

1 **Specific sequence of arrival promotes coexistence via spatial niche preemption by the**  
2 **weak competitor**

3 Inês Fragata<sup>1</sup>, Raul Costa-Pereira<sup>2</sup>, Mariya Kozak<sup>1</sup>, Agnieszka Majer<sup>3</sup>, Oscar Godoy<sup>4\*</sup>, Sara  
4 Magalhães<sup>1\*</sup>

5

6 1 – Centre for Ecology, Evolution and Environmental Changes; Department of Animal  
7 Biology, Faculty of Sciences, University of Lisbon, Portugal

8 2 – Department of Animal Biology, Institute of Biology, Universidade Estadual de Campinas,  
9 Brazil ORCID 0000-0003-2370-5866

10 3 – Population Ecology Lab, Faculty of Biology, Adam Mickiewicz University, Poland ORCID  
11 0000-0002-2425-7885

12 4 – Department of Biology, Instituto Universitario de Investigación Marina (INMAR),  
13 Universidad de Cádiz, Puerto Real. 11510, Spain. ORCID 0000-0003-4988-6626

14

15 \*Co-last authorship

16

17 **Running title:** Niche preemption facilitates coexistence

18

19 **Keywords:** Order of arrival, Priority effects, Modern coexistence theory, Spatial segregation,  
20 *Tetranychus urticae* and *T. evansi*, Herbivores, Niche modification, Competitive ability

21

22 **Article type:** Letter

23

24 **Number of words in abstract:** 150

25

26 **Number of words main text: 5000**

27

28 **Number of references: 66**

29

30 **Number of figures: 3**

31

32 **Corresponding Author:** Inês Fragata, [irfragata@fc.ul.pt](mailto:irfragata@fc.ul.pt), cE3c, Centre for Ecology, Evolution  
33 and Environmental changes, Faculdade de Ciências da Universidade de Lisboa, Edifício C2,  
34 Campo Grande 1749-016 Lisbon, Portugal, Phone. +351 217500577, ext. 22311.

35

36 **Authorship statement:** IF, OG and SM designed the experiment, IF, AM, MK and RCP  
37 collected data, IF and OG performed modelling work and analysed data. IF and SM wrote the  
38 first draft of the manuscript, and all authors contributed substantially to revisions.

39

40 **Data accessibility statement:** Data and scripts for data analyses will be deposited in a public  
41 repository upon acceptance.

42

43

44 **Abstract**

45 Historical contingency, such as the order of species arrival, can modify competitive outcomes  
46 via niche modification or preemption. However, how these mechanisms ultimately modify  
47 stabilising niche and average fitness differences remains largely unknown. By experimentally  
48 assembling two congeneric spider mite species feeding on tomato plants during two  
49 generations, we show that order of arrival affects species' competitive ability and changes the  
50 outcome of competition. Contrary to expectations, order of arrival did not cause positive  
51 frequency dependent priority effects. Instead, coexistence was predicted when the inferior  
52 competitor (*Tetranychus urticae*) arrived first. In that case, *T. urticae* colonised the preferred  
53 feeding stratum (leaves) of *T. evansi* leading to spatial niche preemption, which equalised  
54 fitness and reduced niche differences, driving community assembly to a close-to-neutrality  
55 scenario. Our study demonstrates how the order of species arrival and the spatial context of  
56 competitive interactions can jointly determine whether species can coexist.

57

58

59

60

## 61 **Introduction**

62 Priority effects are broadly defined as the process by which historical contingencies in  
63 community assembly (e.g. order and/or timing of arrival) change the outcome of interspecific  
64 interactions (Chase 2003; Fukami 2015). Inhibitory priority effects, when earlier arrival by one  
65 species inhibits the growth of the species arriving next, are expected to result in alternative  
66 stable states hampering coexistence (Chase 2003; Fukami 2015; Ke & Letten 2018). In turn,  
67 facilitative priority effects, when population growth is higher if individuals arrive after the  
68 settlement of a first species, do not always promote coexistence. Rather, the outcome depends  
69 on the interaction strength among species and on the environmental context in which they  
70 interact (Bulleri *et al.* 2016; Bimler *et al.* 2018). These effects have been less often observed  
71 in natural communities (Queijeiro-Bolaños *et al.* 2017; Clay *et al.* 2019; Halliday *et al.* 2020).

72 Two major mechanisms are predicted to cause priority effects: niche preemption, in which  
73 early colonisers reduce the amount of resource available to late colonisers, and niche  
74 modification, in which the species arriving first modifies the environment, thereby inhibiting  
75 or facilitating later colonisation (Kardol *et al.* 2013; Vannette & Fukami 2014; Fukami 2015;  
76 Delory *et al.* 2019, 2021; Grainger *et al.* 2019). Niche preemption in plant communities was  
77 found to be strong in environments with high nutrient supply, as early arriving plants grew  
78 quickly and prevented growth of later colonisers by depleting space and light (Kardol *et al.*  
79 2013). Niche modification was also detected in plants, as early colonisations modified the soil  
80 metabolome and inhibited population growth of forb, but not grass species arriving later  
81 (Delory *et al.* 2021). Although distinguishing among niche preemption and modification is not  
82 always possible (Grainger *et al.* 2018; Boyle *et al.* 2021), recent advances in coexistence theory  
83 can serve as a powerful approach to better understand the importance of historical  
84 contingencies for species coexistence. Yet the combination of these theoretical tools has  
85 seldom been applied in empirical settings.

86 Modern coexistence theory posits that the long-term persistence of competing species (i.e.,  
87 species coexistence) can be attained by two non-mutually exclusive mechanisms: (i) equalising  
88 mechanisms that reduce average fitness differences, and therefore, dominance between species  
89 and (ii) stabilising mechanisms, which stabilise the interaction between competitors by  
90 increasing the strength of intraspecific competition relative to interspecific competition  
91 (Chesson 2000). Therefore, species will stably coexist if stabilising niche differences are larger  
92 than differences in fitness between competitors. Otherwise the species with higher fitness will  
93 eventually dominate the community (Chesson 2000; Barabás *et al.* 2018; Spaak & De Laender  
94 2021). Under this framework, priority effects are strictly defined as positive frequency  
95 dependence (i.e., via negative niche differences), leading to the dominance of the early-arriving  
96 species (Ke & Letten 2018; Grainger *et al.* 2019; Spaak & De Laender 2021). Hence, species  
97 cannot coexist unless there is spatial variability in the order of arrival. Although recent theory  
98 offers predictions on the outcome of coexistence in systems with historical contingencies,  
99 empirical tests are conspicuously lacking (but see Cardinaux *et al.* 2018; Grainger *et al.* 2019;  
100 Song *et al.* 2020). Therefore, there is as yet scarce knowledge of which species traits interact  
101 with historical contingencies to determine outcomes of interspecific interactions.

102 For herbivore communities, habitat use and dispersal capacity can affect resource use and  
103 ultimately the spatial distribution of consumers. This may lead to niche preemption, as  
104 herbivores generally have preferred plant strata and the first arriving species may monopolise  
105 that resource (Grainger *et al.* 2018; Godinho *et al.* 2020a). Moreover, herbivores often induce  
106 defences on the plants they colonise, which is expected to entail niche modification for species  
107 arriving later (Erb *et al.* 2011; Moreira *et al.* 2015; Stam *et al.* 2017). For example, Hougens-  
108 Eitzman & Karban (1995) showed that early colonisation of grape vine leaves by Willamette  
109 mites negatively affected the growth of Pacific mites, probably due to systemic induction of  
110 defences. Other herbivore species can instead down-regulate plant defences, improving the

111 performance of later colonisers (Sarmiento *et al.* 2011a; Godinho *et al.* 2016), thereby  
112 potentially causing facilitative priority effects. Overall, given the environmental heterogeneity  
113 that herbivores experience (e.g., variation in leaf quality within and between plants), effects of  
114 the order of arrival on species coexistence are expected to be prevalent in these systems  
115 (Utsumi *et al.* 2010; Erb *et al.* 2011; Moreira *et al.* 2015; Stam *et al.* 2017, 2018; Godinho *et*  
116 *al.* 2020a). Still, what type of competitive outcome we should expect is unclear. Indeed,  
117 although the order of arrival is linked to priority effects, the interaction between the chronology  
118 of community assembly and the impact of species on the environment (e.g. where they grow  
119 and how they modify the habitat) can result in diverse outcomes, from competitive exclusion  
120 to species coexistence. Applying modern coexistence theory to this open question can shed  
121 light on the proximate mechanisms that allow for species to coexist under varied historical  
122 contingencies.

