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## Interaction fidelity is less common than expected in plant-pollinator communities

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2 **Interaction fidelity is less common than expected in plant-pollinator**  
3 **communities**

4  
5 Santiago A. Parra<sup>1\*</sup>, Elisa Thébault<sup>1</sup>, Colin Fontaine<sup>2</sup>, Vasilis Dakos<sup>1,3</sup>

6 **ABSTRACT**

- 7 1. Pairs of plants and pollinators species sometimes consistently interact throughout time and  
8 across space. Such consistency can be interpreted as a sign of interaction fidelity, that is a  
9 consistent interaction between two species when they co-occur in the same place. But how  
10 common interaction fidelity is and what determines interaction fidelity in plant pollinator  
11 communities remain open questions.
- 12 2. We aim to assess how frequent is interaction fidelity between plants and their pollinators and  
13 what drives interaction fidelity across plant-pollinator communities.
- 14 3. Using a dataset of 141 networks around the world, we quantify whether the interaction  
15 between pairs of plant and pollinator species happens more ("interaction fidelity") or less  
16 ("interaction avoidance") often than expected by chance given the structure of the networks  
17 in which they co-occur. We also explore the relationship between interaction fidelity and  
18 species' degree (i.e. number of interactions), and the taxonomy of the species involved in the  
19 interaction.
- 20 4. Our findings reveal that most plant-pollinator interactions do not differ from random  
21 expectations, in other words show neither fidelity nor avoidance. Out of the total 44 814 co-  
22 occurring species pairs we found 7 877 unique pair interactions (18%). Only 551 (7%) of the  
23 7 877 plant-pollinator interactions did show significant interaction fidelity, meaning that  
24 these pairs interact in a consistent and nonrandom way across networks. We also find that 39

25 (0.09%) out of 44 814 plant-pollinator pairs showed significant interaction avoidance. These  
26 results suggest that interactions involving specialist species have a high probability to show  
27 interaction fidelity and a low probability of interaction avoidance. In addition, we find that  
28 particular associations between plant and insect orders, as for example interactions between  
29 Hymenoptera and Fabales showed high fidelity and low avoidance.

30 5. Although niche and neutral processes simultaneously influence patterns of interaction in  
31 ecological communities, our findings suggest that it is rather neutral processes that are  
32 shaping the patterns of interactions in plant-pollinator networks.

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### 45 **KEYWORDS**

46 coevolution, community ecology, interaction turnover, mutualistic interactions, co-occurrence,  
47 pollination networks, specialization

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52 Flowering plants often rely on animal pollination for their reproduction (Willmer, 2011). How  
53 tightly associated are species of plants and pollinators has been a question that has drawn attention  
54 for a long time (Darwin, 1876). An increasing number of studies highlight that interactions between  
55 plants and pollinators greatly vary across space and time (CaraDonna et al., 2017; MacLeod et al.,  
56 2016; Trøjelsgaard et al., 2015). These variations arise because of spatial and temporal turnover in  
57 species composition and also simply because two species do not always interact when they co-occur  
58 (Petanidou et al., 2008; Trøjelsgaard et al., 2015). Understanding what drives the variation in the  
59 interaction between species is an important concern, especially nowadays in the context of global  
60 environmental changes. Climate warming, invasive species, increasing urbanization and agricultural  
61 intensification arise as global pressure on the structure and functioning of plant-pollinator networks  
62 (Bascompte et al., 2019; Emer et al., 2016; Magrach et al., 2017; Trøjelsgaard et al., 2019;  
63 Vanbergen, 2013). Partner fidelity, which corresponds to the tendency for two interacting species  
64 to interact whenever they co-occur (Fortuna et al., 2020) or to the consistency in partner composition  
65 of a given species (MacLeod et al., 2016), may increase species vulnerability to environmental  
66 changes. Indeed, highly fidel species might be less able to change their foraging preferences, i.g. to  
67 re-wire, following a perturbation (Kaiser-Bunbury et al. 2010). Thus, understanding the patterns of  
68 partner fidelity in pollination networks is key if we are to predict the consequences of ongoing  
69 changes in species spatial and temporal distributions on interactions between plants and pollinators  
70 (Redhead et al., 2018; Schleuning et al., 2016).

71 A few recent studies have started to investigate patterns of partner fidelity in plant-pollinator  
72 networks both at the species level, i.e. the consistency in partner composition across space  
73 (Trøjelsgaard et al., 2015; Trøjelsgaard et al., 2019) and time (MacLeod et al., 2016), and at the

74 interaction level, i.e. the consistency in plant-pollinator interactions across networks (Fortuna et al.,  
75 2020) (Table 1). While all these studies revealed the presence of partner fidelity, they also  
76 highlighted very different fidelity degrees, from 27% of bee species with consistent partner choice  
77 in MacLeod et al. (2016) to a probability of partner fidelity of 79% for mutualistic interactions in  
78 Fortuna et al. (2020). However, the factors that determine partner fidelity and its variation among  
79 species and among different communities remain mostly unclear. Studying fidelity at the interaction  
80 level, hereafter interaction fidelity, may clarify what drives it and offers an additional dimension to  
81 partner fidelity studied at species level. Indeed, fidelity degrees may vary greatly among the  
82 interactions of a given species because, for example, some interactions with partners with well-  
83 matched traits might show higher fidelity than interactions with other partners with weaker trait  
84 matching. The opposite side of interaction fidelity is when two species interact less than expected  
85 when they co-occur, hereafter interaction avoidance. Interaction avoidance is related to the classical  
86 notion of forbidden links in pollination networks, that is interactions that do not occur due to  
87 ecological or morphological mismatches between species (Olesen et al., 2011).

88 Different factors are expected to determine patterns of interaction fidelity. First, fidelity might  
89 be related to the species' degree of the interacting species (Trøjelsgaard et al., 2015). Specialist  
90 species are expected to consistently interact with the same few partners throughout their range rather  
91 than with random opportunistic partners due to ecological constraints associated with physiological,  
92 phenological or morphological traits (Cordeiro et al., 2020). On the other hand, generalist species  
93 can have more labile and opportunistic preferences determined by the availability of partner species  
94 and less so by trait matching with interacting partners (Blüthgen et al., 2006; Peralta et al., 2020).  
95 Thus, as partner availability might vary in space, generalists might inconsistently interact with their  
96 partners across space (Waser, 1986). However, as generalist species have more partners, they also  
97 have a greater probability of interacting with any partners wherever they co-occur and so they should

98 show higher interaction fidelity than specialists (Fortuna et al., 2020). Other studies have suggested  
99 that interaction fidelity was independent of whether the species interacted with many or few species  
100 (Benadi et al., 2014; MacLeod et al., 2016). Overall, the links between interaction fidelity and  
101 species' degree remain unclear and need to be better understood.

102 Second, the taxonomy of interacting partners might also affect interaction fidelity. Several  
103 studies have highlighted that interactions between plant and pollinator species are related to their  
104 evolutionary history (Cirtwill et al., 2020; Hutchinson et al., 2017; Rezende et al., 2007), which  
105 could be driven by phenological or morphological matches related to the co-evolutionary dynamics  
106 of interacting species (Thompson, 1999). Thus, particular species groups might interact more often  
107 between them than with others across plant-pollinator networks (Olesen et al., 2007). Interaction  
108 fidelity might thus be related to the phylogeny of interacting partners, and it could also differ among  
109 phylogenetic groups as the strength of phylogenetic signal of species interactions differ among  
110 species groups and clades (Cirtwill et al., 2020; Hutchinson et al., 2017).

111 Third, interactions among species in ecological networks result from niche processes, linked with  
112 morphological and behavioural adaptations of interacting partners, but also from neutral (stochastic)  
113 processes associated with species abundances (Leibold & McPeck, 2006). While interaction fidelity  
114 is expected to originate from niche processes such as trait-matching, neutral processes can also  
115 greatly affect the consistency and rewiring of interaction partners over time and space (CaraDonna  
116 et al., 2017; MacLeod et al., 2016; Petanidou et al., 2008; Vázquez et al., 2009). For instance, some  
117 species might change partners frequently simply as a result of chance due to low sampling and/or  
118 low species abundance, and both rewiring and fidelity have been found less common once the effects  
119 of neutral processes were accounted for (MacLeod et al., 2016). So far, the effects of stochastic  
120 processes on the detection of fidelity patterns in ecological networks have only been considered by  
121 studies focusing on fidelity at species level (MacLeod et al. 2016, Trojelsgaard et al. 2015, 2019).

122 In that case, fidelity is defined as greater consistency in partner choice as compared with  
123 expectations from null models, which are a widespread practice in community ecology to evaluate  
124 the deviation of observed phenomena from random expectations (Gotelli & Graves, 1996; MacLeod  
125 et al., 2016; Veech, 2012). Regarding fidelity at interaction level, it is unknown whether the large  
126 probability of partner fidelity in mutualistic interactions outlined recently by Fortuna et al. (2020)  
127 results mainly from niche processes or could also be explained by neutral processes. Fortuna et al.  
128 (2020) highlighted that generalist species had higher probability of partner fidelity than specialist  
129 species by interacting more frequently with their co-occurring species, which might occur simply  
130 because generalists have more interactions and are often more abundant; they are more prone to  
131 encounter potential interacting partners (Fort et al., 2015). Hence, considering that partner fidelity  
132 could result from neutral processes, it is important to build from the study of Fortuna et al. (2020)  
133 to start disentangling whether the partner fidelity in plant-pollinator interactions is explained by  
134 niche or neutral processes.

135 Here, we assess patterns of interaction fidelity and interaction avoidance in plant-pollinator  
136 communities worldwide, and investigate the relationships between interaction fidelity or interaction  
137 avoidance, and taxonomy and species' degree. We do this by quantifying whether pairs of plant and  
138 pollinator species interact more or less often than expected by chance given the structure of the  
139 networks in which both species co-occur, in order to better account for stochastic (neutral and  
140 sampling) effects. We hypothesize that interaction fidelity depends on the taxonomy of the species,  
141 and we hypothesize that interaction fidelity is negatively related with species' degree as generalist  
142 species might interact in a more random and opportunistic way.

