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

Santiago A. Parra^{1*}, Elisa Thébault¹, Colin Fontaine², Vasilis Dakos^{1,3}

ABSTRACT

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

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

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

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KEYWORDS

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

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

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

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

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

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

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

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

Biological level of organization	Concept	Definition
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

Dataset

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

Defining Interaction fidelity and Interaction avoidance

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

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

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

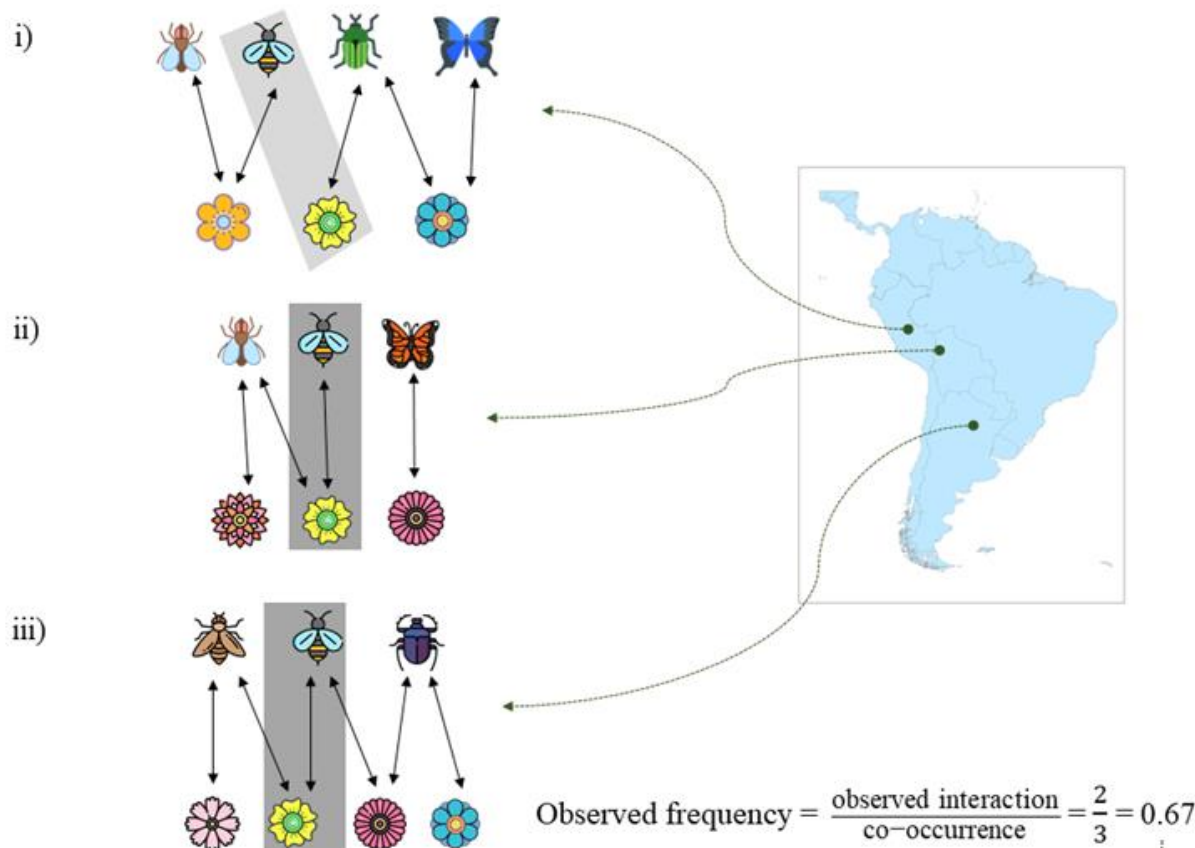
Second, to assess whether the observed frequency of interaction of a plant-pollinator pair differed from random expectations considering networks' structures, we used null models by randomizing the plant-pollinator networks in which the species pair co-occurred. As the null models allowed to generate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

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

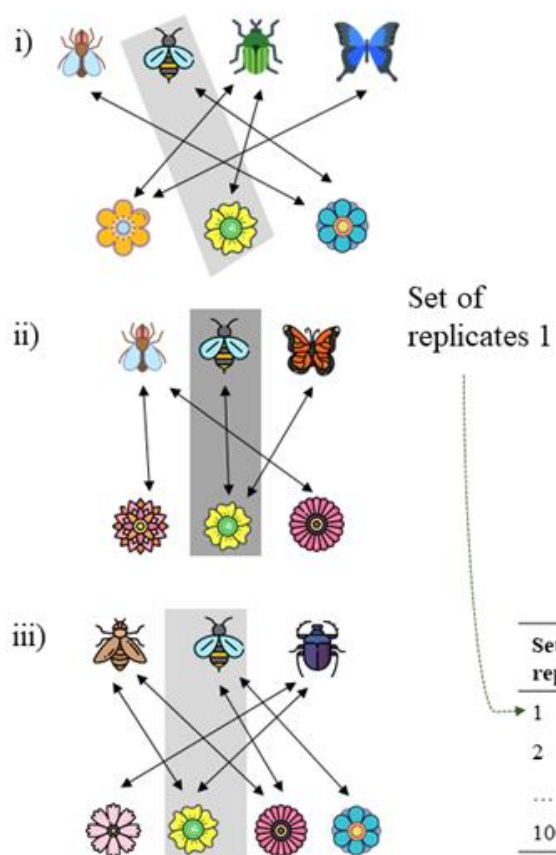
To assess whether the studied plant-pollinator pair showed stronger fidelity than expected at random, we calculated the proportion of values in the null distribution that were equal or greater than the observed frequency of interaction (proportion (observed \leq expected values)), hereafter the *p-value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