123 Here, we investigate the drivers of competitive outcomes by combining theoretical and  
124 empirical tools to test the mechanisms through which order of arrival affects species  
125 coexistence. We use as a model system the two closely-related competing herbivorous species,  
126 the spider mites *Tetranychus urticae* and *T. evansi*. *Tetranychus evansi* generally outcompetes  
127 *T. urticae* on tomato plants (Sarmiento *et al.* 2011b; Orsucci *et al.* 2017; Alzate *et al.* 2020),  
128 although both species are also commonly observed on the same location (Ferragut *et al.* 2013).  
129 Niche modification is expected to be at play in this system, because the two species interact  
130 with plant defences. Indeed, *T. evansi* suppresses plant defences (Sarmiento *et al.* 2011a; Alba  
131 *et al.* 2014), whereas most *T. urticae* populations induce them (Kant *et al.* 2008). This  
132 asymmetrical niche modification is predicted to increase the probability of coexistence by  
133 hampering growth of the stronger competitor and favouring growth of the inferior one, when  
134 the later arrives on plants colonised by the other species. Moreover, niche preemption may  
135 occur, as both *T. evansi* and *T. urticae* prefer the upper, more nutritious leaves of tomato plants,

136 where their performance is higher (Godinho *et al.* 2020a). Thus, early-arriving species could  
137 occupy the preferred niche and displace the other species to lower, less optimal, plant strata.  
138 We tested this by performing a series of multi-generational experiments where we varied order  
139 of arrival and measured space use by the two competing species. To quantify the magnitude of  
140 niche modification, we tested how these species modify the expression of genes associated  
141 with induced defenses on tomato. We then applied modern coexistence theory to unravel the  
142 conditions favouring coexistence or potentially leading to priority effects.

143

## 144 **Material and Methods**

### 145 **Model system, species characteristics, and maintenance of experimental populations**

146 *Tetranychus urticae* is a generalist herbivore that feeds on many economically important crops  
147 (Helle & Sabelis 1985; Grbić *et al.* 2011; Sousa *et al.* 2019), whereas *T. evansi* is a solanaceous  
148 specialist that has recently invaded Europe (Boubou *et al.* 2012). Both species colonise tomato  
149 plants, although *T. urticae* may shift to other hosts if *T. evansi* is present (Ferragut *et al.* 2013).

150 All experiments were performed with outbred populations of *T. urticae* and *T. evansi*  
151 spider mites, formed via controlled crosses among four *T. evansi* and three *T. urticae*  
152 populations collected in different locations in Portugal (Godinho *et al.* 2020b). Populations  
153 were maintained in boxes containing leaves detached from five-week-old tomato plants  
154 (*Solanum lycopersicum*, var MoneyMaker), with their petiole in a small pot containing water  
155 Twice a week, overexploited leaves were removed, and water and new tomato leaves were  
156 added. Before infestation, tomato plants were kept in a separate climatic chamber and watered  
157 three times per week. Mites and plants were kept under controlled conditions (25 °C, 70%  
158 humidity, 16 /8 L/D hours).

159 We created same-age cohorts of mated *T. urticae* and *T. evansi* females for each block. To  
160 this aim, females were placed during 48h in petri dishes (14.5 cm diameter, with a layer of wet

161 cotton watered twice per week) and two freshly cut tomato leaves. One week later, another  
162 tomato leaf was added. In the experiment, we used females with 13-15 days of age.

163

164 **Theoretical approach for predicting competitive outcomes: quantifying niche and fitness**  
165 **differences**

166 Data collected in the experiments were used to parameterise a mathematical model from which  
167 niche and average fitness differences can be quantified to then draw predictions of competitive  
168 outcomes. We assume that the population dynamics in our experiment can be described by a  
169 Beverton-Holt function (Levine & HilleRisLambers 2009; Godoy & Levine 2014):

170 
$$(1) N_{i,t+1} = \frac{\lambda_i * N_{i,t}}{(1 + \alpha_{ii} * N_{i,t} + \alpha_{ij} * N_{j,t})}$$

171 Where  $N_{i,t+1}$  is the number of individuals of species  $i$  in the next generation,  $\lambda_i$  the intrinsic  
172 growth rate of species  $i$  in absence of competitors,  $\alpha_{ii}$  the intraspecific competitive interaction  
173 describing the per-capita effect of species  $i$  on itself,  $\alpha_{ij}$  the interspecific competitive  
174 interactions describing the per-capita effect of species  $j$  on species  $i$ , and  $N_{i,t}$ ,  $N_{j,t}$  the number of  
175 individuals of species  $i$  and  $j$  in the current generation, respectively. We assume that spider  
176 mites do not have a dormant stage. Thus,  $\lambda_i$  represents the fraction of eggs that hatch and  
177 become females that reproduce in the next generation. One of the predictions of modern  
178 coexistence theory is that, for species to coexist, they must invade the resident species from  
179 rare. Because for our system equilibrium densities are difficult to attain within a time frame  
180 fast enough to study the impact of priority effects on species coexistence, we instead used  
181 experimental gradients of density and relative frequency to estimate intra and interspecific  
182 competitive interactions (the  $\alpha$ 's) and intrinsic growth rate ( $\lambda$ ) for each species, an approach  
183 well established and validated by previous work (Godoy & Levine 2014; Matías *et al.* 2018;  
184 Song *et al.* 2020).



185 From the above mentioned model, niche overlap ( $\rho$ ) is defined as follows (see details in  
186 Chesson 2012; Godoy & Levine 2014).

$$187 \quad (2) \quad \rho = \frac{\sqrt{\alpha_{ij} \alpha_{ji}}}{\sqrt{\alpha_{jj} \alpha_{ii}}}$$

188 This formula reflects the average degree to which species limit individuals of their own  
189 species relative to heterospecific competitors. If species limit population growth of their own  
190 species more strongly than that of their competitors ( $\alpha_{jj}$ ,  $\alpha_{ii}$ , are much greater than  $\alpha_{ij}$ ,  $\alpha_{ji}$ ),  
191 then niche overlap will be low, favouring coexistence. Alternatively, niche overlap will  
192 approach one, which hampers stable coexistence. Stabilising niche differences are thus  
193 expressed as  $1-\rho$ .

194 Average fitness differences ( $\frac{\kappa_j}{\kappa_i}$ ) (Chesson 2012; Godoy & Levine 2014) are defined as:

$$195 \quad (3) \quad \frac{\kappa_j}{\kappa_i} = \frac{\lambda_j - 1}{\lambda_i - 1} * \frac{\sqrt{\alpha_{ij} * \alpha_{ii}}}{\sqrt{\alpha_{ji} * \alpha_{jj}}}$$

196 The greater the ratio, ( $\frac{\kappa_j}{\kappa_i}$ ), the greater the fitness advantage of species  $j$  over  $i$ . If this ratio  
197 is one, species are equivalent competitors. Coexistence requires both species to invade when  
198 rare (Chesson 2012), which is satisfied when (Godoy & Levine 2014):

$$199 \quad (4) \quad \rho < \frac{\kappa_j}{\kappa_i} < \frac{1}{\rho}$$

200 Stable coexistence is possible whenever species have either large stabilising niche  
201 differences (corresponding to small niche overlap) that overcome large average fitness  
202 differences, or at the other extreme, via an a close-to-neutral scenario (Scheffer *et al.* 2018),  
203 where, even with weak niche differences, small fitness differences stabilise the interaction  
204 between competitors. If no coexistence is predicted, we can pinpoint if this is due to  
205 competitive exclusion (when fitness differences are larger than niche differences) or to priority  
206 effects, leading to alternative states when niche differences are negative. Negative niche  
207

208 differences imply that each species limits the growth of the competitor more than their own  
209 (Fukami & Nakajima 2011; Ke & Letten 2018).

210 We used maximum likelihood techniques to parameterise the population model following  
211 a nested approach. That is, we first created a single model for which we estimate the intrinsic  
212 growth rate in absence of competitors ( $\lambda$ ), and then we used this information as prior for  
213 subsequent more complex models that include intra and interspecific competitive interactions  
214 (the  $\alpha$ 's) (Matías et al. 2018).  $\lambda$  values were considered fixed per species across empirical  
215 treatments, but competition varied across treatments because mite species can differentially  
216 disperse and modify leaf quality and availability (see the full details in the Supplementary  
217 Material and Methods).