143

144 Table 1. Overview of fidelity related definitions in plant-pollinator communities.

<b>Biological level of organization</b>	<b>Concept</b>	<b>Definition</b>
Individual level	Flower constancy or floral fidelity	Short-term specialization: The tendency of an individual to visit the same plant species as the one last visited in a foraging event. (Brosi, 2016; Cane & Sipes, 2006)
Species level	Species fidelity	Consistency in partner choice across time and/or places. (MacLeod et al., 2016; Trøjelsgaard et al., 2015)
	Species' degree	Measure of interacting partners within a network: i) Qualitative approach: Number of interacting partners that a species has within a network. In other words, the number of pollinator visitors of a plant species and, from the pollinator's perspective, the number of plant species visited. ii) Quantitative approach: Combine the proportion of the interaction with each partner to the overall partner availability. Highly generalist species use resources in proportion to their availability. (Blüthgen et al., 2006)
	Pollen specialization	Pollinator dietary niche breadths defined by pollen host taxa. Three big categories: oligolectic species that gather pollen solely from a few host genera, mesolectic species rely on several genera from the same few families and polylectic species that gather pollen from several families. (Cane & Sipes, 2006)
Interaction level	Interaction fidelity	The consistency in plant-pollinator interactions across networks. (This work; Fortuna et al., 2020)

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## MATERIALS AND METHODS

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### 152 **Dataset**

153 We compiled an extensive database of plant- insect pollinator networks from existing databases  
154 (e.g. Web of Life database) as well as from additional studies published between 1923 and 2019.  
155 The database comprised 87 385 interactions between plants and pollinators embedded in 435  
156 networks that were from different parts of the world. To avoid pseudoreplication, the networks in  
157 close locations from the same study were aggregated, generating 141 aggregate networks (Fig. S1).  
158 In our dataset, we checked different scientific names' spelling and we looked at synonyms in the  
159 names of pollinators and plants through the GBIF database. Also, thanks to studies that have revised  
160 scientific names (Tooker and Hanks 2000; Tooker et al. 2002; Tooker et al. 2006 and Graham et al.  
161 2012), we updated scientific names of ancient networks, as Robertson (1929), in our dataset. We  
162 focused our work on interactions between partners identified at the species-level, with 7 646 insect  
163 pollinators and 5 130 plants identified within the dataset.

164

### 165 **Defining Interaction fidelity and Interaction avoidance**

166 Fidelity at the interaction level has been defined as the tendency for two interacting species to  
167 interact wherever they co-occur (Fortuna et al. 2020) that takes into account the number of networks  
168 in which an interaction was observed and the number of networks in which both species co-occurred.  
169 This definition, however, implicitly assumes that random processes are explaining fidelity along  
170 with other (i.e. niche) processes. To separate fidelity from random processes, we defined here  
171 interaction fidelity as a plant-pollinator interaction that occurs more frequently across different  
172 networks than expected by chance, given the structure of the networks in which the two interacting

173 species co-occur. By analogy, we defined interaction avoidance of a plant-pollinator pair if that pair  
174 interacts fewer times than expected by chance.

175 First, we estimated the observed frequency of interaction of each plant-pollinator pair, that is the  
176 number of networks in which a given interaction is observed divided by the number of networks in  
177 which the corresponding plant and pollinator species co-occur (Fig.1; Fortuna et al., 2020). In our  
178 dataset, we considered plant-pollinator pairs present in at least two networks, which was the case  
179 for 44 814 pairs between 1 519 pollinators and 910 plants. As sampling effort might make more  
180 difficult to assess fidelity for ecologically rare species for which we have less data on their  
181 interactions (MacLeod et al., 2016; Olesen et al., 2011), we evaluated whether species presence and  
182 species co-occurrence across networks affected the ability to detect interaction fidelity or avoidance.  
183 To do so, we included in the analysis the number of networks in which a species is present and the  
184 number of networks in which a plant and pollinator species co-occur. Moreover, as pairs of species  
185 co-occurring in very few networks could lead to a reduced probability of detecting significant  
186 interaction fidelity or avoidance, we tested the robustness of our results removing from the analysis  
187 the species pairs that were present in only two and three networks. The results without pairs present  
188 in two and three networks were consistent with the results including all the species pairs present in  
189 at least two networks (Fig. S2).

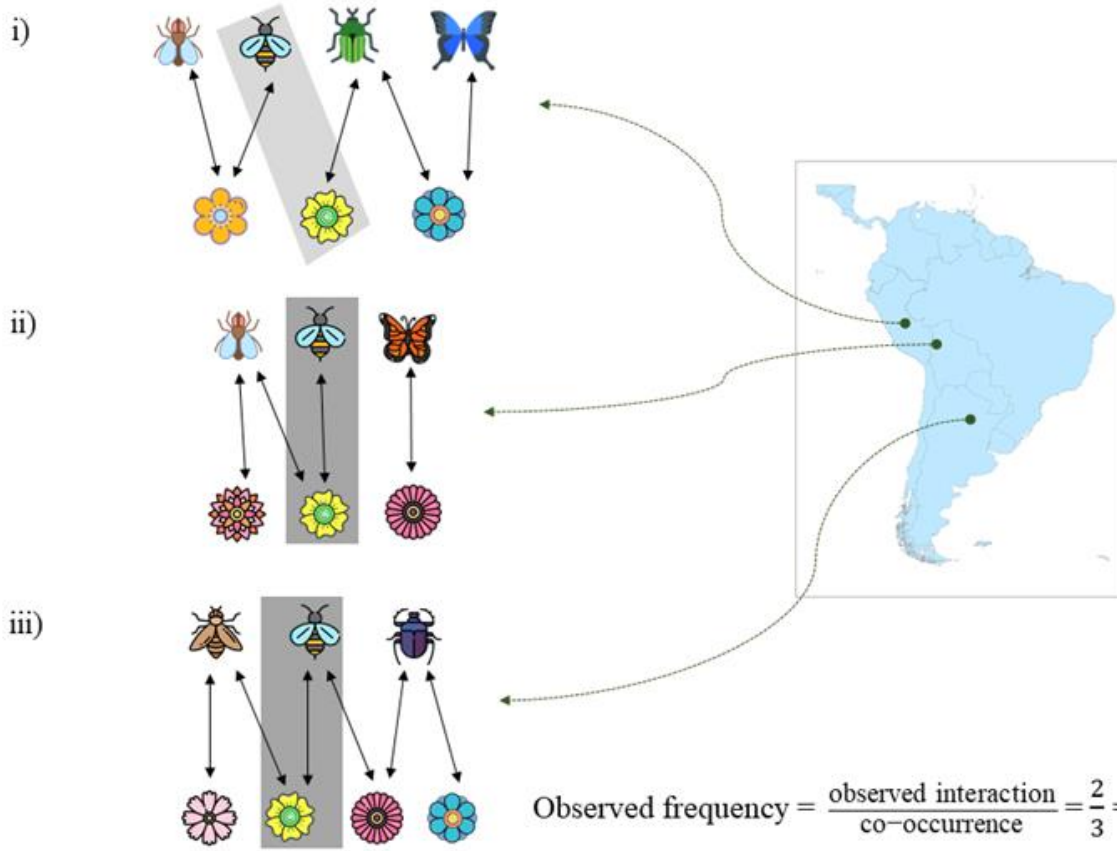
190 Second, to assess whether the observed frequency of interaction of a plant-pollinator pair differed  
191 from random expectations considering networks' structures, we used null models by randomizing  
192 the plant-pollinator networks in which the species pair co-occurred. As the null models allowed to  
193 generate random networks keeping constant the degree distribution of plants and pollinators (i.e.  
194 the number of interactions that a species has to other species within a network), they take into  
195 account that generalist species have greater chance than specialists to interact in the network. Plant-  
196 pollinator networks were arranged in matrices with plant species in rows and pollinator species in

197 columns. In order to keep the degree distribution constant, we preserved rows and columns total in  
198 the randomizations of each network thanks to the algorithms of Miklo and Podani (2004) for binary  
199 matrices. We performed the randomisations using the method *quasiswap* in *Vegan* package for R  
200 statistical software (Oksanen et al., 2019). To compare the observed frequency of interaction with  
201 the expected frequency of interaction for each species pair, we randomized 1000 times the networks  
202 and we generated a null dataset of the 141 networks and their 1000 replicates. For a given plant-  
203 pollinator pair, we picked up the networks in which this pair was present and their respective  
204 replicates, generating a specific set of randomized networks for each pair. Then, for each replication  
205 within this specific set, we divided the number of networks in which the random interaction  
206 happened by the number of networks in which the pair was present, here coined expected frequency  
207 of interaction (Fig.1c). By doing so for the 1000 set of replicates, we generated a null distribution  
208 of the expected frequencies of interaction with 1000 values. The expected frequencies of interaction  
209 had enough variability independent of connectance or plant or pollinator richness of the empirical  
210 networks (Fig. S3).

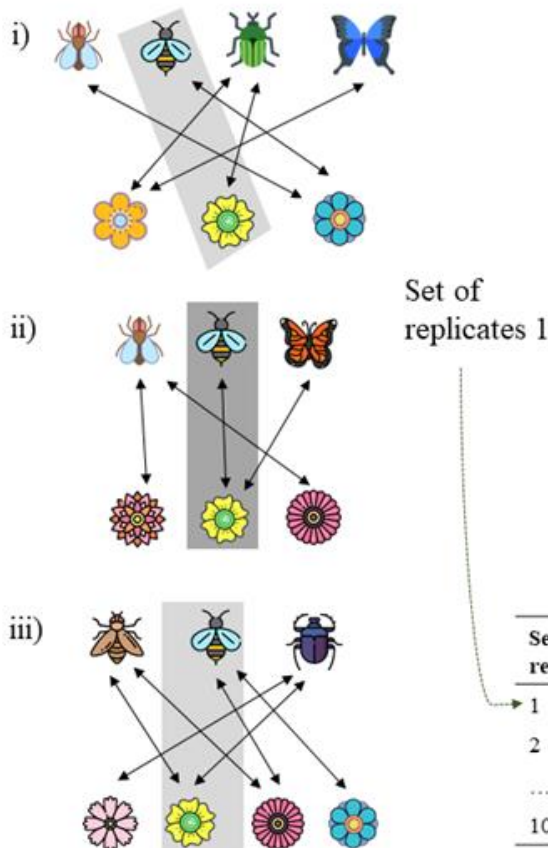
211 To assess whether the studied plant-pollinator pair showed stronger fidelity than expected at  
212 random, we calculated the proportion of values in the null distribution that were equal or greater  
213 than the observed frequency of interaction (proportion (observed  $\leq$  expected values)), hereafter  
214 the *p-value of fidelity*. We did this procedure for plant-pollinator pairs that interact in at least one  
215 network as these were the species pairs that potentially could show interaction fidelity (i.e. 7 877  
216 pairs out of the total 44 814). We then performed a two-tailed test, fixing a significance level at  
217 0.050 and tail cutoff of 0.025 such that interactions with a *p-value of fidelity* less or equal than 0.025  
218 corresponded to species pairs interacting more times than expected by chance and were considered  
219 as showing significant interaction fidelity. To assess whether the species pairs showed stronger  
220 interaction avoidance than expected at random, we calculated the proportion of values in the null

221 distribution that were equal or less than the observed frequency of interaction (proportion  
222 (observed  $\geq$  expected values)), hereafter the *p-value of avoidance*. We did so for all the pairs that  
223 potentially could show avoidance (i.e. all 44 814 pairs of plants and pollinators co-occurring in at  
224 least two networks). Following the two-tailed test, pairs with a *p-value of avoidance* less or equal  
225 than 0.025 corresponded to species pairs interacting fewer times than expected by chance and were  
226 considered as showing significant interaction avoidance.