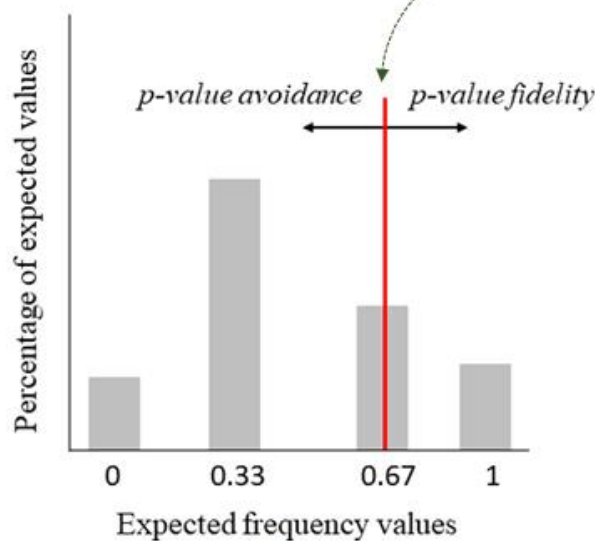
(a) Observed frequency of interaction



(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

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

Statistical analyses

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

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

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

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

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

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

$$\begin{aligned} \text{significant fidelity (sf)} \sim & \text{pair co-occurrence} + \text{plant presence} + \text{pollinator presence} + \\ & \text{normalized degree of the pollinator} + \text{normalized degree of the plant} + \text{plant order} * \text{insect order} \\ & (\text{model 1}) \end{aligned}$$