218

## 219 **Experiments**

220 To test the impact of order of arrival on coexistence, we performed a series of experiments in  
221 which we either manipulated the order of arrival and relative frequency (i.e., relative initial  
222 abundance with a constant density of 20 individuals), or the initial density of each of two  
223 species of competing spider mites. Furthermore, to estimate the effect of order of arrival on  
224 promoting niche preemption, we quantified leaf occupation for both species at the end of the  
225 experiment. Finally, to estimate the effect of order of arrival on promoting niche modification,  
226 we quantified induction of plant defences of both species.

227 In the first experiment, both species were introduced simultaneously using the following  
228 proportions of *T. evansi* : *T. urticae*: 1:19; 10:10 and 19:1, along with the single-species  
229 controls (20:0 and 0:20). To manipulate the order of arrival, we introduced (i) 10 *T. evansi*  
230 females 48h before 10 *T. urticae* females and vice versa and (ii) 19 *T. evansi* females 48h  
231 before 1 *T. urticae* female and vice versa (Figure S1). The experiment was done in two blocks,  
232 one week apart. Each block contained five boxes of each experimental treatment (nine

233 treatments, n=10), each with a pot filled with water and two freshly cut tomato leaves from  
234 five-week-old tomato plants. Leaf pairs consisted of leaves 2 and 4 or 3 and 5 (leaf number is  
235 inversely proportional to leaf age), to ensure that each box contained a younger and an older  
236 leaf, since both species prefer younger leaves (Godinho *et al.* 2020a). Adult females were  
237 distributed by the two leaves, following the treatments described above. After one generation  
238 (circa 14 days), two more leaves were added to ensure enough resources for the second mite  
239 generation. Boxes that initially received the leaf pair 2-4, received leaves 3-5 and vice versa.  
240 After two generations, we counted the number of adult females of each species on each leaf.

241 Next, we estimated the growth rate of each species by counting the number of adult  
242 females obtained from the progeny of a single *T. urticae* or *T. evansi* female ovipositing for  
243 48h in two overlapping 18mm leaf disks (n=10). These disks were placed in square petri dishes  
244 with a layer of wet cotton and were watered every two days. The number of adult females  
245 produced was assessed after one generation.

246

#### 247 Quantification of niche modification

248 To quantify the magnitude of niche modification induced by *T. urticae* and *T. evansi*, we  
249 investigated how these two species modified the expression of genes associated with plant  
250 defences. As controls, we quantified the expression of the same genes upon infestation with  
251 spider mites from *T. urticae* Santpoort and *T. evansi* Viçosa populations, known to induce and  
252 suppress tomato defences, respectively (Alba *et al.* 2014). Details of this experiment are given  
253 in the Supplementary Material and Methods and Table S1.

254

#### 255 **Data Analyses**

256 *Effect of order of arrival and initial frequency on species abundance*

257 To test the impact of order of arrival, frequency and their interaction on the proportion of adult  
258 females of each species after two generations, we performed the following general linear mixed  
259 model (lme4 package, Bates et al. 2015), using the binomial family:

$$260 \quad (5) Y = \text{Treatment} + \text{Block} + \varepsilon$$

261 Where Y corresponds to the combination of two vectors with the number of *T. evansi* and  
262 *T. urticae* females after two generations, Treatment (fixed factor) to the combination of  
263 different orders of arrival and initial frequencies, Block (random factor) to whether the  
264 experiment was performed on week one or two, and  $\varepsilon$  to the residual error. We then performed  
265 *a priori* contrasts, using testInteractions fromphia package (Rosario-Martinez 2015) as our  
266 experimental design was not orthogonal. To compare the effect of different orders of arrival,  
267 we performed contrasts between the treatments with same initial frequency but different orders  
268 of arrival. To compare the effect of frequency, we performed contrasts between treatments with  
269 same order of arrival but different initial frequencies. Contrasts were corrected for multiple  
270 comparisons using FDR correction (Benjamini & Yekutieli 2001). To test whether the results  
271 were biased by the order in which the leaf pairs were added to the boxes, we repeated these  
272 statistical analyses separately for each leaf pair.

273

#### 274 *Effect of order or arrival and initial frequency on leaf occupancy and aggregation*

275 To test if coexistence outcomes could be explained by niche preemption, we compared  
276 occupancy patterns of each species across the four leaves. For the single species treatment, we  
277 tested if the number of females differed across leaves (model 6). For the double species  
278 treatment, we tested if the order of arrival, initial frequency, or their interaction changed mite  
279 distribution (model 7), by comparing it to the distribution of the single species treatment.

280 We applied the following binomial models, with Leaf and/or Treatment and their  
281 interaction as fixed factors, for the control (model 6) and experimental (model 7) treatments:

282 
$$(6) Y = \text{Leaf} + \varepsilon$$

283 
$$(7) Y = \text{Leaf} + \text{Treatment} + \text{Leaf} \times \text{Treatment} + \varepsilon$$

284 where Y corresponds to the combination of two vectors with the number of *T. evansi* (or  
285 *T. urticae*) females on each leaf and the total number of individuals on each box that were not  
286 on that leaf. To test whether the results were biased by the order in which the leaf pairs were  
287 added to the boxes, we repeated these statistical analyses accounting for the preference of each  
288 species for each leaf pair. For the double treatment, a posteriori contrasts were done between  
289 each treatment and the corresponding single species treatment. The initial fitting with Block as  
290 a random factor, indicated no variance in this factor, thus we fitted only fixed factors. We also  
291 tested in changes in order of arrival affected aggregation scores (see details in Supplementary  
292 Material and Methods).

293

294 All analyses were done using R (R Core Team 2021). To predict coexistence outcomes we  
295 used the package “cxr” (García-Callejas *et al.* 2020). Plots were done using “ggplot2”  
296 (Wickham 2016) and “cowplot” (Wilke 2020) packages. Data and scripts are available in the  
297 github repository: [https://github.com/irfragata/order\\_arrival\\_niche\\_preemption](https://github.com/irfragata/order_arrival_niche_preemption).

298

## 299 **Results**

### 300 Effect of order of arrival and initial frequency on species abundance

301 The number of individuals of each species on tomato plants were affected by the order of arrival  
302 (contrasts between *T. evansi* arriving first vs. simultaneously:  $\chi^2 = 44.252$ ,  $df = 1$ ,  $p\text{-value} <$   
303  $0.0001$ ; or *T. urticae* arriving first vs. simultaneously:  $\chi^2 = 375.860$ ,  $df = 1$ ,  $p\text{-value} <$   $0.0001$ ),  
304 and their initial frequency (contrasts between *T. evansi* starting at equal vs. higher frequency.  
305 :  $\chi^2 = 784.335$ ,  $df = 1$ ,  $p\text{-value} <$   $0.0001$ ; or *T. urticae* starting at equal vs. higher frequency:  $\chi^2$   
306 =  $654.903$ ,  $df = 1$ ,  $p\text{-value} <$   $0.0001$ ). Specifically, the abundance of *T. evansi* females after

307 two generations was higher when this species arrived first or simultaneously with *T. urticae*,  
308 independently of initial frequencies. However, the additional advantage provided by arriving  
309 first was much larger in the equal frequency treatment (Table S2, Fig.1). The abundance of *T.*  
310 *urticae* after two generations was also affected by initial frequency and order of arrival. Indeed,  
311 the final number of *T. urticae* females was higher when this species arrived first and was at  
312 high initial frequency, than in the equal frequency treatment (Table S2, Fig. 1). We observed  
313 the same patterns when performing these analyses per leaf pair (Table S3). Overall, these  
314 results confirm that *T. evansi* is a superior competitor as observed in previous studies  
315 (Sarmiento *et al.* 2011b; Ferragut *et al.* 2013; Alzate *et al.* 2020).