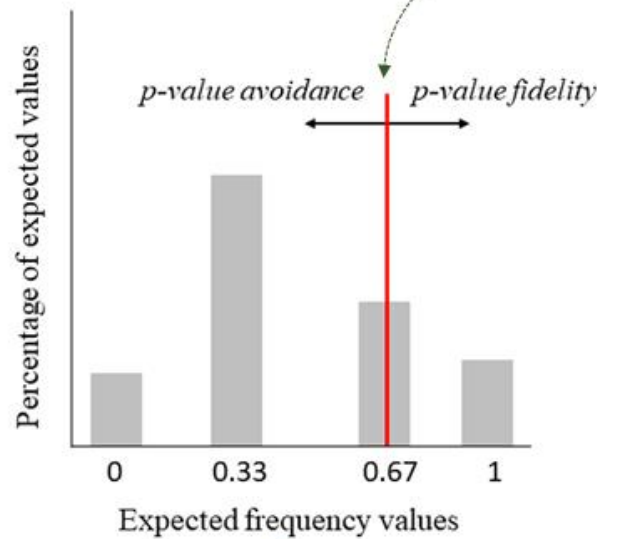
**(a) Observed frequency of interaction**



**(b) Random interaction**



**(c) Null distribution**



Set of replicates	Network i	Network ii	Network iii	Expected frequency
1	0	1	0	0.33
2	1	1	1	1
...	...	...	...	...
1000	0	0	0	0

228 Fig. 1. Quantitatively assessing interaction fidelity and interaction avoidance. Calculation of  
229 interaction fidelity across three hypothetical plant-pollinator networks (a). The pair highlighted in  
230 grey is present in three networks and interacts in two of these networks. The observed frequency of  
231 interaction is the number of networks in which the interaction is observed divided by the number of  
232 networks in which the corresponding plant and pollinator species co-occur (a). In this example, the  
233 observed frequency is  $\frac{2}{3} = 0.67$ . One example set of a randomized three plant-pollinator networks  
234 (b). For each randomization replicate, we divide the number of random interactions by the number  
235 of networks where the species co-occur. By doing so for the 1000 set of replicates, we get 1000  
236 expected frequencies of interactions to generate a null distribution (c). Then, we calculate the  
237 proportion of values in the null distribution that are equal or greater than the observed frequency of  
238 interaction (*p-value of fidelity*) and the proportion of values in the null distribution that are equal or  
239 less than the observed frequency (*p-value of avoidance*)(c). A *p-value of fidelity*  $\leq 0.025$  means a  
240 significantly fidel interaction, while a *p-value of avoidance*  $\leq 0.025$  means a significantly avoided  
241 interaction.

242

### 243 **Statistical analyses**

244 We assessed whether the probability of an interaction to show either significant fidelity or  
245 significant avoidance was related to the taxonomy of the plants and the pollinators, the species  
246 presence, the pair-occurrence and the degree of both plant and pollinator species involved in the  
247 interaction.

248 The taxonomic level analyzed was the pollinator's order and plant's order. The species presence  
249 was the number of networks in which a species was present. We considered the pair co-occurrence  
250 as the number of networks in which the plant and the pollinator co-occur. Finally, we accounted for  
251 the degree of plant and pollinator species (species' degree) as well as of the pair of species that make  
252 up an interaction (link's degree) (Aizen et al., 2012). The normalized degree of a species in a  
253 network was calculated as the number of realized interactions (i.e. degree) of this species divided  
254 by the total number of potential partners in the network. The normalized degree of generalist species

255 is near to one, unlike specialist species which have normalized degrees near to zero. This metric  
256 was calculated for all the networks where a species was present, and we used the median of the  
257 normalized degrees across networks in our statistical models. To calculate the normalized degree of  
258 a link (Aizen et al., 2012), we averaged the median normalized degree of the plant and the pollinator  
259 involved in the interaction. The normalized species degree was calculated using the *Bipartite*  
260 package for R (Dormann et al., 2020).

261 We used the taxonomy, the species presence, pair co-occurrence and species' degree as  
262 explanatory variables to fit two models: one with the probability of an interaction to show *significant*  
263 *fidelity (sf)* as the response variable, and the other with the probability of an interaction to show  
264 *significant avoidance (sa)*. Our two response variables followed a Binomial distribution, therefore,  
265 we used generalized linear models with a Binomial distribution (link = logit). To deal with  
266 imbalanced data among the plant and pollinator orders, in the models of *sf* as response variables,  
267 we filtered out orders that were present less than 300 times in the dataset. Thus, we carried out the  
268 statistical models with 5 744 interactions considering the insect orders of Coleoptera, Diptera,  
269 Hymenoptera and Lepidoptera and the plant orders of Apiales, Asterales, Caryophyllales,  
270 Dipsacales, Fabales, Lamiales, Ranunculales and Rosales. To interpret the relationship between our  
271 response variables and the explanatory quantitative variables, we used beta coefficients standardized  
272 by the standard deviations of predictor and response variables (Bring, 1994).

273 To avoid collinearity in our models, we used a threshold correlation coefficient of  $|r| > 0.7$   
274 between the explanatory variables (Dormann et al., 2013). Among the explanatory variables,  
275 normalized degree (ND) of the link was highly correlated with ND of the pollinator ( $r = 0.78$ ). Thus,  
276 we compared a model with ND of the link to a model with both ND of the pollinator and ND of the  
277 plant (Table S1). We selected the latter model as it was more parsimonious based on the Akaike's  
278 Information Criterion (AIC). Then, we tested whether the relationship between interaction fidelity

279 and ND differed between orders (i.e. whether there is a significant statistical interaction between  
280 ND of the plant or ND of the pollinator and plant or pollinator order) and whether there was an  
281 interaction between the effects of pollinator and plant orders on interaction fidelity. Simplifying the  
282 model when the interactions between explanatory variables were not significant and given that the  
283 Variance Inflation Factor (VIF) (O'brien, 2007) among the remaining quantitative explanatory  
284 variables was lower than three, we excluded the effect of collinearity in the model's results to reach  
285 the following model:

286

287 *significant fidelity (sf) ~ pair co-occurrence + plant presence + pollinator presence +*  
288 *normalized degree of the pollinator + normalized degree of the plant+ plant order \* insect order*  
289 *(model 1)*

290 In order to obtain comparable results between our two models (*sf* and *sa*), we studied the same  
291 quantitative variables and the same plant and insect orders as in the *sf* model. We also excluded the  
292 effect of collinearity in the *sa* model's results. In the *sa* model we considered 32 033 plant-  
293 pollinators pairs and we had to deal with the issue of separation, that is when an explanatory  
294 variable, in our case the interaction between plant and insect orders, perfectly predicts the binary  
295 response variable (Zorn, 2005). Several interactions involving particular pairs of plant and insect  
296 orders never showed significant avoidance. For example, interactions between Coleoptera and  
297 Caryophyllales never showed significant interaction avoidance (Table S3), which meant that the  
298 corresponding binary variable (*sa*) completely belonged to the case *not avoidance* (*sa* = 0). When  
299 this issue of separation occurs, the maximum likelihood estimation might produce infinite  
300 coefficients and standard errors (Zorn, 2005). Thus, we applied the penalized-likelihood method

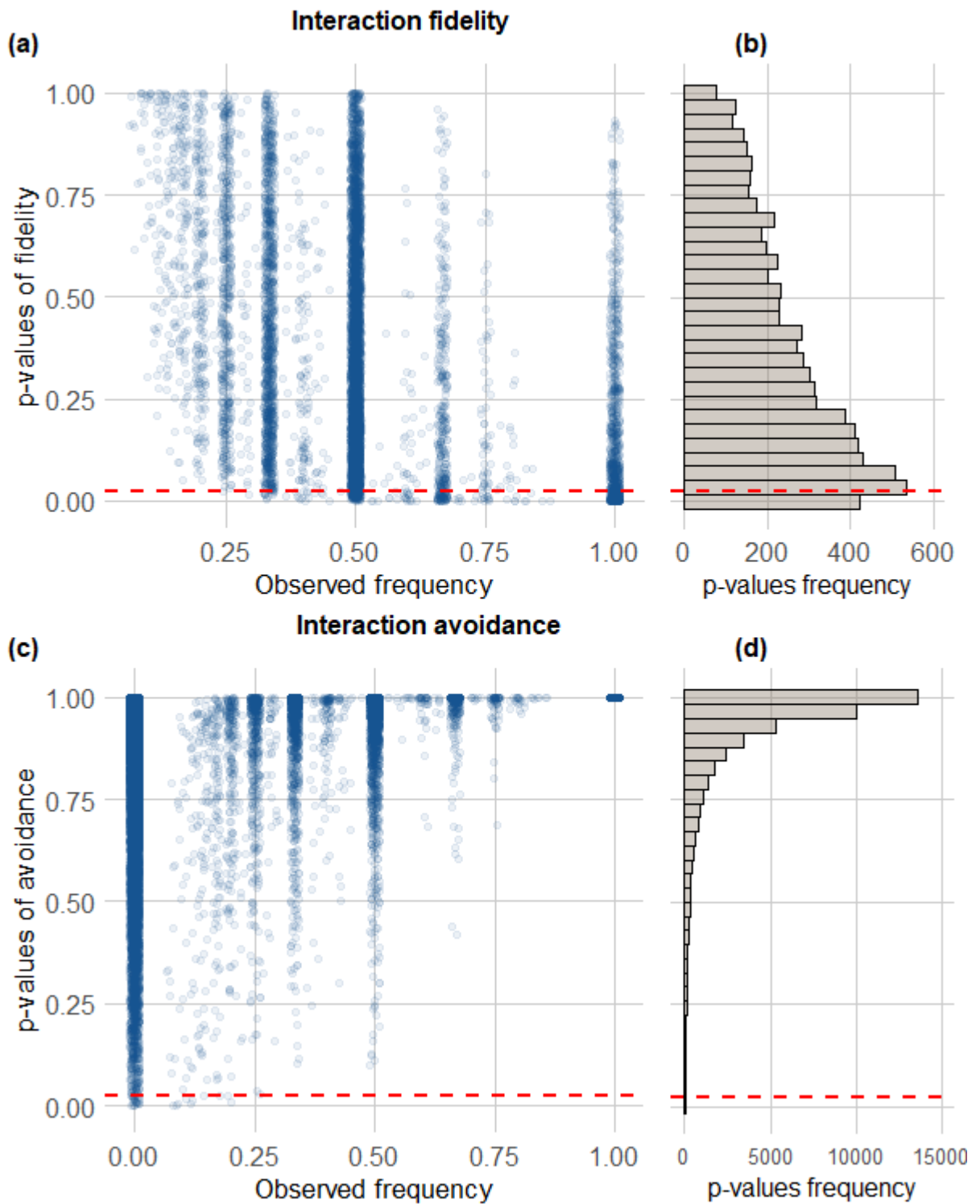


301 using Jeffreys' invariant prior in our generalized linear model (Zorn, 2005) from the package  
302 *Brglm2* in R (Kosmidis, 2020).