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

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

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

RESULTS

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

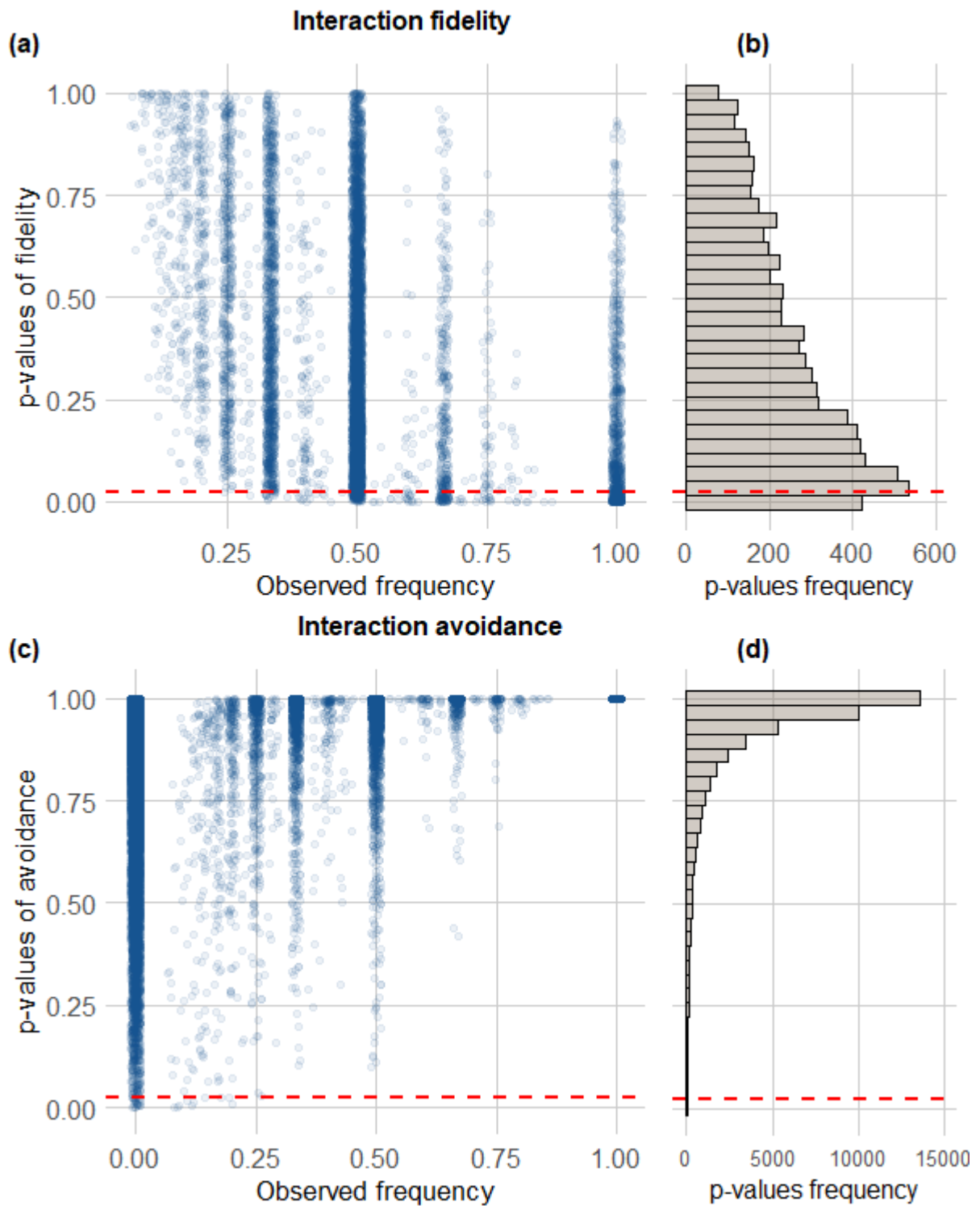


Fig. 2. Distribution of observed frequency (i.e. the number of networks in which the interaction is observed divided by the number of networks in which the corresponding plant and pollinator species co-occur) of 7 877 plant-pollinator pairs, which interact in at least one network (i.e. observed frequency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

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

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

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

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

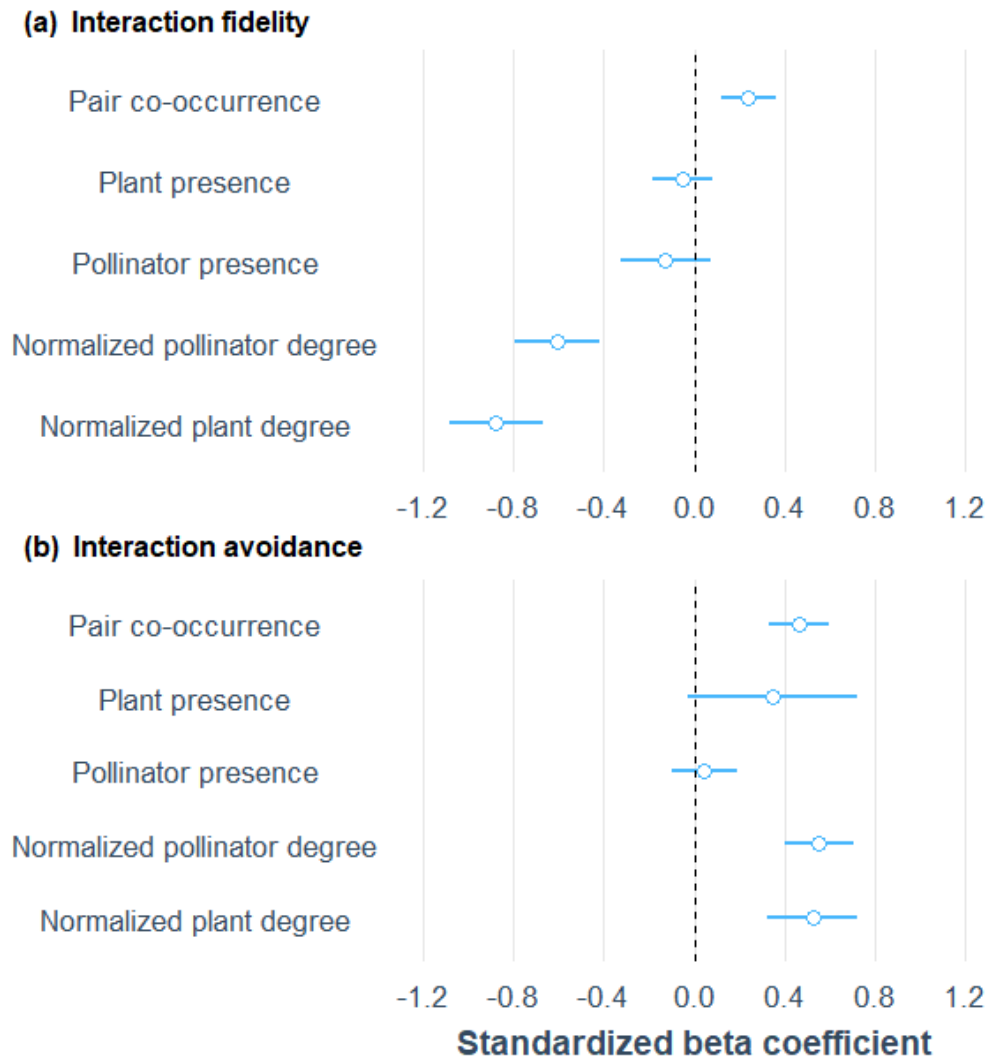


Fig. 3. Standardized beta coefficients and their 95% confidence intervals of explanatory quantitative variables from the generalized linear model with interaction fidelity as response variable (a) and from the generalized linear model with interaction avoidance as response variable