316

### 317 Effect of order of arrival on coexistence

318 The order of arrival modified the outcome of competition between the two species. *Tetranychus*  
319 *evansi* (the superior competitor) is predicted to exclude *T. urticae* when it arrives first or at the  
320 same time. Under this exclusion scenario, the rate of competitive exclusion is expected to be  
321 faster when *T. evansi* arrives first due to a decrease in niche differences (Fig 2). The small  
322 overlap between the lower confidence interval with the priority effects region suggests that  
323 positive frequency dependence might also emerge in this system. Interestingly, coexistence  
324 was only possible when *T. urticae* arrived first (Fig. 2). This outcome was due to small niche  
325 and fitness differences among competitors, leading to a quasi-neutral scenario. Specifically,  
326 when *T. urticae* arrived first, we observed similar strengths of intra- and interspecific  
327 interactions among species (Fig S2A). Contrary to expectations and previous studies, the order  
328 of arrival was not associated with positive frequency dependence leading to priority effects.  
329 However, since the order of arrival modified the outcome of the interactions between *T. urticae*  
330 and *T. evansi*, we can also interpret these results as priority effects (*sensu* (Chase 2003; Fukami  
331 2015) allowing for coexistence between species in our system.

332

333 Effect of order of arrival and initial frequency on leaf occupancy and aggregation

334 When *T. evansi* was alone, it reached higher abundances on leaves 3 and 4 (Table S4A, Fig  
335 3B), whereas *T. urticae* was less abundant on leaf 2 in comparison to all others (Table S4A,  
336 Fig 3D). Fewer *T. evansi* females were found on leaf 4 when *T. urticae* arrived first, and on  
337 leaf 3 when *T. urticae* started with higher frequency and both species arrived at the same time  
338 (Fig 3, Fig S3A, Table S4B). When *T. evansi* arrived first or started at higher frequency, we  
339 observed fewer changes on its own leaf occupancy (Fig S4A). The distribution of *T. urticae*  
340 showed a slight shift when it arrived first, with a reduction on the prevalence of leaves 2 and 5  
341 and slightly higher occupation of leaves 3 and 4 (Fig. S3B, Table S4B). When *T. evansi* started  
342 at high frequency, there was also a shift in *T. urticae* distribution, with a lower occupancy of  
343 leaves 2 and 5 (Fig S3B). We observed similar shifts in leaf occupation when performing the  
344 analyses accounting for the order in which each leaf pair was added (Fig S4, Table S5).

345 Spatial aggregation significantly differed among treatments ( $\chi^2 = 18.186$ ,  $df = 6$ ,  $p$ -value  
346 = 0.01279), being higher in treatments with similar initial densities (cf. Fig S5 with Fig 1, Table  
347 S5). We observed a significant difference in C-score, with higher aggregation when both  
348 species arrived at the same time and had equal frequency, and a lower aggregation when both  
349 species arrived at the same time and *T. evansi* started at higher frequency (Table S6). Order of  
350 arrival did not change the C-score (Fig. S5, Table S6).

351

352 Quantification of niche modification

353 Plants infested by *T. urticae* or *T. evansi* populations showed patterns of gene expression  
354 similar to those of Viçosa, the suppression control, and significant differences with Santpoort,  
355 the induction control (Fig. S6; Table S7). We thus conclude that, both populations suppress  
356 plant defences.

357

## 358 **Discussion**

359 This study shows that order of arrival interacts with competitive ability to determine the  
360 probability of coexistence between congeneric species that share common resources. When  
361 both species arrive at the same time or the superior competitor (*Tetranychus evansi*) arrived  
362 first, *T. urticae* was predicted to be excluded. Coexistence was only predicted when the inferior  
363 competitor (*T. urticae*) was the first species colonising the habitat. Analyses of leaf occupancy  
364 show that these competition outcomes are linked to a spatial niche preemption process in which  
365 *T. evansi* was displaced from its preferred food stratum when *T. urticae* arrived first. As a result  
366 of this complex interaction between order of arrival, species competitive ability, and spatial  
367 occupancy, we observed a particular configuration that allows species coexistence: both  
368 species equalised their fitness differences to the extent that they can coexist despite small niche  
369 differences. These multiple lines of evidence challenge the common understanding of the  
370 inhibitory role of niche preemption in coexistence between species.

371 We found that *T. evansi* had higher competitive ability and growth rate, and often excluded  
372 *T. urticae* (Fig 1, 2). This is in line with laboratory observations showing that *T. evansi*  
373 outcompeted *T. urticae* on tomato plants (Sarmiento *et al.* 2011b; Alzate *et al.* 2020, but see  
374 Orsucci *et al.* 2017) and with field observations showing a shift in host use in *T. urticae* upon  
375 invasion by *T. evansi* (Ferragut *et al.* 2013). Still, these two species can co-occur in the field in  
376 the same plant species (Ferragut *et al.* 2013; Orsucci *et al.* 2017; Zélé *et al.* 2018). The  
377 advantage created by the earlier arrival of *T. urticae*, and associated reduction in interspecific  
378 competition by *T. evansi*, could be one of the possible mechanisms fostering their coexistence.  
379 Indeed, *T. urticae* can withstand colder temperatures than *T. evansi* (Gotoh *et al.* 2010;  
380 Khodayari *et al.* 2013; Riahi *et al.* 2013; White *et al.* 2018), hence it is expected to arrive first



381 in the season. Field surveys that sample both species in the same location across seasons are  
382 needed to further explore this hypothesis.

383 Historical contingencies emerging from order of arrival can happen through two main  
384 mechanisms: niche modification or niche preemption (Fukami 2015). In our system, niche  
385 modification may arise via interactions between spider mites and plant defences. However, we  
386 observe that both species suppress plant defenses. If suppression would affect species  
387 performance, we would expect higher production of offspring when the competitor arrives first.  
388 We did not observe this, suggesting that this mechanism of niche modification does not affect  
389 the outcome of competition in this system.

390 Niche preemption can occur through monopolisation of nutrients or space, which can be  
391 particularly important among competitors with similar requirements (Grainger *et al.* 2018;  
392 Holditch & Smith 2020). In our study, we observed a shift in the leaf occupancy pattern of *T.*  
393 *evansi* females when *T. urticae* arrived first. This displacement of *T. evansi* from the preferred  
394 food stratum (i.e., younger, more nutritious leaves) by early-arriving *T. urticae* can explain the  
395 decreased performance of the superior competitor. Thus, our results indicate that variation in  
396 species performance driven by habitat quality heterogeneity (Orians *et al.* 2000; Orians & Jones  
397 2001) combines with order of arrival to generate niche preemption, providing a mechanism for  
398 the two herbivores to coexist.

399 Order of arrival is a major determinant of community assembly across diverse taxa, from  
400 microbes to plants (Chase 2003; Erb *et al.* 2011; Kardol *et al.* 2013; Stam *et al.* 2017; Grainger  
401 *et al.* 2018, 2019; Clay *et al.* 2019, 2020; Halliday *et al.* 2020). Most of these studies show that  
402 early colonisers inhibit growth and decrease performance of late arriving species, especially in  
403 those that occupy very similar niches (Fargione *et al.* 2003; Vannette & Fukami 2014; Delory  
404 *et al.* 2019, 2021; Grainger *et al.* 2019), although very few concern herbivorous species  
405 competing for the same niche (e.g. Grainger *et al.* 2018; Holditch & Smith 2020). Other studies

406 found that order of arrival does not affect community assembly (e.g. Delory *et al.* 2021) or that  
407 initial colonisers facilitate later colonisation of other species (e.g. Queijeiro-Bolaños *et al.*  
408 2017; Delory *et al.* 2019). Here, we show that coexistence is promoted by niche preemption  
409 because early colonisation by the inferior competitor leads to increased intraspecific  
410 competition for the superior competitor and reduced interspecific competition for itself. . As a  
411 result, both species can coexist under a quasi-neutral scenario because this equalising effect on  
412 fitness differences is enough to fit within the constraints of small niche differences. Our study  
413 adds a novel perspective to the growing body of evidence that historical contingencies shape  
414 ecological communities, by showing that the probability of coexistence of two competing  
415 herbivores changes due to an interaction between order of arrival and species competitive  
416 ability.

417 Priority effects were recently incorporated into modern coexistence theory (Ke & Letten  
418 2018; Spaak & De Laender 2021), but empirical tests quantifying the effects of order of arrival  
419 on species coexistence remain very rare. In another study, Grainger *et al.* (2019) documented  
420 that positive frequency dependence, due to strong priority effects, arose from changes in order  
421 or arrival in yeast species feeding on floral nectars. In contrast, our results show that order of  
422 arrival did not lead to alternative states caused by priority effects under positive frequency  
423 dependence. Rather, we predicted either competitive exclusion when *T. evansi* arrived first  
424 because it excluded *T. urticae* or coexistence when *T. urticae* arrived first. Overall, these results  
425 suggest that in this system deterministic expectations, stemming from theory, can be strongly  
426 influenced by small stochastic events, such as changes in order of arrival, because it affects the  
427 timing of dispersal across and within host plants.