303 If the orders had a significant effect on our response variable, we performed a post-hoc test, with  
304 a Bonferroni correction to adjust the p-values, using the *Emmeans* package for R (Lenth et al., 2020).  
305 We made comparisons between insect orders within each plant order and comparisons between  
306 plant orders within each insect order.

## 307 **RESULTS**

308 We found that 551 interactions out of 7 877 interacting pairs showed significant fidelity (7.00%).  
309 Species involved in these interactions interacted significantly more frequently across networks than  
310 expected by chance (Fig. 2a). On the other hand, 39 pairs out of 44 814 showed significant avoidance  
311 (0.09%), meaning that plant-pollinator pairs interacted significantly less often than expected by  
312 chance (Fig. 2c). Whether the p-value was close to zero, either few or none of the 1000 expected  
313 frequencies of interaction were greater than the observed frequency of interaction. Regarding  
314 interaction avoidance, most of the expected frequency values were lower or equal to the observed  
315 frequency of interaction (peak of p-values of avoidance close to one, Fig. 2d).



316

317 Fig. 2. Distribution of observed frequency (i.e. the number of networks in which the interaction  
 318 is observed divided by the number of networks in which the corresponding plant and pollinator  
 319 species co-occur) of 7 877 plant-pollinator pairs, which interact in at least one network (i.e. observed  
 320 frequency  $\neq 0$ ), and the distribution of the p-value of fidelity (i.e. the proportion of expected values

321 equal or greater than the observed (equation 1)). When the observed frequency is high, pairs were  
322 more likely to show significant fidelity (a). Distribution of observed frequency of 44 814 pairs and  
323 the p-value of avoidance. When the observed frequency is low, pairs were more likely to show  
324 significant avoidance. Most of the pairs do not interact in the networks where they co-occurred so  
325 the observed frequency is equal to zero (c). Lower bound ( $p = 0.025$ ) of significance level  
326 represented by dashed red lines (a, b, c, d). None of the species pairs shows at the same time  
327 significant fidelity and avoidance. Peak of the frequency of p-value of fidelity is near zero as most  
328 of the expected frequency values are below the observed frequency of interaction (b). Peak of the  
329 frequency of p-value of avoidance is one, as most of the expected frequency values are equal or  
330 below the observed frequency of interaction (d).

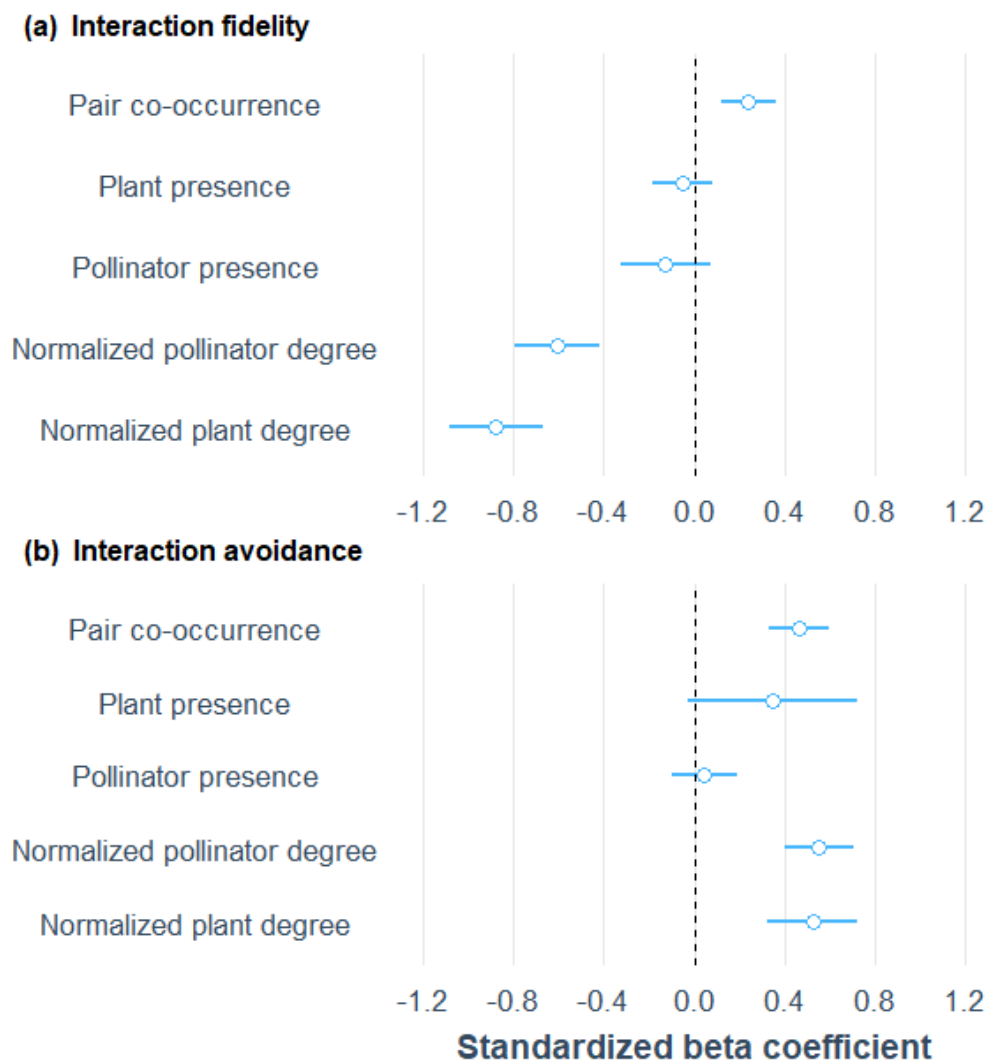
331

332 Most of the pairs were present in two or three networks (Fig. S4). The number of networks in  
333 which both species co-occurred (i.e. pair co-occurrence) was positively and significantly related to  
334 both fidelity (estimate = 0.24 [SE = 0.06];  $p = 0.0001$ ) and avoidance (estimate = 0.47 [SE = 0.07];  
335  $p < 0.0001$ ) (Fig. 3a-b). Thus, interactions between species that co-occurred in more networks  
336 showed more frequently significant fidelity and avoidance. The probability of detecting significant  
337 fidelity and avoidance was very low when the pairs were present in less than 10 networks (Fig. 4c-  
338 f; Fig. S4). Fidelity was not significantly related to the number of networks in which pollinators and  
339 plants were present ( $p > 0.05$ ) (Fig. 3a). Also, avoidance was not significantly related to the presence  
340 of pollinators and plants ( $p > 0.05$ ) (Fig. 3b).

341 Interactions involving pollinators with greater normalized degree showed a lower probability of  
342 significant fidelity (estimate = -0.61 [Standard Error (SE) = 0.10];  $p < 0.0001$ ) (Fig. 3a). Similarly,  
343 interactions involving plants with greater normalized degree showed a lower probability of fidelity  
344 (estimate = -0.88 [SE = 0.10];  $p < 0.0001$ ). In contrast, avoidance was positively related to the  
345 normalized pollinator degree and the normalized plant degree (estimate = 0.55 [SE = 0.08];  $p <$   
346  $0.0001$ , and estimate = 0.52 [SE = 0.10];  $p < 0.0001$ ). In other words, interactions between specialist

347 species tended to show more frequently significant fidelity than interactions involving more  
 348 generalist species, whereas we found the opposite for avoidance. The probability of detecting  
 349 significant fidelity was considerably low when the normalized degree of the species was higher than  
 350 0.2 (Fig. 4a-b), whereas when the normalized degree was higher than 0.4 the probability of  
 351 significant avoidance increases sharply (Fig. 4d-e).