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

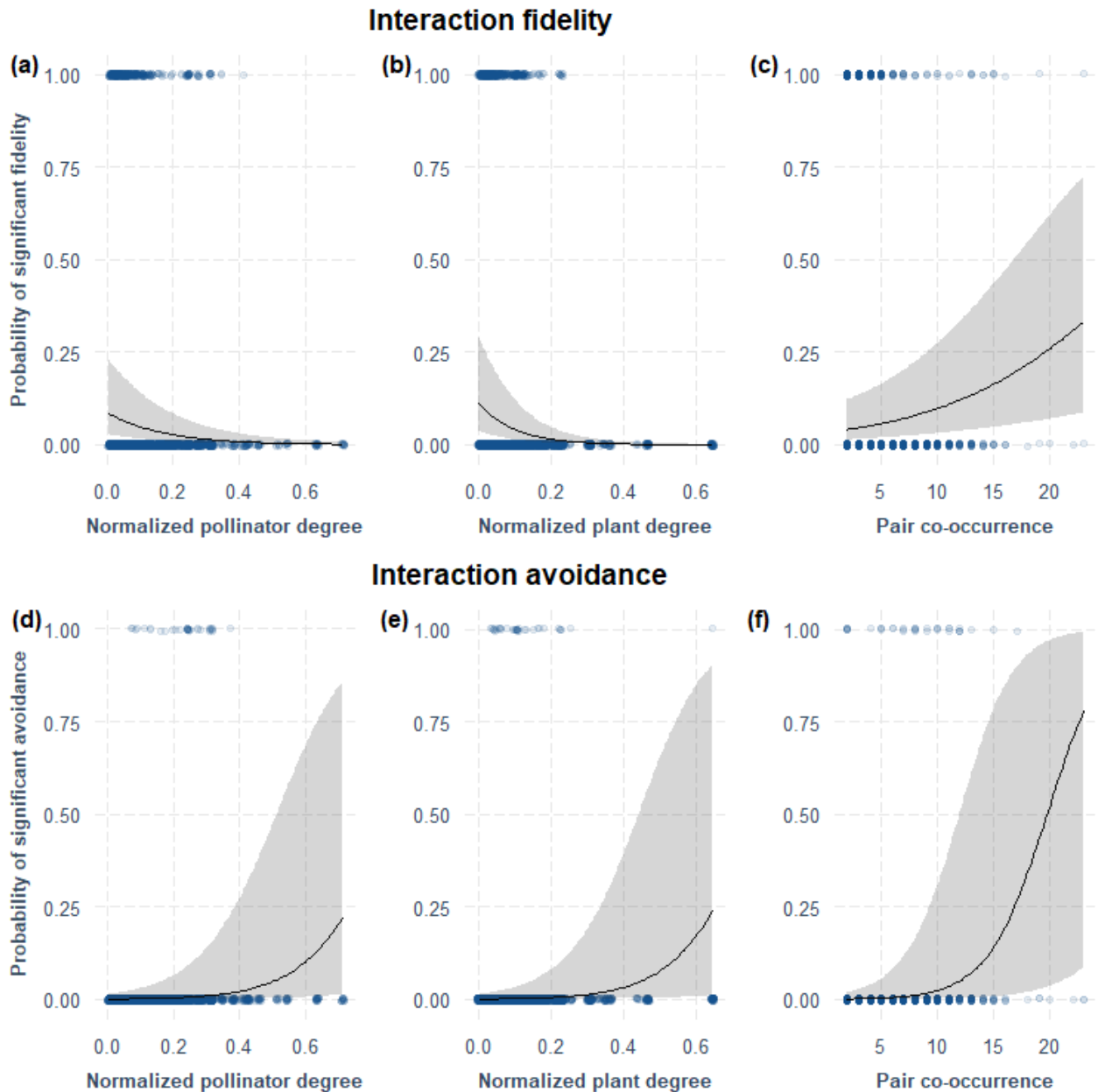


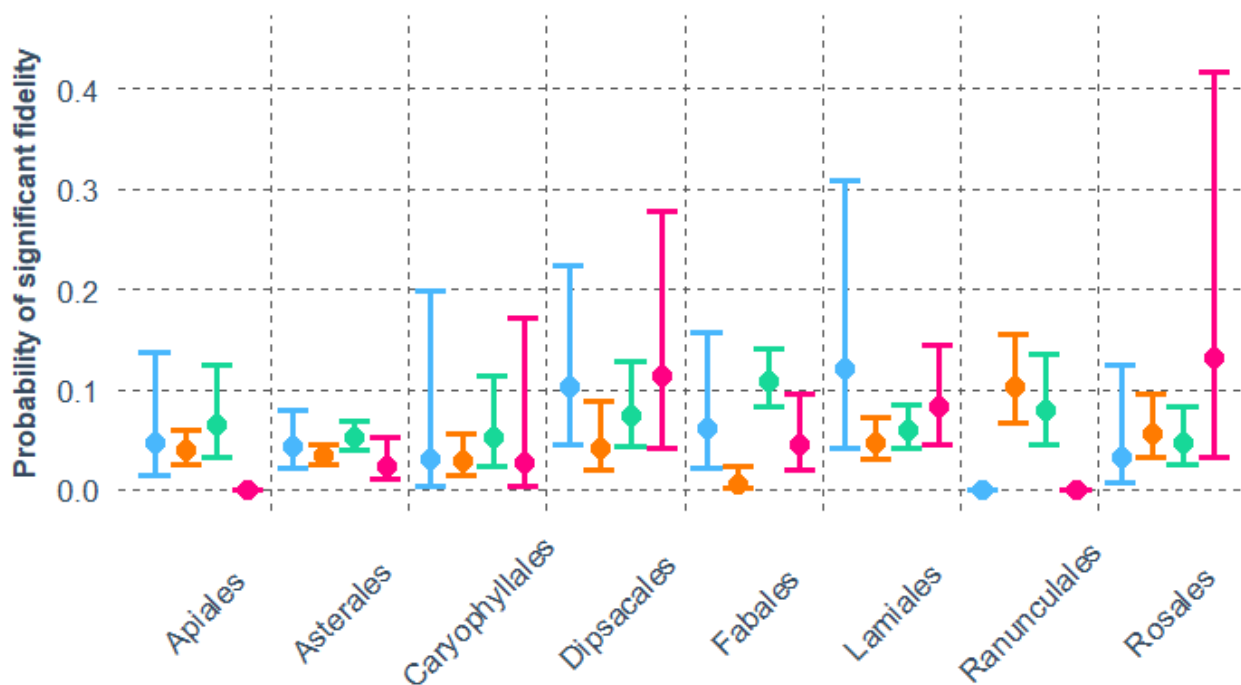
Fig. 4. Effects of normalized degree of the pollinator and the plant on the probability of significant fidelity (a, b) and avoidance (d, e) and effects of pair co-occurrence on the probability

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

We also found a significant interaction effect of plant and pollinator orders on the probability of detecting interaction fidelity. This means that some interactions between specific plant and pollinator orders had higher probability to show significant fidelity than others. Specifically, interactions between Lepidoptera and Rosales as well as Coleoptera and Lamiales showed the greatest probability of significant fidelity (Fig. 5a). In contrast, Coleoptera and Ranunculales or Lepidoptera and Apiales or Ranunculales never showed significant interaction fidelity (Table S2). The comparison between insect orders within plant orders, from the post-hoc test, pointed out that within the order Fabales, interactions between Fabales and Diptera had a lower probability to show fidelity than interactions between Fabales and Coleoptera (Effect Size[ES] = -2.42; $p = 0.0424$) and than interactions between Fabales and Hymenoptera (ES = -3.05; $p = 0.0002$). The comparison between plant orders within Diptera highlighted again that pairs between Diptera and Fabales had a low probability of significant fidelity, these pairs had lower probability to show fidelity than pairs between Diptera and Ranunculales (ES = -2.99 ; $p = 0.0026$). These latter pairs also had a greater probability to show significant fidelity than pairs between Diptera and Apiales (ES = 1.04; $p = 0.0461$) and than between Diptera and Asterales (ES = 1.20; $p = 0.0012$) (Fig. 5a). Within Hymenoptera, the contrast between plant orders pointed out that pairs between Hymenoptera and Fabales had a greater probability to show significant fidelity than pairs between Hymenoptera and 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; $p = 0.0475$).