428 Framing priority effects in the modern coexistence theory (Ke & Letten 2018) is  
429 undoubtedly an important step to mechanistically understand how order of arrival affects  
430 community assembly processes. However, in this framework, priority effects are only caused

431 by positive frequency dependence (i.e., population growth rate is higher as individuals become  
432 relatively more abundant) (Fukami 2015; Song *et al.* 2020). Including other types of  
433 interactions and outcomes into modern coexistence framework is fundamental to improve our  
434 ability to understand how species coexist (Spaak *et al.* 2021). Here we show that order of arrival  
435 can lead to coexistence via niche preemption by the inferior competitor. Thus, our results show  
436 that changes in the order of arrival can produce a wide range of competitive outcomes from  
437 coexistence to competitive exclusion due to positive and negative frequency dependence.  
438 Therefore, it is urgent that ecologists widen the scope of the multiple outcomes that historical  
439 contingency can produce on species coexistence.

440 Most empirical and theoretical studies emphasize the inhibitory nature of niche preemption  
441 (Fargione *et al.* 2003; Fukami 2015; Vieira *et al.* 2018; Delory *et al.* 2019), with the early  
442 arriving species outcompeting the other. However, recent theory suggests that, in a resource  
443 competition model of two species, niche preemption by the inferior competitor could facilitate  
444 coexistence under a trade-off between order of arrival and the resource levels of zero net growth  
445 ( $R^*$ ) (Qi *et al.* 2021). Our study is, to the best of our knowledge, the first empirical study  
446 showing that niche preemption by the weaker competitor promotes coexistence. This striking  
447 change in the outcome of competitive interactions emerges mostly due to a decrease in niche  
448 overlap, shifting niche differences from negative to positive. This suggests that even small  
449 differences in order of arrival can be sufficient for the monopolisation of a resources in plant-  
450 herbivore interactions, which may suffice to allow coexistence between competitor species.  
451 Therefore, our results demonstrate how small temporal differences percolate into small spatial  
452 heterogeneities, fostering coexistence and the maintenance of diversity.

453

454 **Acknowledgments:** This work was financed by an ERC (European Research Council)  
455 consolidator grant COMPCON, GA 725419 attributed to SM and by FCT (Fundação para

456 Ciência e Tecnologia) with the Junior researcher contract (CEECIND/02616/2018) attributed  
457 to IF. RC-P is supported by grant #2020/11953-2 São Paulo Research Foundation (FAPESP)  
458 and grant R-2011-37572 Instituto Serrapilheira. OG acknowledges financial support provided  
459 by the Spanish Ministry of Economy and Competitiveness (MINECO) and by the European  
460 Social Fund through the Ramón y Cajal Program (RYC-2017-23666). AM was funded by  
461 National Science Centre, Poland (grant no. 2018/28/T/NZ8/00060) and Excellence Initiative -  
462 Research University programme (support for the internationalization of the Adam Mickiewicz  
463 University PhD students, no. 003/13/UAM/0018). The authors acknowledge stimulating  
464 discussion with all members of the Mite Squad, in particular Flore Zélé and Diogo Godinho,  
465 which have significantly improved the experimental design and interpretation of the results,  
466 and Marta Artal for invaluable infrastructure at meetings in Sevilla.

467

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

469

470

471

472 **Bibliography**

- 473 Alba, J.M., Schimmel, B.C.J., Glas, J.J., Ataide, L.M.S., Pappas, M.L., Villarroel, C.A., *et al.*  
474 (2014). Spider mites suppress tomato defenses downstream of jasmonate and salicylate  
475 independently of hormonal crosstalk. *New Phytol.*, 205, 828–840.
- 476 Alzate, A., Onstein, R.E., Etienne, R.S. & Bonte, D. (2020). The role of preadaptation,  
477 propagule pressure and competition in the colonization of new habitats. *Oikos*, 129,  
478 820–829.
- 479 Barabás, G., D’Andrea, R. & Stump, S.M. (2018). Chesson’s coexistence theory. *Ecol.*  
480 *Monogr.*, 88, 277–303.
- 481 Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models  
482 Using lme4. *J. Stat. Softw.*, 67, 1–48.
- 483 Benjamini, Y. & Yekutieli, D. (2001). The control of the false discovery rate in multiple  
484 testing under dependency. *Ann. Stat.*, 29, 1165–1188.
- 485 Bimler, M.D., Stouffer, D.B., Lai, H.R. & Mayfield, M.M. (2018). Accurate predictions of  
486 coexistence in natural systems require the inclusion of facilitative interactions and  
487 environmental dependency. *J. Ecol.*, 106, 1839–1852.
- 488 Boubou, A., Migeon, A., Roderick, G.K., Auger, P., Cornuet, J.M., Magalhães, S., *et al.*  
489 (2012). Test of colonisation scenarios reveals complex invasion history of the red  
490 tomato spider mite *tetranychus evansi*. *PLoS One*, 7.
- 491 Boyle, J.A., Simonsen, A.K., Frederickson, M.E. & Stinchcombe, J.R. (2021). Priority effects  
492 alter interaction outcomes in a legume-rhizobium mutualism. *Proc. R. Soc. B Biol. Sci.*,  
493 288, 1–8.
- 494 Bulleri, F., Bruno, J.F., Silliman, B.R. & Stachowicz, J.J. (2016). Facilitation and the niche:  
495 Implications for coexistence, range shifts and ecosystem functioning. *Funct. Ecol.*, 30,  
496 70–78.

- 497 Cardinaux, A., Hart, S.P. & Alexander, J.M. (2018). Do soil biota influence the outcome of  
498 novel interactions between plant competitors? *J. Ecol.*, 106, 1853–1863.
- 499 Chase, J.M. (2003). Community assembly: When should history matter? *Oecologia*, 136,  
500 489–498.
- 501 Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*,  
502 31, 343–366.
- 503 Chesson, P. (2012). Species Competition and Predation. In: *Encyclopedia of Sustainability*  
504 *Science and Technology* (ed. Meyers, R.A.). Springer, New York, pp. 10 061–10 085.
- 505 Clay, P.A., Dhir, K., Rudolf, V.H.W. & Duffy, M.A. (2019). Within-host priority effects  
506 systematically alter pathogen coexistence. *Am. Nat.*, 193, 187–199.
- 507 Clay, P.A., Duffy, M.A. & Rudolf, V.H.W. (2020). Within-host priority effects and epidemic  
508 timing determine outbreak severity in co-infected populations. *Proc. R. Soc. B Biol. Sci.*,  
509 287.
- 510 Delory, B.M., Weidlich, E.W.A., von Gillhaussen, P. & Temperton, V.M. (2019). When  
511 history matters: The overlooked role of priority effects in grassland overyielding. *Funct.*  
512 *Ecol.*, 33, 2369–2380.
- 513 Delory, B.M., Schempp, H., Spachmann, S.M., Störzer, L., van Dam, N.M., Temperton,  
514 V.M., *et al.* (2021). Soil chemical legacies trigger species-specific and context-  
515 dependent root responses in later arriving plants. *Plant Cell Environ.*, 44, 1215–1230.
- 516 Erb, M., Robert, C.A.M., Hibbard, B.E. & Turlings, T.C.J. (2011). Sequence of arrival  
517 determines plant-mediated interactions between herbivores. *J. Ecol.*, 99, 7–15.
- 518 Fargione, J., Brown, C.S. & Tilman, D. (2003). Community Assembly and Invasion: An  
519 Experimental Test of Neutral versus Niche Processes. *Proc. Natl. Acad. Sci. U. S. A.*,  
520 100, 8916–8920.
- 521 Ferragut, F., Garzón-Luque, E. & Pekas, A. (2013). The invasive spider mite *Tetranychus*