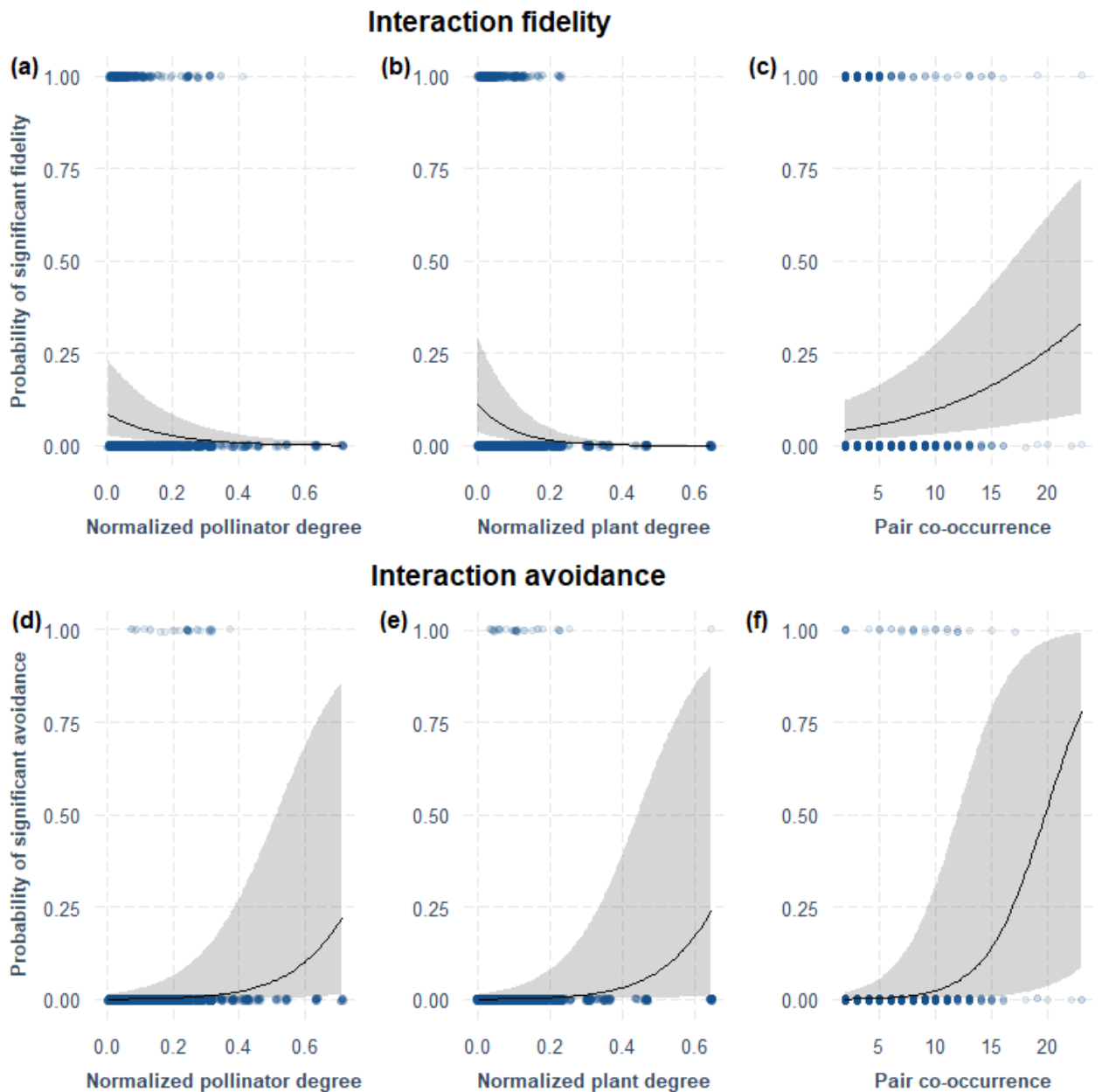
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353

354 Fig. 3. Standardized beta coefficients and their 95% confidence intervals of explanatory  
 355 quantitative variables from the generalized linear model with interaction fidelity as response  
 356 variable (a) and from the generalized linear model with interaction avoidance as response variable

357 (b). The X-axis shows the sign of beta coefficient that indicates the relationship between the  
 358 explanatory variable and the response variable. Confidence intervals not touching the zero line have  
 359 a significant effect on the response variable. Y-axis: Plant and pollinator presence correspond to the  
 360 number of presence of the pollinators or the plants across all networks. Pair co-occurrence  
 361 corresponds to the number of networks in which the plant and the pollinator co-occur. Normalized  
 362 degree is the median of the normalized degree of the plant or the pollinator.



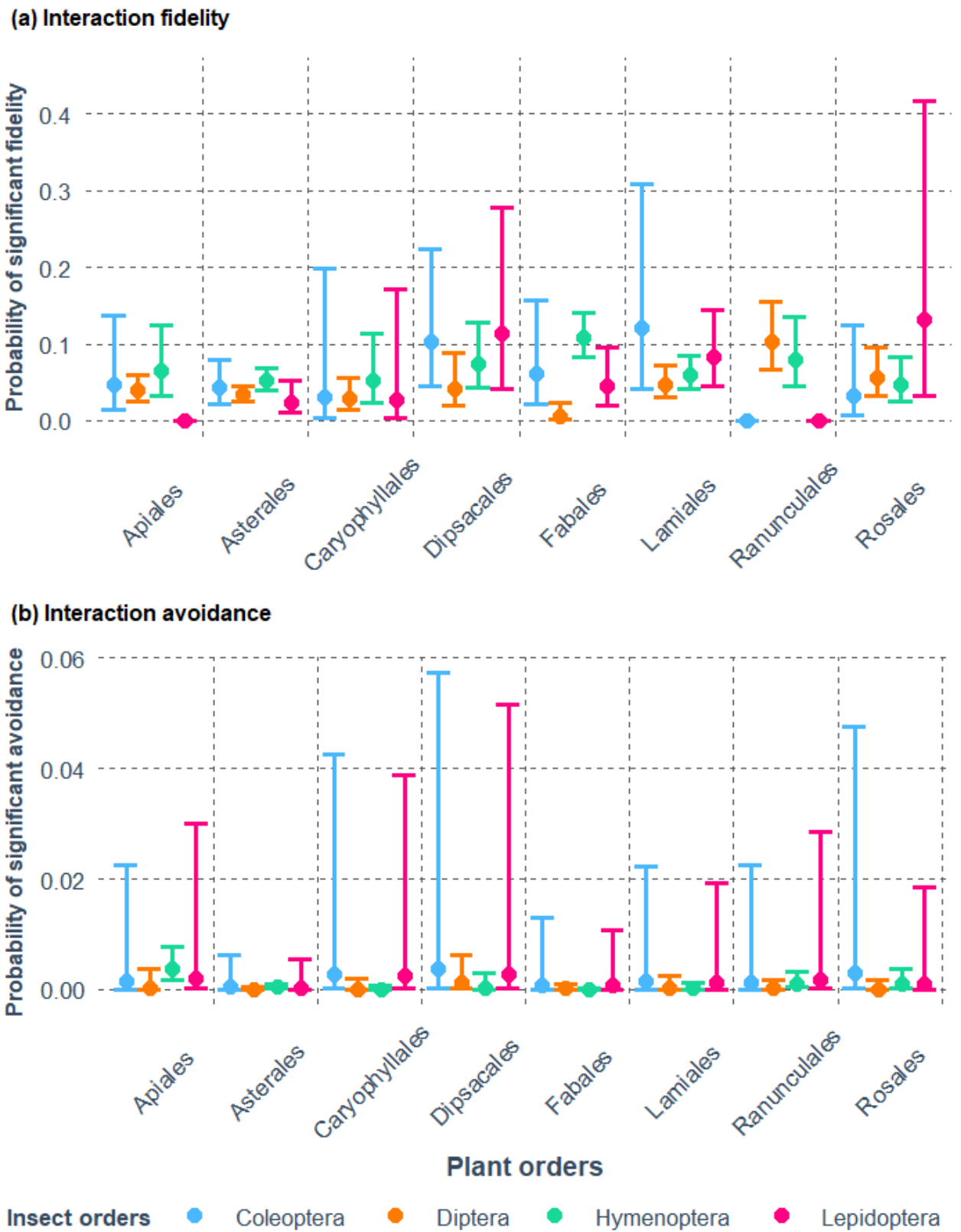
363  
 364 Fig. 4. Effects of normalized degree of the pollinator and the plant on the probability of  
 365 significant fidelity (a, b) and avoidance (d, e) and effects of pair co-occurrence on the probability

366 of significant fidelity (c) and avoidance (f). The black line represents the predicted values from the  
367 generalized linear model with interaction fidelity as response variable (a, b, c) and from the  
368 generalized linear model with interaction avoidance as response variable (d, c, f). The grey area  
369 represents the 95% confidence interval of the predicted values. Blue dots correspond to the response  
370 variables.

371

372 We also found a significant interaction effect of plant and pollinator orders on the probability of  
373 detecting interaction fidelity. This means that some interactions between specific plant and  
374 pollinator orders had higher probability to show significant fidelity than others. Specifically,  
375 interactions between Lepidoptera and Rosales as well as Coleoptera and Lamiales showed the  
376 greatest probability of significant fidelity (Fig. 5a). In contrast, Coleoptera and Ranunculales or  
377 Lepidoptera and Apiales or Ranunculales never showed significant interaction fidelity (Table S2).  
378 The comparison between insect orders within plant orders, from the post-hoc test, pointed out that  
379 within the order Fabales, interactions between Fabales and Diptera had a lower probability to show  
380 fidelity than interactions between Fabales and Coleoptera (Effect Size[ES] = -2.42;  $p = 0.0424$ ) and  
381 than interactions between Fabales and Hymenoptera (ES = -3.05;  $p = 0.0002$ ). The comparison  
382 between plant orders within Diptera highlighted again that pairs between Diptera and Fabales had a  
383 low probability of significant fidelity, these pairs had lower probability to show fidelity than pairs  
384 between Diptera and Ranunculales (ES = -2.99 ;  $p = 0.0026$ ). These latter pairs also had a greater  
385 probability to show significant fidelity than pairs between Diptera and Apiales (ES = 1.04;  $p =$   
386 0.0461) and than between Diptera and Asterales (ES = 1.20;  $p = 0.0012$ ) (Fig. 5a). Within  
387 Hymenoptera, the contrast between plant orders pointed out that pairs between Hymenoptera and  
388 Fabales had a greater probability to show significant fidelity than pairs between Hymenoptera and  
389 Asterales (ES = 0.80;  $p = 0.0021$ ).

390 Certain pollinator orders never showed avoidance, as for example pairs involving Lepidoptera  
391 (Table S3). Whereas pairs between Hymenoptera and Apiales showed the greatest probability of  
392 avoidance (Fig. 5b). Apiales showed greater probability of significant avoidance than Asterales (ES  
393 = 2.16;  $p = 0.0006$ ), than Caryophyllales (ES = 3.99;  $p = 0.0466$ ), than Fabales (ES = 5.24;  $p =$   
394 0.0009) and than Lamiales (ES = 2.95;  $p = 0.0421$ ) in their interaction with Hymenoptera. Besides,  
395 interactions between Hymenoptera and Ranunculales had a greater probability to show avoidance  
396 than interactions between Hymenoptera and Fabales (ES = 4.00;  $p = 0.0475$ ).



397

398

399

Fig. 5. Probability of significant fidelity (a) and significant avoidance (b) with 95% confidence interval of the interactions between insect and plant orders. Four different colours represent the four



400 insect orders (Coleoptera = light blue, Diptera = orange, Hymenoptera = green, Lepidoptera = pink)  
401 and their interaction with the eight plant orders.

402

403

## DISCUSSION

404 Our analysis of 141 plant pollinator networks worldwide reveals that, overall, the 7 817  
405 interacting pairs do not differ from random expectations as about 7% of pair interactions show  
406 significant fidelity and only less than 0.1% out of the 44 814 plant-pollinator co-occurring pairs  
407 show significant avoidance when compared to null model expectations. While specialist species  
408 show more fidelity in their interactions, interaction avoidance is mostly detected for generalist  
409 species. These interacting patterns are probably due to specialist species, with more fixed  
410 preferences, consistently interacting with the same few partners throughout their range while  
411 generalist species might have more opportunistic and labile preferences (Blüthgen et al., 2006;  
412 Cordeiro et al., 2020; Waser, 1986). Interestingly, however, generalist species have a higher  
413 probability of avoidance (Fig. 4). Our results highlight the importance of the taxonomy of plant and  
414 pollinator interacting partners as some combinations of plant and pollinator orders show distinctive  
415 patterns of avoidance and fidelity.