(a) Interaction fidelity



(b) Interaction avoidance



Insect orders ● Coleoptera ● Diptera ● Hymenoptera ● Lepidoptera

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

SUPPORTING INFORMATION



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

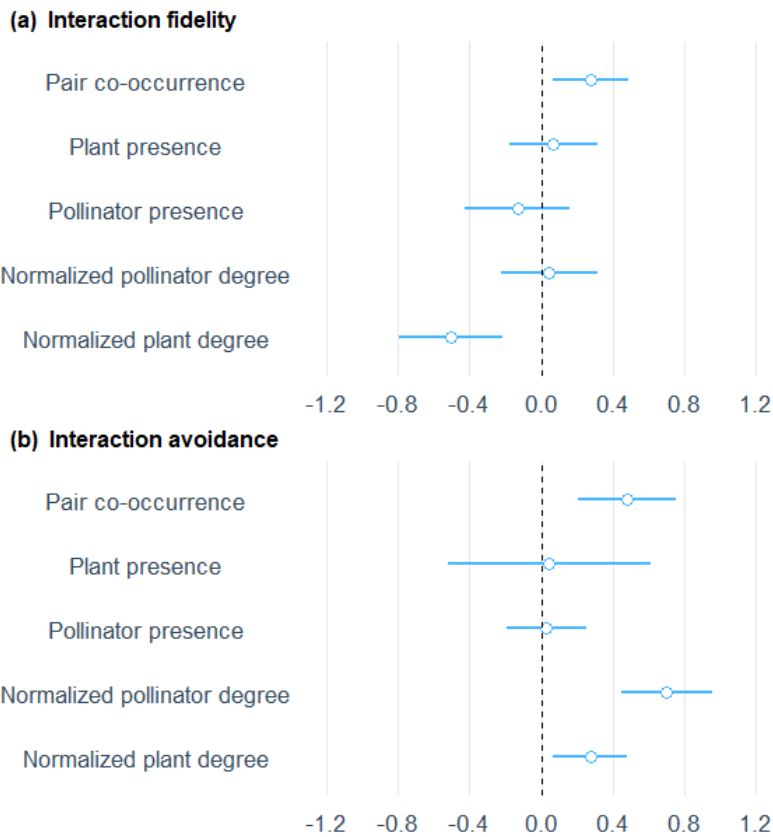


Fig. S2: Species pairs co-occurring in very few networks could lead to a reduced probability of detecting significant interaction fidelity or avoidance because there are less possibilities in the null distribution. Subsequently, it is more possible in the randomisations to obtain expected values equal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

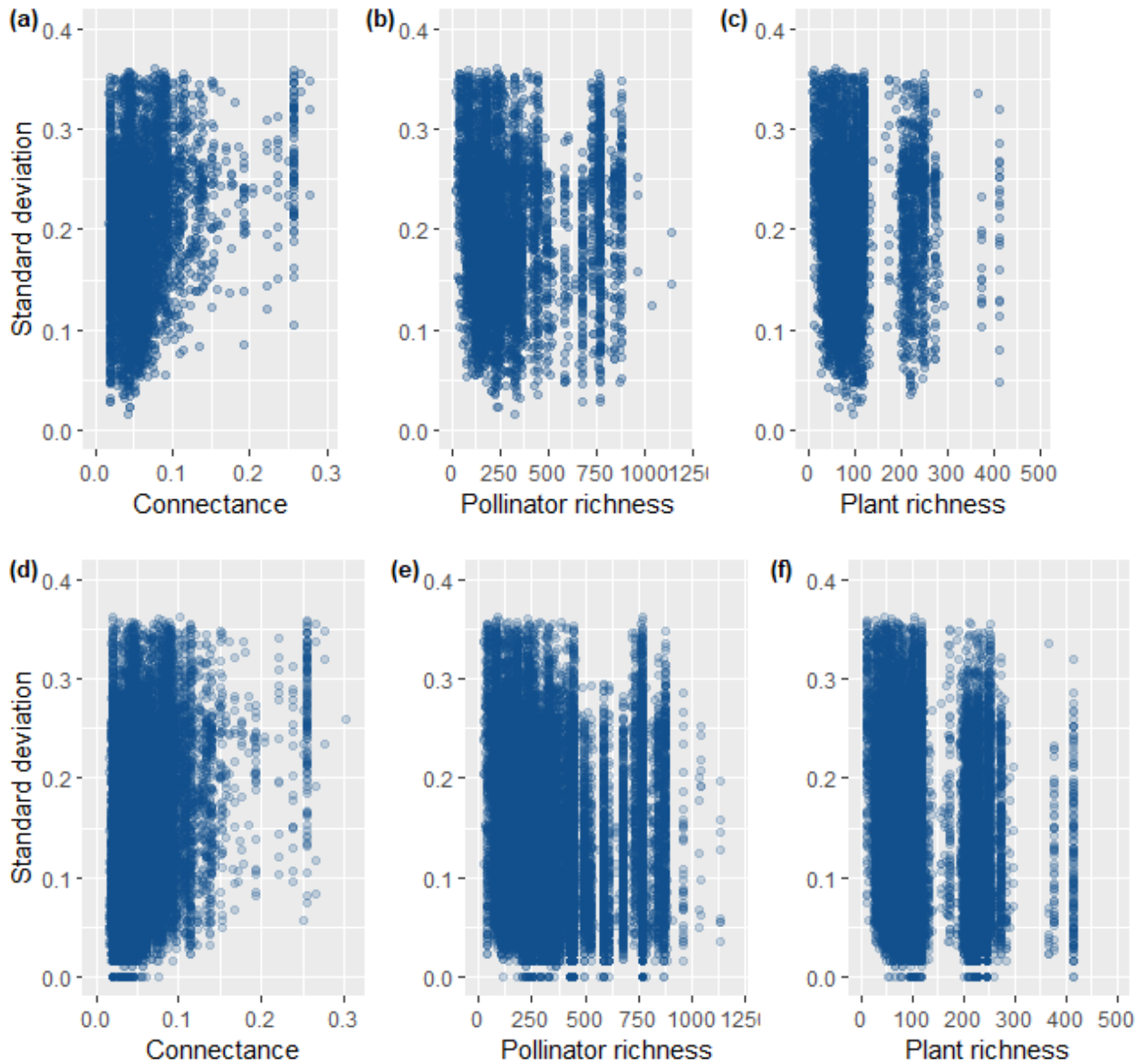


Fig. S3: Standard deviation of expected frequency of interaction of each plant-pollinator pair derived from the null set of networks created by the swap algorithm in relation to median connectance, median pollinator richness and median plant richness of the empirical networks in which the pairs are present.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