- 522 evansi (Acari: Tetranychidae) alters community composition and host-plant use of  
523 native relatives. *Exp. Appl. Acarol.*, 60, 321–341.
- 524 Fukami, T. & Nakajima, M. (2011). Community assembly: Alternative stable states or  
525 alternative transient states? *Ecol. Lett.*, 14, 973–984.
- 526 Fukami, T. (2015). Historical Contingency in Community Assembly: Integrating Niches,  
527 Species Pools, and Priority Effects. *Annu. Rev. Ecol. Evol. Syst.*, 46, 1–23.
- 528 García-Callejas, D., Godoy, O. & Bartomeus, I. (2020). cxr: A toolbox for modelling species  
529 coexistence in R. *Methods Ecol. Evol.*, 11, 1221–1226.
- 530 Godinho, D.P., Janssen, A., Dias, T., Cruz, C. & Magalhães, S. (2016). Down - regulation of  
531 plant defence in a resident spider mite species and its effect upon con - and  
532 heterospecifics. *Oecologia*, 180, 161–167.
- 533 Godinho, D.P., Janssen, A., Li, D., Cruz, C. & Magalhães, S. (2020a). The distribution of  
534 herbivores between leaves matches their performance only in the absence of  
535 competitors. *Ecol. Evol.*, 10, 8405–8415.
- 536 Godinho, D.P., Cruz, M.A., Charlery de la Masselière, M., Teodoro-Paulo, J., Eira, C.,  
537 Fragata, I., *et al.* (2020b). Creating outbred and inbred populations in haplodiploids to  
538 measure adaptive responses in the laboratory. *Ecol. Evol.*, 10, 7291–7305.
- 539 Godoy, O. & Levine, J.M. (2014). Phenology effects on invasion success: Insights from  
540 coupling field experiments to coexistence theory. *Ecology*, 95, 726–736.
- 541 Gotoh, T., Sugimoto, N., Pallini, A., Knapp, M., Hernandez-Suarez, E., Ferragut, F., *et al.*  
542 (2010). Reproductive performance of seven strains of the tomato red spider mite  
543 *Tetranychus evansi* (Acari: Tetranychidae) at five temperatures. *Exp. Appl. Acarol.*, 52,  
544 239–259.
- 545 Grainger, T.N., Rego, A.I. & Gilbert, B. (2018). Temperature-dependent species interactions  
546 shape priority effects and the persistence of unequal competitors. *Am. Nat.*, 191, 197–

- 547           209.
- 548 Grainger, T.N., Letten, A.D., Gilbert, B. & Fukami, T. (2019). Applying modern coexistence  
549 theory to priority effects. *Proc. Natl. Acad. Sci. U. S. A.*, 116, 6205–6210.
- 550 Grbić, M., Van Leeuwen, T., Clark, R.M., Rombauts, S., Rouzé, P., Grbić, V., *et al.* (2011).  
551 The genome of *Tetranychus urticae* reveals herbivorous pest adaptations. *Nature*, 479,  
552 487–492.
- 553 Halliday, F.W., Penczykowski, R.M., Barrès, B., Eck, J.L., Numminen, E. & Laine, A.L.  
554 (2020). Facilitative priority effects drive parasite assembly under coinfection. *Nat. Ecol.*  
555 *Evol.*, 4, 1510–1521.
- 556 Helle, W. & Sabelis, M.W. (1985). *Spider mites their biology, natural enemies and control.*  
557 *World Crop Pests*. Elsevier Science Publishers, Amsterdam.
- 558 Holditch, Z. & Smith, A.D. (2020). Priority determines *Tribolium* competitive outcome in a  
559 food-limited environment. *PLoS One*, 15, 1–14.
- 560 Hougren-Eitzman, D. & Karban, R. (1995). Mechanisms of interspecific competition that  
561 result in successful control of Pacific mites following inoculations of Willamette mites  
562 on grapevines. *Oecologia*, 103, 157–161.
- 563 Kant, M.R., Sabelis, M.W., Haring, M.A. & Schuurink, R.C. (2008). Intraspecific variation in  
564 a generalist herbivore accounts for differential induction and impact of host plant  
565 defences. *Proc. R. Soc. B Biol. Sci.*, 275, 443–452.
- 566 Kardol, P., Souza, L. & Classen, A.T. (2013). Resource availability mediates the importance  
567 of priority effects in plant community assembly and ecosystem function. *Oikos*, 122, 84–  
568 94.
- 569 Ke, P.J. & Letten, A.D. (2018). Coexistence theory and the frequency-dependence of priority  
570 effects. *Nat. Ecol. Evol.*, 2, 1691–1695.
- 571 Khodayari, S., Colinet, H., Moharramipour, S. & Renault, D. (2013). Seasonal changes in the



- 572 cold hardiness of the two-spotted spider mite females (Acari: Tetranychidae). *Environ.*  
573 *Entomol.*, 42, 1415–1421.
- 574 Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of  
575 species diversity. *Nature*, 461, 254–257.
- 576 Matías, L., Godoy, O., Gómez-Aparicio, L. & Pérez-Ramos, I.M. (2018). An experimental  
577 extreme drought reduces the likelihood of species to coexist despite increasing  
578 intransitivity in competitive networks. *J. Ecol.*, 106, 826–837.
- 579 Moreira, X., Abdala-Roberts, L., Hernández-Cumplido, J., Cuny, M.A.C., Glauser, G. &  
580 Benrey, B. (2015). Specificity of induced defenses, growth, and reproduction in lima  
581 bean (*Phaseolus lunatus*) in response to multispecies herbivory. *Am. J. Bot.*, 102,  
582 1300–1308.
- 583 Orians, C.M., Pomerleau, J. & Ricco, R. (2000). Vascular architecture generates fine scale  
584 variation in systemic induction of proteinase inhibitors in tomato. *J. Chem. Ecol.*, 26,  
585 471–485.
- 586 Orians, C.M. & Jones, C.G. (2001). Plants as resource mosaics: A functional model for  
587 predicting patterns of within-plant resource heterogeneity to consumers based on  
588 vascular architecture and local environmental variability. *Oikos*, 94, 493–504.
- 589 Orsucci, M., Navajas, M. & Fellous, S. (2017). Genotype-specific interactions between  
590 parasitic arthropods. *Heredity (Edinb.)*, 118, 260–265.
- 591 Qi, M., DeMalach, N., Sun, T. & Zhang, H. (2021). Coexistence under hierarchical resource  
592 exploitation: the role of R\*-preemption tradeoff. *bioRxiv*, 1–23.
- 593 Queijeiro-Bolaños, M.E., González, E.J., Martorell, C. & Cano-Santana, Z. (2017).  
594 Competition and facilitation determine dwarf mistletoe infection dynamics. *J. Ecol.*,  
595 105, 775–785.
- 596 R Core Team. (2021). R: A language and environment for statistical computing.

- 597 Riahi, E., Shishehbor, P., Nemati, A.R. & Saeidi, Z. (2013). Temperature effects on  
598 development and life table parameters of *Tetranychus urticae* (Acari: Tetranychidae). *J.*  
599 *Agric. Sci. Technol.*, 15, 661–672.
- 600 Rosario-Martinez, H. De. (2015). *phia*: Post-Hoc Interaction Analysis.
- 601 Sarmiento, R.A., Lemos, F., Bleeker, P.M., Schuurink, R.C., Pallini, A., Oliveira, M.G.A., *et*  
602 *al.* (2011a). A herbivore that manipulates plant defence. *Ecol. Lett.*, 14, 229–236.
- 603 Sarmiento, R.A., Lemos, F., Dias, C.R., Kikuchi, W.T., Rodrigues, J.C.P., Pallini, A., *et al.*  
604 (2011b). A herbivorous mite down-regulates plant defence and produces web to exclude  
605 competitors. *PLoS One*, 6, 8–14.
- 606 Scheffer, M., Van Nes, E.H. & Vergnon, R. (2018). Toward a unifying theory of biodiversity.  
607 *Proc. Natl. Acad. Sci. U. S. A.*, 115, 639–641.
- 608 Song, C., Rohr, R.P., Vasseur, D. & Saavedra, S. (2020). Disentangling the effects of  
609 external perturbations on coexistence and priority effects. *J. Ecol.*, 108, 1677–1689.
- 610 Sousa, V.C., Zélé, F., Rodrigues, L.R., Godinho, D.P., Charlery de la Masselière, M. &  
611 Magalhães, S. (2019). Rapid host-plant adaptation in the herbivorous spider mite  
612 *Tetranychus urticae* occurs at low cost. *Curr. Opin. Insect Sci.*, 36, 82–89.
- 613 Spaak, J.W., Godoy, O. & Laender, F. (2021). Mapping species niche and fitness differences  
614 for communities with multiple interaction types. *Oikos*, 1–13.
- 615 Spaak, J.W. & De Laender, F. (2021). Intuitive and broadly applicable definitions of niche  
616 and fitness differences. *Ecol. Lett.*, 23, 1117–1128.
- 617 Stam, J.M., ChrÉtien, L., Dicke, M. & Poelman, E.H. (2017). Response of *Brassica oleracea*  
618 to temporal variation in attack by two herbivores affects preference and performance of  
619 a third herbivore. *Ecol. Entomol.*, 42, 803–815.
- 620 Stam, J.M., Dicke, M. & Poelman, E.H. (2018). Order of herbivore arrival on wild cabbage  
621 populations influences subsequent arthropod community development. *Oikos*, 127,