416 While our results still support the presence of interaction fidelity across space as found by  
417 previous studies, we report lower levels of fidelity than previously found. Trøjelsgaard et al. (2015),  
418 assessing the consistency in partner choice across geographically close networks, highlighted that  
419 about 50% of the pollinators (25 of 48) and most of the plants (18 of 19) showed partner fidelity  
420 across sites. MacLeod et al. (2016) working at the species level across 3 years in an experimental  
421 array found that 27% of bee species (14 of 52) showed consistency in partner choice over time. Part  
422 of the discrepancy with these studies lies in the fact that we studied fidelity at the level of the  
423 interaction instead of the level of species (Table 1). Moreover, the spatial scale of these studies is

424 much more restricted than the worldwide approach we present. Our approach includes networks  
425 from different environmental and community contexts that could lead to a greater variability on the  
426 realization of an interaction of a given plant-pollinator pair and the overall low interaction fidelity  
427 we observed across networks.

428 Similarly, we report much lower fidelity compared to the 79% found by Fortuna et al. (2020)  
429 who worked at the same interaction level as ours across 102 mutualistic networks that included 68  
430 plant-pollinator and 34 plant seed-disperser networks. The difference lies in the definition of  
431 interaction fidelity quantified as the probability for two species to interact wherever they co-occur  
432 (Fortuna et al. 2020). Although this is a valid definition, here we postulate that by comparing the  
433 observed frequency of interaction to a null model expectation enables us to test for other than  
434 random processes in the probability of interaction between a pair of species. Inevitably under this  
435 definition the number of interactions exhibiting fidelity naturally reduces.

436 Yet, perhaps the most striking result is that we found a considerably reduced number of fidel  
437 interactions as well as a very low number (0.09%) of species pairs showing interaction avoidance.  
438 In community ecology both niche and neutral processes influence patterns of interaction in  
439 ecological networks (Leibold & McPeck, 2006). In niche processes, species' features modulate the  
440 interactions in ecological networks (MacLeod et al., 2016; Sazatornil et al., 2016; Vizentin-Bugoni  
441 et al., 2018). Thus, niche processes, like phenological or morphological matches between species,  
442 could be modulating the significant interaction fidelity that we found here but equally so the  
443 interaction avoidance. Our concept of interaction avoidance is closely related to the forbidden links  
444 hypothesis. Although in our case the plant-pollinator pairs involved in interaction avoidance could  
445 interact or not (i.e. the interaction is not fully forbidden), they interact fewer times than would be  
446 expected by chance. Still the number of interaction avoidance we report appears very low (39 out  
447 of 44 814 plant-pollinator pairs). The forbidden links hypothesis posits that unobserved interactions

448 are driven by species' biological traits that constrain interactions by means of mismatches on  
449 ecological and morphological traits of species, such as phenological uncoupling or size constraints  
450 (Jordano, Bascompte, & Olesen, 2003; Olesen et al., 2011; Vizentin-Bugoni et al., 2018). At the  
451 same time, in neutral processes, species are ecologically equivalent, and species might interact  
452 randomly in the community depending on local species abundances (Petanidou et al., 2008; Vázquez  
453 et al., 2009). These neutral processes could be explaining the remaining 92.91% of plant-pollinator  
454 interactions (Fig. 2), since their interacting patterns do not differ from random expectations  
455 considering network structure. This is especially true in the case of pairs with unobserved  
456 interactions, as few of these pairs show interaction avoidance. Hence, the unobserved links could  
457 be related to the low species abundance as ecologically rare species might have a low probability of  
458 encounter between them (Canard et al., 2012).

459 The low levels of interaction fidelity and avoidance we found might also partly arise from a  
460 failure to reject the null hypothesis (i.e. no fidelity nor avoidance) as a result of insufficient sample  
461 sizes and associated low statistical power. Indeed, the positive relations between the number of  
462 networks in which species pair co-occurred and both interaction fidelity and avoidance suggest that  
463 the less co-occurrence, the less power to detect interaction fidelity and avoidance (Fig. 4). The  
464 standard deviations of expected frequencies from the null models show an important heterogeneity  
465 for pairs co-occurring in very few networks with high standard deviations denoting reduced ability  
466 to detect significant fidelity and avoidance in these cases (Fig. S5). However, significant fidelity  
467 can still be detectable even in pairs present in only very few networks as exemplified by the presence  
468 of significant interaction fidelity for pairs present in only two or three networks (Fig. S4). More  
469 importantly, when we remove pairs which are present in only two or three networks, we do not find  
470 strong differences in our results for fidelity and avoidance (compare Fig. 3 and Fig. S2), suggesting  
471 that our results are not driven by cases with very low detection power.

472 The relations between species degree and fidelity and avoidance might also partly arise from  
473 differences in statistical power for specialist and generalist species. By focusing on the species level,  
474 MacLeod et al. (2016) showed that significant fidelity was more easily detected at small to moderate  
475 species abundance and significant rewiring at large abundance. Since generalism is often strongly  
476 correlated to abundance (Fort et al. 2016), the positive relations between specialism and fidelity and  
477 between generalism and avoidance that we found might thus also result from statistical power issues.  
478 Indeed, the species' degree is positively correlated to both the mean and the standard deviation of  
479 expected frequencies of interaction (Fig. S6), meaning that interaction fidelity might be more  
480 difficult to detect for generalist whereas it is the opposite for specialist. However, it should be noted  
481 that in our case these correlations are rather weak (Fig. S6), and it is unclear whether these are  
482 enough to generate our findings. Whether there is an artifactual or ecologically driven relationship  
483 between interaction fidelity and species' degree thus remains an open question. Better  
484 acknowledging the effects of sampling and statistical power for detecting interaction patterns across  
485 networks arise as an important future perspective of this type of studies.

486 Despite low levels of significant fidelity and avoidance, and even though we are working at the  
487 order level, that is a high hierarchy of biological classification, we find significant associations  
488 between plant and insect orders, for either fidelity or avoidance. Particular associations between  
489 orders might be the result of co-evolutionary dynamics of co-occurring species (Olesen et al., 2007;  
490 Thompson, 1999). As a result, particular plant and pollinator orders interact more often between  
491 them than with other orders across ecological networks (Cordeiro et al., 2020; Olesen et al., 2007).  
492 The significant associations between particular plant and pollinator orders can be related to what is  
493 known in the natural history and ecology of pollination. A broad overview of pollination patterns  
494 of these orders highlights that Lamiales, Fabaceas, and Dipsacales show relatively high interaction  
495 fidelity with Coleoptera which might be linked to Coleoptera's preferences for scented flowers

496 arranged in racemes, terminal inflorescence or dense clusters such as pea-like flowers (Willmer,  
497 2011). Among Diptera, interactions between Diptera and Fabales show low fidelity. Such  
498 interacting patterns might be related to Fabaceae's long corolla tubes and hidden nectar, while the  
499 myophily pollination syndrome is linked with generalist and short-tongued flies (Willmer, 2011).  
500 Meanwhile, the relationship between Diptera and Ranunculales show a high probability of fidelity  
501 (Fig. 5). This association might be related to the fact that in our dataset there are hoverflies  
502 (Syrphidae) described as specialist and constant flies that are good pollinators of Ranunculaceae  
503 among other plant families (Willmer, 2011). As some Ranunculaceae's plants have bowl and disc  
504 flowers and also do solar tracking (flower heliotropism), they can absorb radiation and reach greater  
505 temperatures (Luzar & Gottsberger, 2001). In cold habitats, Ranunculaceae are usually visited by  
506 hoverflies, since these plants provide, besides nectar and pollen, heat reward for pollinators (Luzar  
507 & Gottsberger, 2001; Stanton & Galen, 1989). Regarding Hymenoptera, bees and bumblebees  
508 usually visit zygomorphic tubular flowers such as Fabaceae (Goulson et al., 2008), which is  
509 reflected in high fidelity and low avoidance between Hymenoptera and Fabales orders (Fig. 5).  
510 However, the orders' associations should be interpreted with caution as bumblebees also often  
511 pollinate Ranunculaceae (Willmer, 2011), but in contrast our results point out a relatively high  
512 probability of avoidance between Hymenoptera and Ranunculales orders (Fig. 5). Probably other  
513 groups of Hymenoptera are driving this orders' association.

514       Nonetheless, the heterogeneity within plant and pollinator orders we report suggests that it might  
515 be fruitful to dig deeper in the taxonomical associations found. It will be a step forward to work at  
516 the family or genus level to test which are the underlying morphological traits or phenological  
517 overlap that are behind the orders' association in the probability of significant fidelity or avoidance.  
518 Future work should also take into account the intra-specific variation in partner choice across space  
519 and time as some species could show generalist behaviour in one location and specialist in another,

520 or being specialists in the short-term and generalists over a long-term period (Brosi, 2016; Petanidou  
521 et al., 2008). Behind the intra-specific variation can lie the community context in which species are  
522 embedded, since the dietary niche breadth of a pollinator can be mediated by competition. For  
523 example, interspecific competition can reduce the niche breadth of a given pollinator, which in turn  
524 may positively affect interaction fidelity of this pollinator (Brosi, 2016). Assessing the relationship  
525 between interaction fidelity and avoidance in mutualistic interactions and competition could shed  
526 light upon the underlying drivers shaping the structure of ecological communities and their response  
527 to global anthropogenic change.