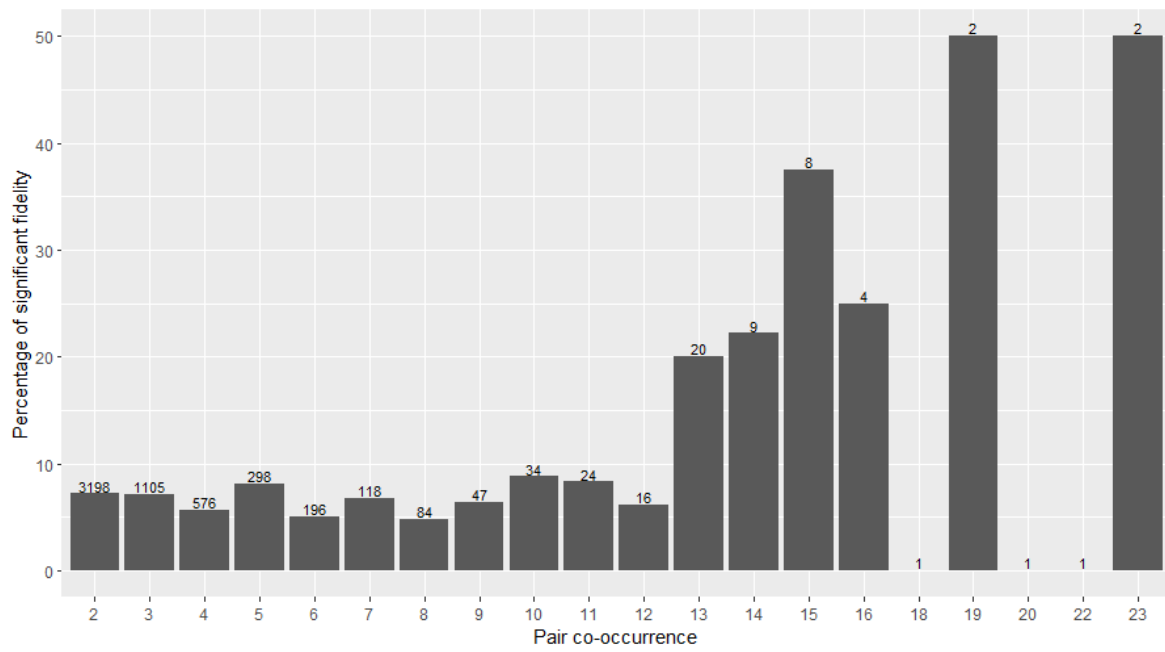


Fig. S4: Percentage is the ratio between the pair showing significant fidelity and the total number of pairs of given co-occurrence (i.e., number of networks in which a plant-pollinator pair is present). In the top of each bar, it is indicated the total number of plant-pollinator pairs with a given co-occurrence.

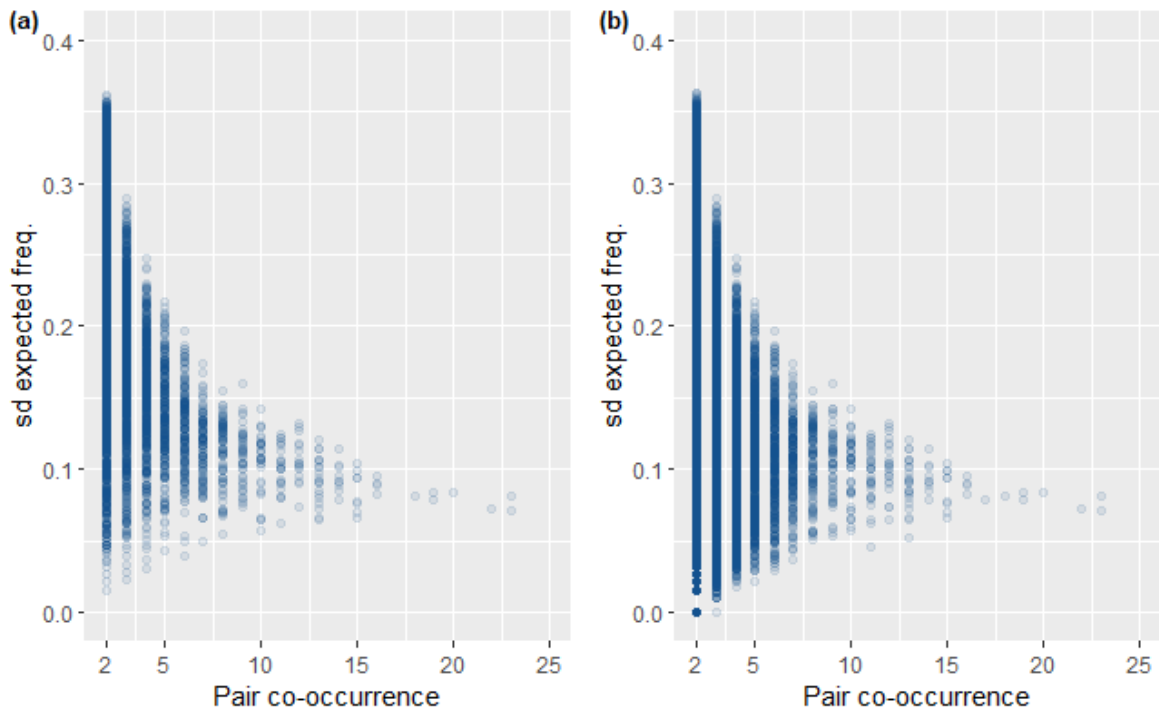


Fig. S5: Standard deviation of expected frequency of interactions considered in the model of fidelity (a) and avoidance (b) and pair co-occurrence (Spearman coefficient: -0.58 and -0.03, respectively).