- 622 1482–1493.
- 623 Utsumi, S., Ando, Y. & Miki, T. (2010). Linkages among trait-mediated indirect effects: A  
624 new framework for the indirect interaction web. *Popul. Ecol.*, 52, 485–497.
- 625 Vannette, R.L. & Fukami, T. (2014). Historical contingency in species interactions: Towards  
626 niche-based predictions. *Ecol. Lett.*, 17, 115–124.
- 627 Vieira, E.A., Flores, A.A.V. & Dias, G.M. (2018). Persistence and space preemption explain  
628 species-specific founder effects on the organization of marine sessile communities. *Ecol.*  
629 *Evol.*, 8, 3430–3442.
- 630 White, N., Bale, J.S. & Hayward, S.A.L. (2018). Life-history changes in the cold tolerance of  
631 the two-spot spider mite *Tetranychus urticae*: applications in pest control and  
632 establishment risk assessment. *Physiol. Entomol.*, 43, 334–345.
- 633 Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*.
- 634 Wilke, C. (2020). *cowplot: Streamlined Plot Theme and Plot Annotations for “ggplot2.”*
- 635 Zélé, F., Santos, I., Olivieri, I., Weill, M., Duron, O. & Magalhães, S. (2018). Endosymbiont  
636 diversity and prevalence in herbivorous spider mite populations in South-Western  
637 Europe. *FEMS Microbiol. Ecol.*, 94, 1–11.
- 638
- 639

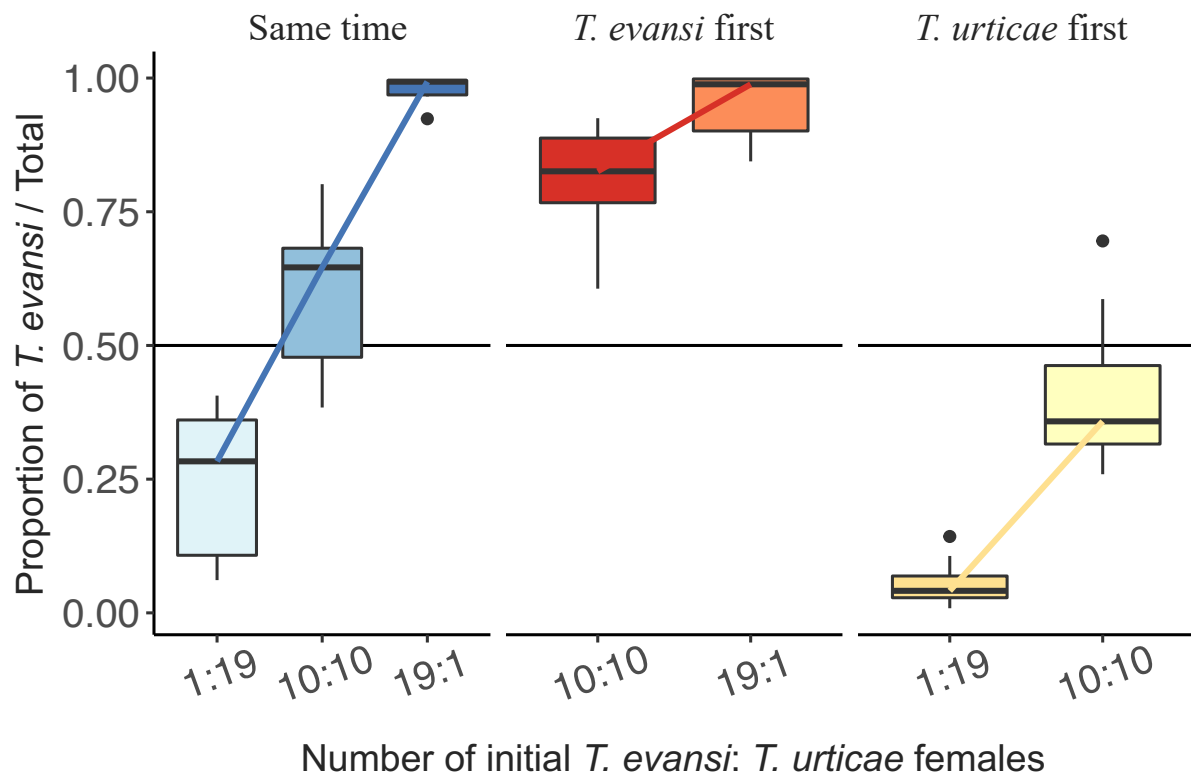
640 Figure 1 – Proportion of spider mites *Tetranychus evansi* females (y-axis) depending on initial  
641 frequency (number of initial females *T. evansi*: *T. urticae*, x-axis) and order of arrival (same  
642 time vs. *T. evansi* or *T. urticae* arriving 48h before its competitor) after two generations.  
643 *Tetranychus evansi* is the better competitor overall (ratio above 0.5), unless *T. urticae* arrives  
644 first or is at higher initial frequency. A posteriori contrasts show a strong effect of order of  
645 arrival in the proportion of females of the two species (Table S2B). Initial frequency also  
646 impacts the final ratio, with a stronger effect when *T. urticae* arrives first or at the same time  
647 than *T. evansi* (Table S2B). Boxplots represent median and quartiles of the 10 boxes within  
648 treatment.

649  
650 Figure 2 – Relationship between average fitness differences ( $\frac{\kappa_j}{\kappa_i}$ , y-axis) and stabilising niche  
651 differences ( $1 - \rho$ , x-axis) for different orders of arrival (*Tetranychus evansi* first – red, same  
652 time – blue, *T. urticae* first – yellow). Plotting average fitness differences against niche  
653 differences allows mapping different competitive outcomes predicted by modern coexistence  
654 theory. The coexistence condition (eq. 4) and its symmetrical for each competing species,  
655 represented by the two solid black lines, allow defining the space in which species can coexist  
656 due to negative frequency dependence or enter alternative stable states due to positive  
657 frequency dependence, whenever niche differences are greater or smaller than zero  
658 respectively. Otherwise, the species with higher fitness will exclude the other. In our case, the  
659 only scenario in which species are predicted to coexist is when *T. urticae* arrives first (yellow).  
660 Error bars for each outcome indicate the 95% confidence interval from the maximum  
661 likelihood estimates. For the other two cases, it is predicted that the superior competitor *T.*  
662 *evansi* will exclude *T. urticae*.

663

664 Figure 3 – Differences between expected and observed leaf occupancy for *Tetranychus evansi*  
665 (A) and *T. urticae* (C) for a subset of the experimental treatments (when *T. urticae* arrived first  
666 or at the same time as *T. evansi*, note that Figure S3 includes all treatments); leaf occupancy  
667 for *T. evansi* (B) and *T. urticae* (D) in the control, single species, treatments. Leaf 2 corresponds  
668 to the oldest leaf and leaf 5 to the youngest. For each box, we calculated the ratio of females  
669 occupying each leaf in relation to the total number of females present. For the experimental  
670 treatments we calculated the difference between this ratio and the average ratio for the control  
671 treatments. Thus, positive values indicate that there are more females on that leaf than expected  
672 based on the single-species treatment and negative values indicate the reverse pattern. Overall,  
673 we see that *T. evansi* reduces occupancy on leaf 4 when *T. urticae* arrives first and on leaf 3  
674 when the two species arrive at the same time. In contrasts, *T. urticae* shows a slight increase in  
675 occupancy of leaf 4 when it arrives first and a slight decrease in occupancy of leaves 2 and 5.  
676  
677  
678