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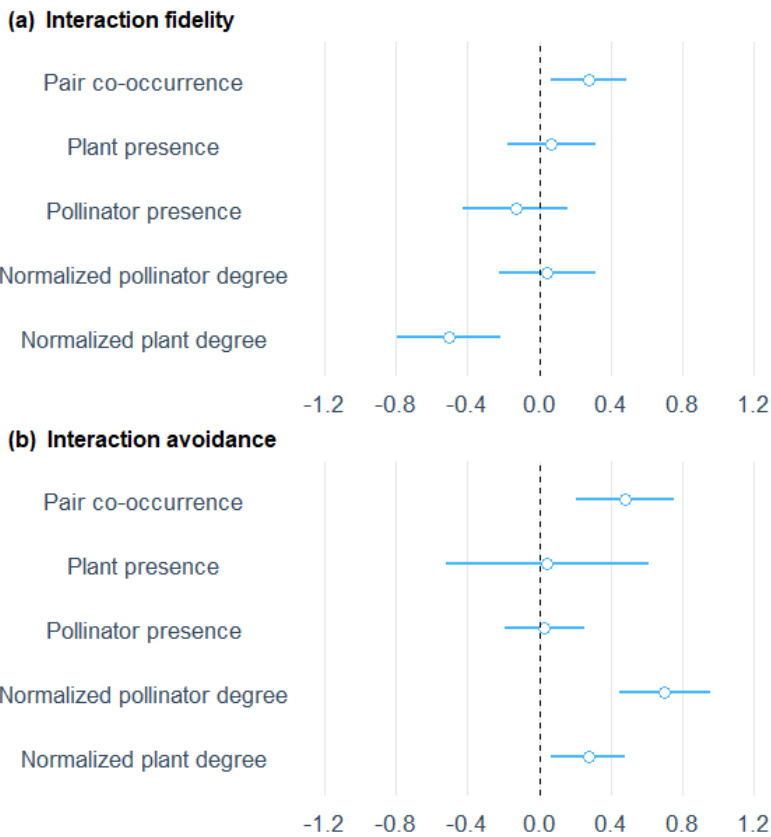
### SUPPORTING INFORMATION

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530

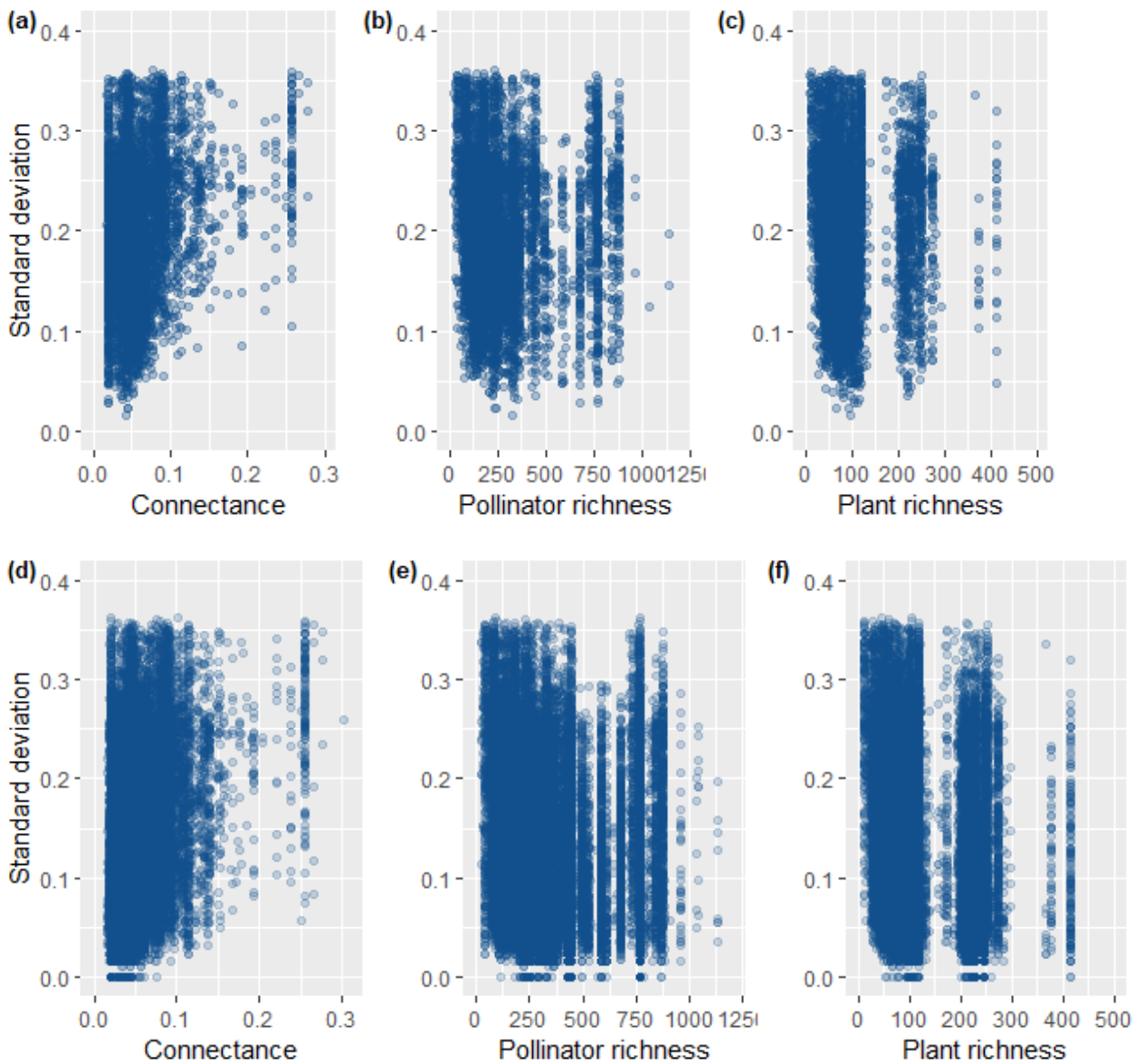
531 Fig. S1: Geographical distribution of the 141 aggregate plant-pollinator networks analysed in our  
532 study.



533

534 Fig. S2: Species pairs co-occurring in very few networks could lead to a reduced probability of  
 535 detecting significant interaction fidelity or avoidance because there are less possibilities in the null  
 536 distribution. Subsequently, it is more possible in the randomisations to obtain expected values equal  
 537 or close to the observed frequency of interaction, outputting an insignificant p-value. We tested the  
 538 robustness of our results removing from the analysis the species pairs that were present in only two  
 539 and three networks. Standardized beta coefficients and their 95% confidence intervals of  
 540 explanatory variables from the new generalized linear models (GLM) with interaction fidelity as  
 541 response variable (a) and with interaction avoidance as response variable (b). We present results  
 542 without pairs present in only two and three networks.

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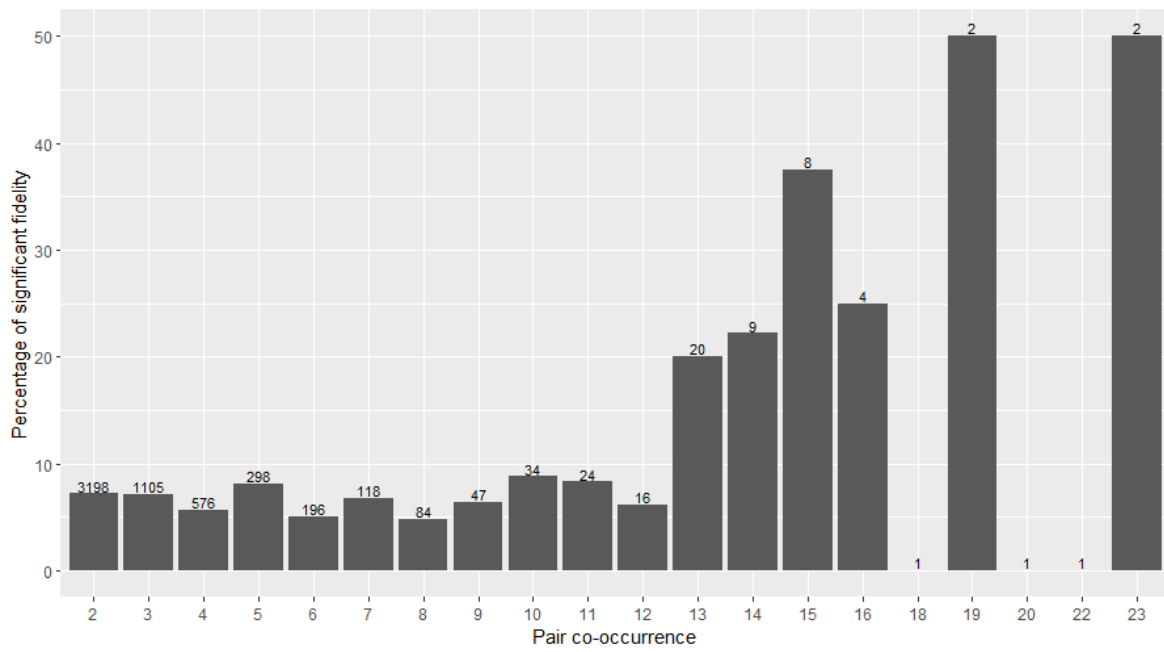
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546 Fig. S3: Standard deviation of expected frequency of interaction of each plant-pollinator pair  
 547 derived from the null set of networks created by the swap algorithm in relation to median  
 548 connectance, median pollinator richness and median plant richness of the empirical networks in  
 549 which the pairs are present. Panel a,b,c correspond to interactions considered in the model of fidelity  
 550 and panel d, e, f correspond to interactions considered in the model of avoidance .We find that the  
 551 swap model creates enough variability (SD far from zero in most of the cases) that is only weakly  
 552 correlated to connectance (Spearman coefficient: 0.17 and 0.31) (a-d) and pollinator (Spearman  
 553 coefficient: -0.03 and -0.20) (b-e) or plant richness (Spearman coefficient: 0.01 and -0.22) (c-f).