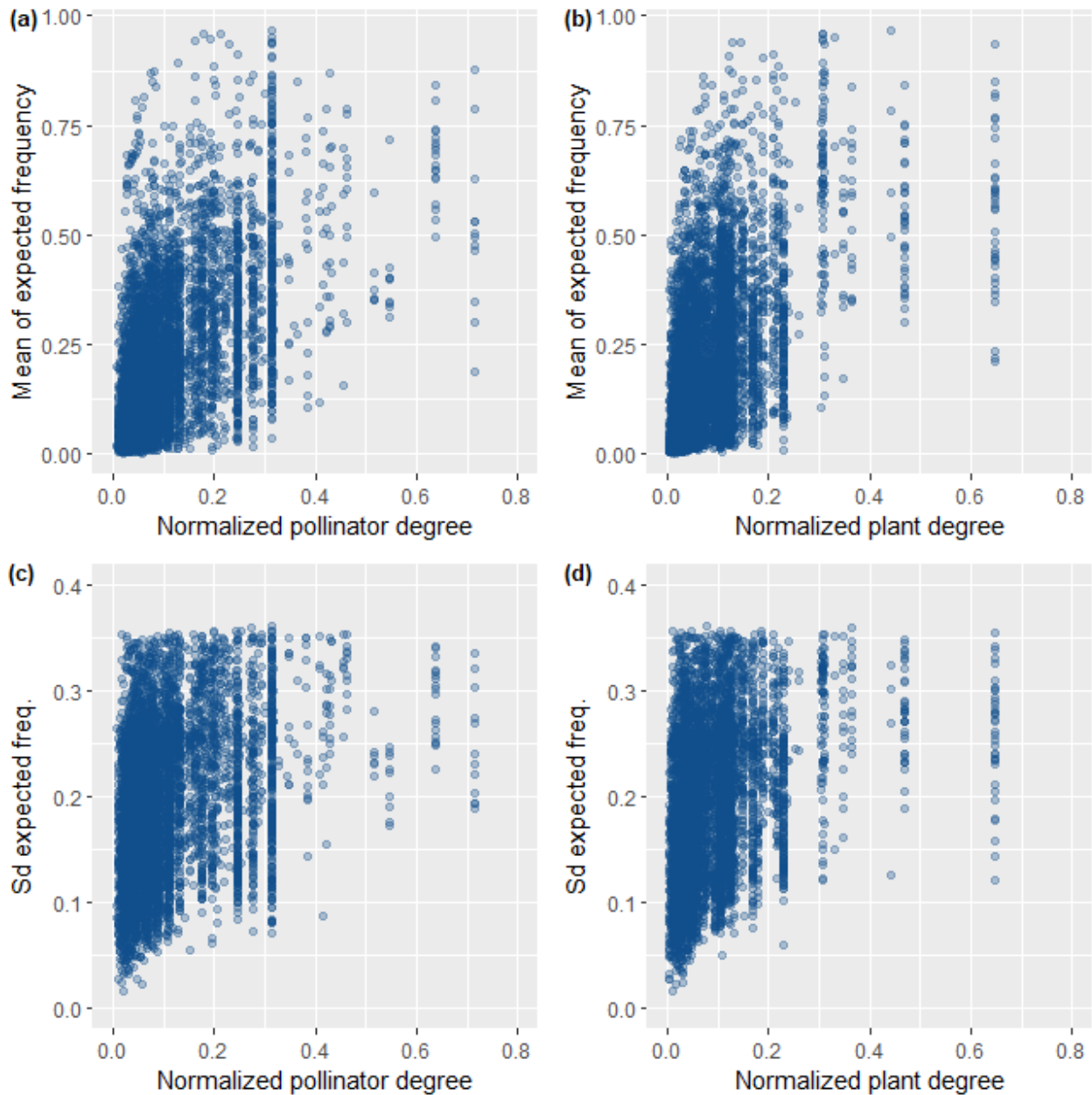


Fig. S6: Mean expected frequency of interactions considered in the model of fidelity and degree of the pollinator (a) and of the plant (b) ($r = 0.55$ and $r = 0.45$, respectively). Standard deviation of expected frequency of interaction and degree of the pollinator (c) and of the plant (d) ($r = 0.34$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

Appendix S2. GLModel of Interaction Avoidance

- Null deviance: 547.31 on 32032 degrees of freedom
- Residual deviance: 312.50 on 31996 degrees of freedom
- AIC: 386.5

Table S3. Interaction Avoidance and species' orders

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

	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

DATA AVAILABILITY STATEMENT

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

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