679

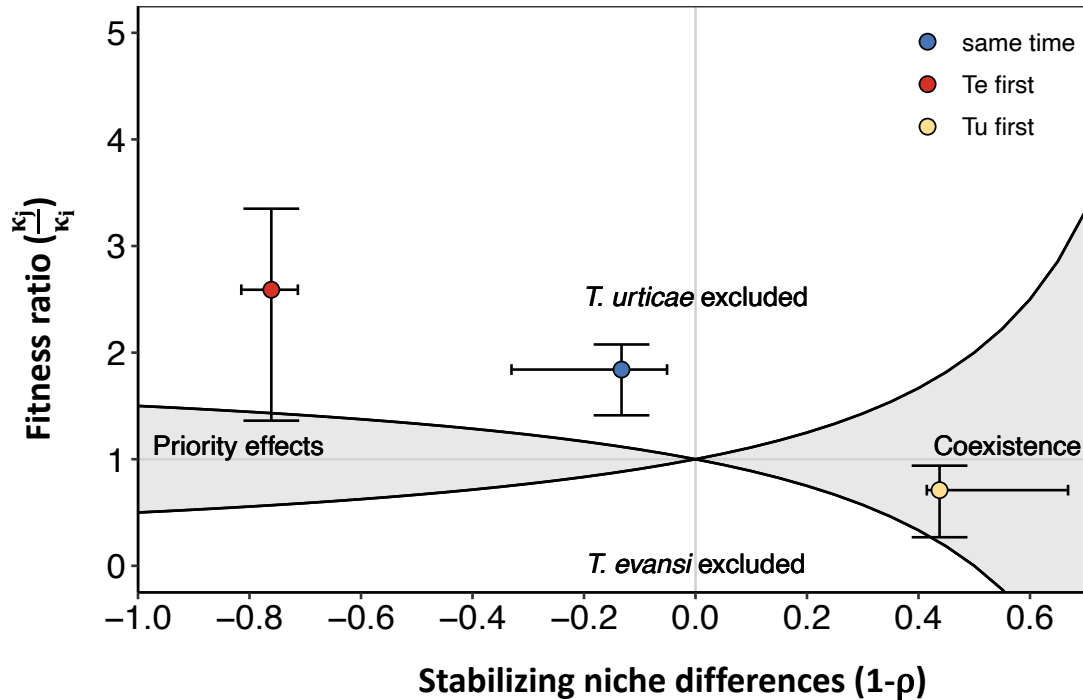


680

681 Figure 1 – Proportion of spider mites *Tetranychus evansi* females (y-axis) depending on initial  
682 frequency (number of initial females *T. evansi*: *T. urticae*, x-axis) and order of arrival (same  
683 time vs. *T. evansi* or *T. urticae* arriving 48h before its competitor) after two generations.  
684 *Tetranychus evansi* is the better competitor overall (ratio above 0.5), unless *T. urticae* arrives  
685 first or is at higher initial frequency. A posteriori contrasts show a strong effect of order of  
686 arrival in the proportion of females of the two species (Table S2B). Initial frequency also  
687 impacts the final ratio, with a stronger effect when *T. urticae* arrives first or at the same time  
688 than *T. evansi* (Table S2B). Boxplots represent median and quartiles of the 10 boxes within  
689 treatment.

690

691



692

693 Figure 2 – Relationship between average fitness differences ( $\frac{\kappa_j}{\kappa_i}$ , y-axis) and stabilising niche

694 differences ( $1 - \rho$ , x-axis) for different orders of arrival (*Tetranychus evansi* first – red, same

695 time – blue, *T. urticae* first – yellow). Plotting average fitness differences against niche

696 differences allows mapping different competitive outcomes predicted by modern coexistence

697 theory. The coexistence condition (eq. 4) and its symmetrical for each competing species,

698 represented by the two solid black lines, allow defining the space in which species can coexist

699 due to negative frequency dependence or enter alternative stable states due to positive

700 frequency dependence, whenever niche differences are greater or smaller than zero

701 respectively. Otherwise, the species with higher fitness will exclude the other. In our case, the

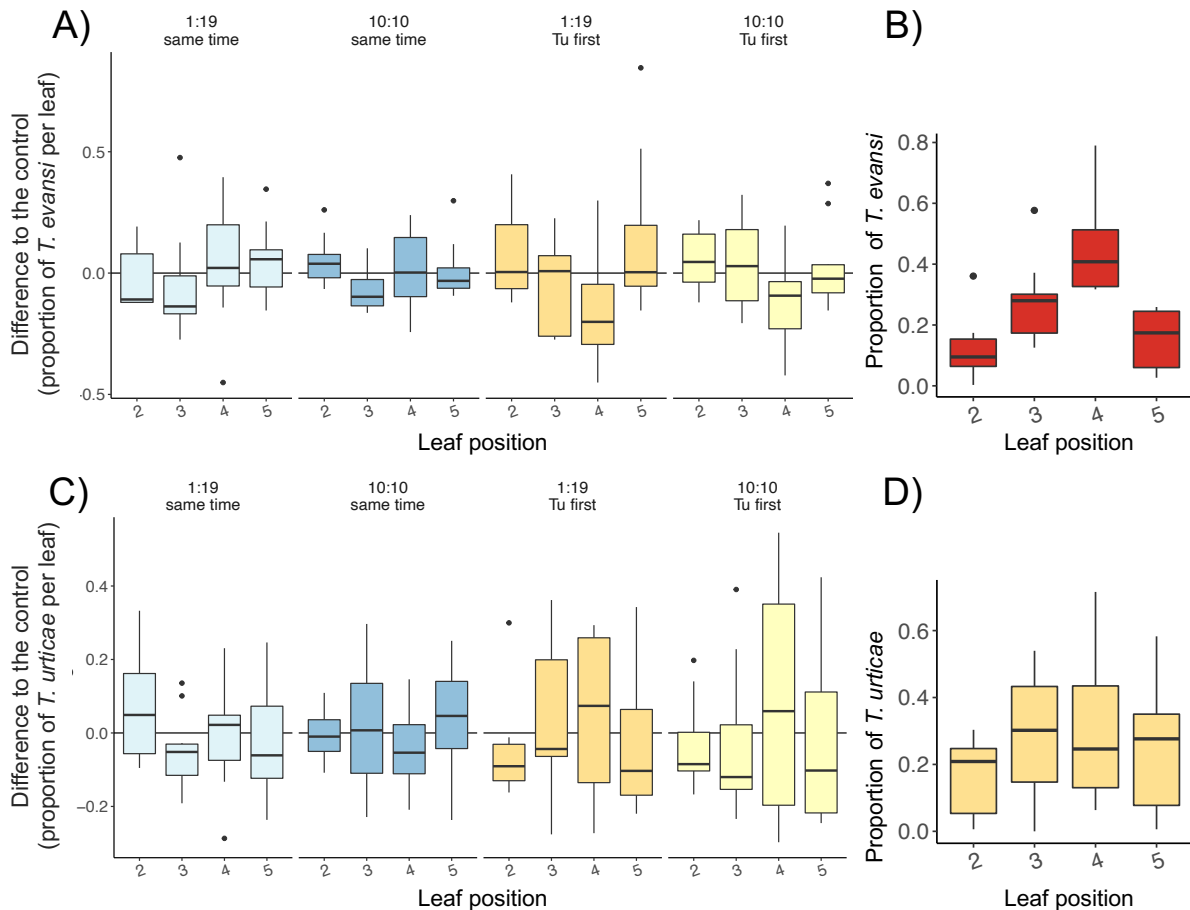
702 only scenario in which species are predicted to coexist is when *T. urticae* arrives first (yellow).

703 Error bars for each outcome indicate the 95% confidence interval from the maximum

704 likelihood estimates. For the other two cases, it is predicted that the superior competitor *T.*

705 *evansi* will exclude *T. urticae*.

706



707

708 Figure 3 – Differences between expected and observed leaf occupancy for *Tetranychus evansi*

709 (A) and *T. urticae* (C) for a subset of the experimental treatments (when *T. urticae* arrived first

710 or at the same time as *T. evansi*, note that Figure S3 includes all treatments); leaf occupancy

711 for *T. evansi* (B) and *T. urticae* (D) in the control, single species, treatments. Leaf 2 corresponds

712 to the oldest leaf and leaf 5 to the youngest. For each box, we calculated for each species the

713 proportion of females occupying each leaf in relation to the total number of females present.

714 For the experimental treatments we calculated the difference between this proportion and the

715 average proportion for the control treatments. Thus, positive values indicate that there are more

716 females on that leaf than expected based on the single-species treatment and negative values

717 indicate the reverse pattern. Overall, we see that *T. evansi* reduces occupancy on leaf 4 when

718 *T. urticae* arrives first and on leaf 3 when the two species arrive at the same time. In contrasts,



719 *T. urticae* shows a slight increase in occupancy of leaf 4 when it arrives first and a slight  
720 decrease in occupancy of leaves 2 and 5.