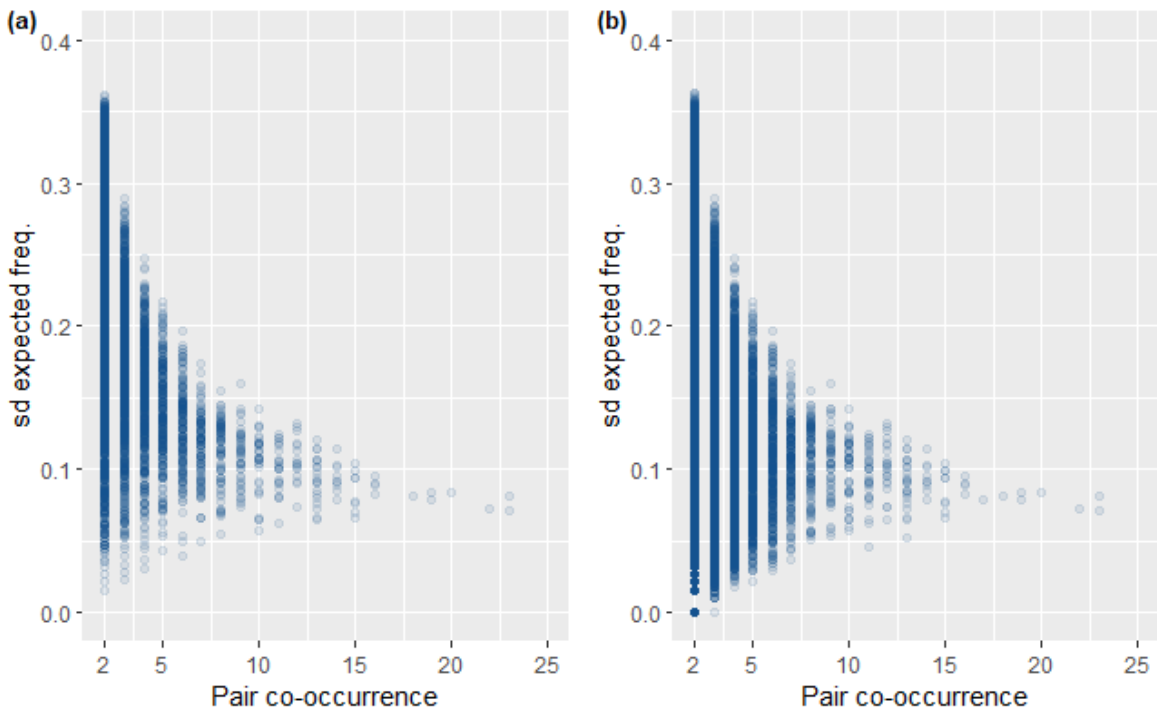
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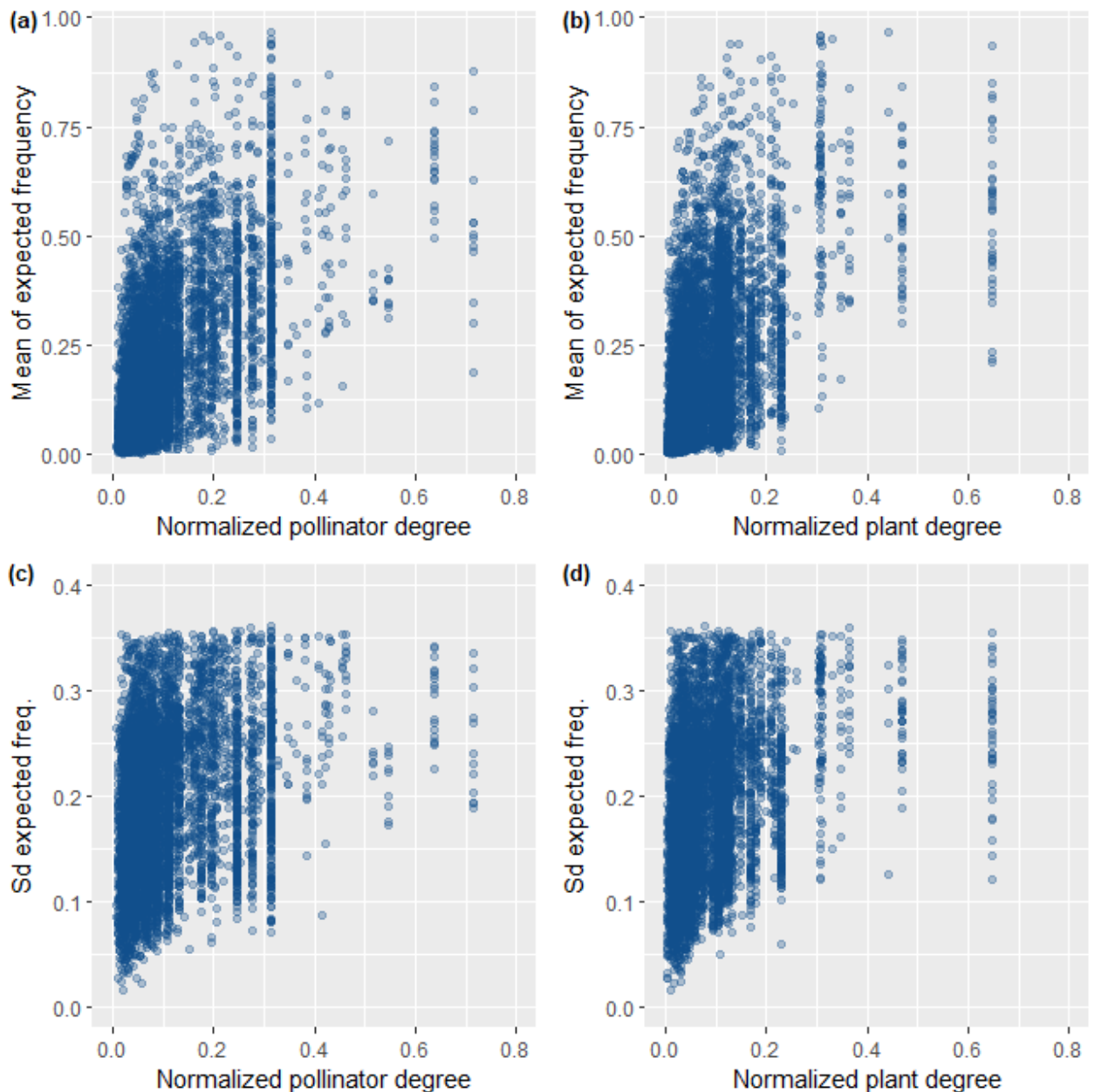
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556 Fig. S4: Percentage is the ratio between the pair showing significant fidelity and the total number  
 557 of pairs of given co-occurrence (i.e., number of networks in which a plant-pollinator pair is present).  
 558 In the top of each bar, it is indicated the total number of plant-pollinator pairs with a given co-  
 559 occurrence.



560

561 Fig. S5: Standard deviation of expected frequency of interactions considered in the model of  
 562 fidelity (a) and avoidance (b) and pair co-occurrence (Spearman coefficient: -0.58 and -0.03,  
 563 respectively).



564  
 565 Fig. S6: Mean expected frequency of interactions considered in the model of fidelity and degree of  
 566 the pollinator (a) and of the plant (b) ( $r = 0.55$  and  $r = 0.45$ , respectively). Standard deviation of  
 567 expected frequency of interaction and degree of the pollinator (c) and of the plant (d) ( $r = 0.34$  and  
 568  $r = 0.32$ , respectively). In the case of interaction avoidance, the mean is also positively correlated to  
 569 the degree of the pollinator or the plant ( $r = 0.55$  and  $r = 0.57$ , respectively), while the correlations

570 between deviation and pollinator or plant degree are slightly stronger ( $r = 0.50$  and  $r = 0.55$ ,  
 571 respectively).

572 Table S1. Model of Interaction Fidelity. Correlation matrix of quantitative explanatory variables.

	Pair co-occurrence	Normalized link degree	Normalized pollinator degree	Normalized plant degree	Pollinator presence	Plant presence
Pair co-occurrence	1					
Normalized link degree	0.00	1				
Normalized pollinator degree	0.05	0.78	1			
Normalized plant degree	-0.05	0.66	0.04	1		
Pollinator presence	0.24	0.29	0.46	-0.09	1	
Plant presence	0.46	-0.14	-0.17	-0.02	-0.11	1

573

574 **Appendix S1. GLModel of Interaction Fidelity**

- 575 ● Null deviance: 2949.5 on 5743 degrees of freedom
- 576 ● Residual deviance: 2671.4 on 5707 degrees of freedom
- 577 ● AIC: 2745.4

578

579 **Table S2. Fidelity and species' orders**

580 Fidelity between plant-pollinator orders: Interaction fidelity between plant-pollinator orders: Total  
 581 (T) numbers of pairs of a given insect and plant orders, number of and percentage of pairs  
 582 showing significant fidelity (sf).

583

	Coleoptera	Diptera	Hymenoptera	Lepidoptera	Total plant orders

	T	sf	%	T	sf	%	T	sf	%	T	sf	%	T	sf	%
Apiales	50	3	6	377	22	5.8	107	8	7.5	16	0	0.0	550	33	6.0
Asterales	144	10	6.9	927	46	5.0	913	56	6.1	177	6	3.4	2161	118	5.5
Caryophyllales	14	1	7.1	187	8	4.3	126	6	4.8	27	1	3.7	354	16	4.5
Dipsacales	33	6	18.2	109	7	6.4	136	13	9.6	28	4	14.3	306	30	9.8
Fabales	37	4	10.8	143	2	1.4	440	68	15.5	77	7	9.1	697	81	11.6
Lamiales	16	4	25.0	242	22	9.1	454	32	7.0	91	12	13.2	803	70	8.7
Ranunculales	23	0	0.0	236	20	8.5	167	13	7.8	17	0	0.0	443	33	7.4
Rosales	38	2	5.3	188	13	6.9	183	11	6.0	21	2	9.5	430	28	6.5
Total insect orders	355	30	8.5	2409	140	5.8	2526	207	8.2	454	32	7.0	5744	409	7.1

584

585

586

587

588 **Appendix S2. GLModel of Interaction Avoidance**

- 589 ● Null deviance: 547.31 on 32032 degrees of freedom
- 590 ● Residual deviance: 312.50 on 31996 degrees of freedom
- 591 ● AIC: 386.5

592

593 **Table S3. Interaction Avoidance and species' orders**

594 Interaction avoidance between plant-pollinator orders: Total numbers of pairs of a given insect  
595 and plant orders, number of and percentage of pairs showing significant avoidance (sa).

596

	Coleoptera			Diptera			Hymenoptera			Lepidoptera			Total plant orders		
	T	sf	%	T	sf	%	T	sf	%	T	sf	%	T	sf	%
Apiales	314	0	0	1373	0	0	1002	9	0.9	213	0	0	2902	9	0.31

Asterales	812	0	0	4063	1	0.02	4073	11	0.27	718	0	0	9666	12	0.12
Caryophyllales	349	0	0	1142	0	0	955	1	0.1	226	0	0	2672	1	0.04
Dipsacales	193	0	0	599	1	0.17	718	0	0	109	0	0	1619	1	0.06
Fabales	441	0	0	1880	3	0.16	1974	1	0.05	456	0	0	4751	4	0.08
Lamiales	505	0	0	2394	0	0	2351	1	0.04	482	0	0	5732	1	0.02
Ranunculales	190	0	0	1105	0	0	837	5	0.6	140	0	0	2272	5	0.22
Rosales	274	0	0	994	0	0	992	2	0.2	159	0	0	2419	2	0.08
Total insect orders	3078	0	0	13550	5	0.35	12902	30	2.16	2503	0	0	32033	35	0.11

597

598

#### DATA AVAILABILITY STATEMENT

599 We intend to archive our dataset in the digital repository Zenodo (<https://zenodo.org/>) upon  
600 acceptance of the manuscript.

601

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