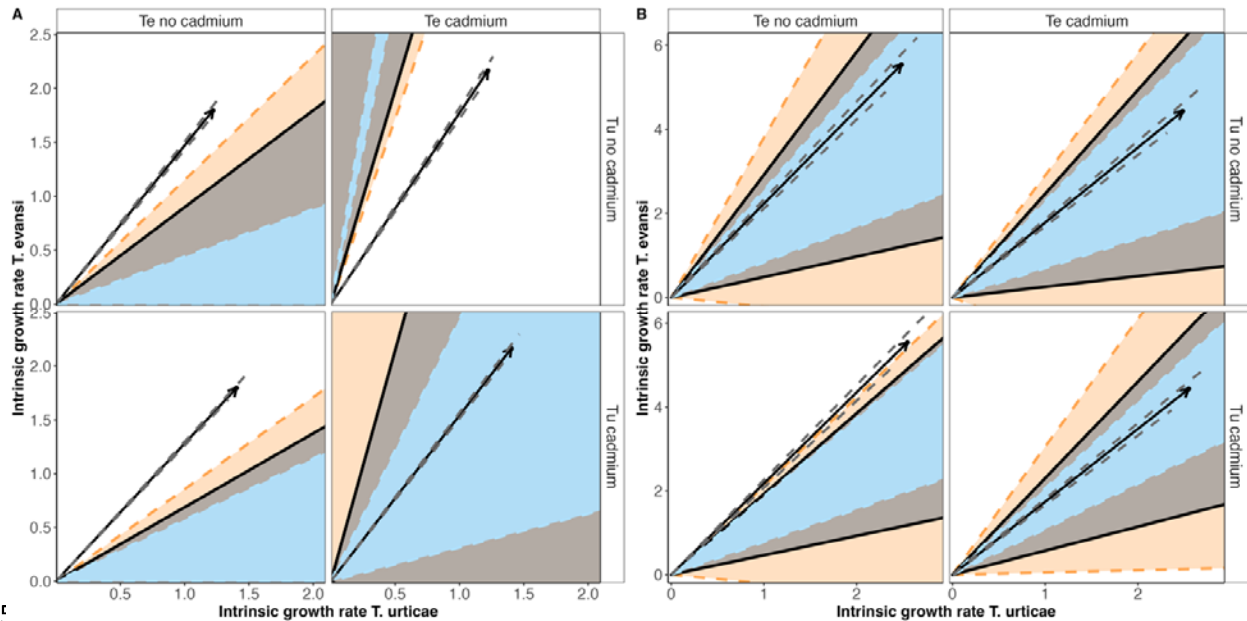
Figures



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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 (λ), 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

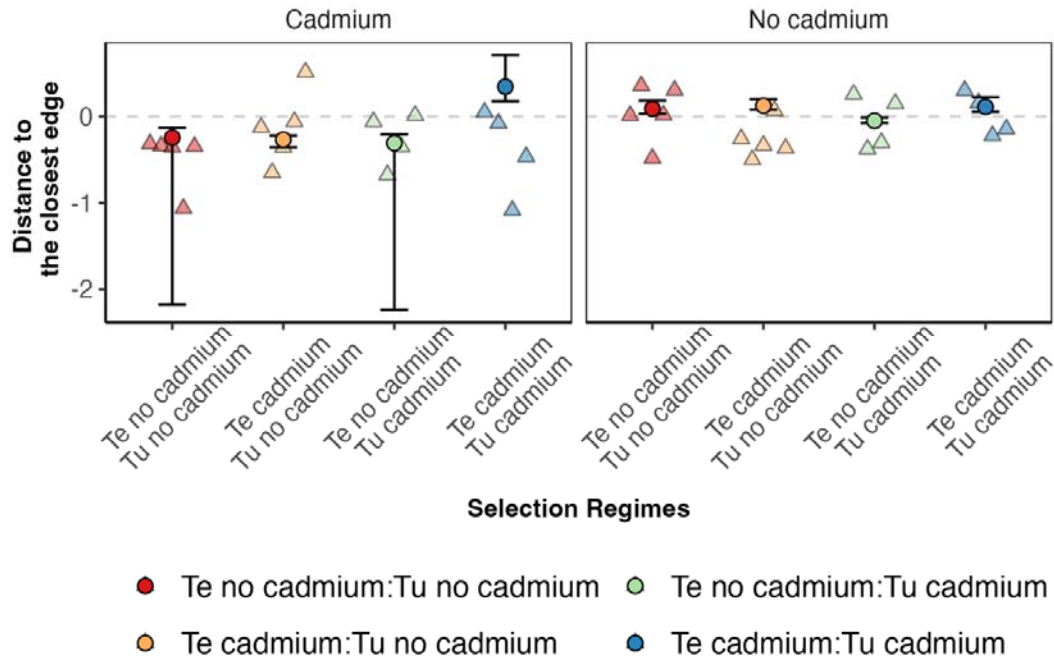
780 (and). Starting conditions for simulations: 10 individuals of each species.
781 Treatments correspond to combinations of *T. evansi* (Te) and *T. urticae* (Tu) selection
782 regimes (cf. colour code). Note the different scales on the X-axis between the two species (A
783 vs B).
784



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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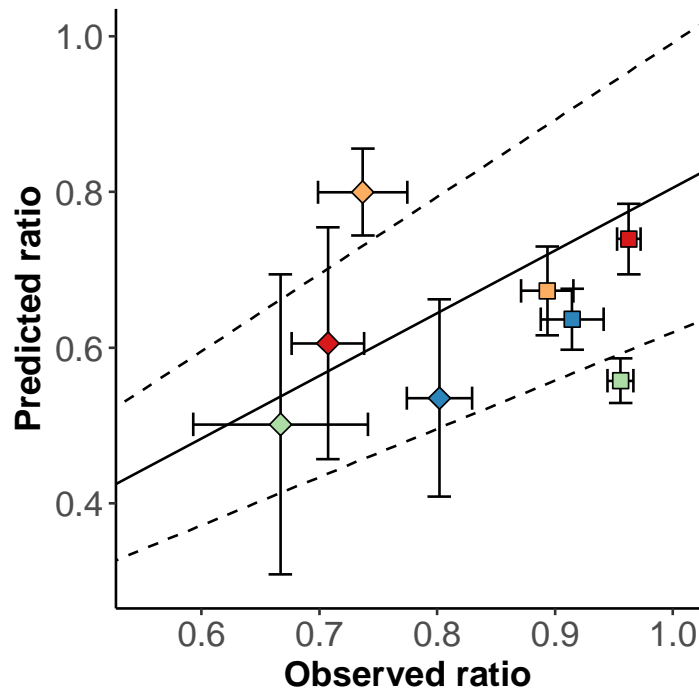
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806 Figure 3 – Distance between the vector of intrinsic growth rates and the closest edge of the
807 feasibility domain in environments with (left panel) or without (right panel) cadmium for the
808 different combinations of no-cadmium or cadmium selection 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).

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