

1        **Interaction network structure maximizes community-level**  
2                **plant reproduction success via niche complementarity**

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5    Short running title: Network structure effects on ecosystem functioning

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18    interactions

19 **Abstract**

20 Declines in pollinator diversity and abundance have been reported across different  
21 regions, with implications for the reproductive success of plant species. However,  
22 research has focused primarily on pairwise plant-pollinator interactions, largely  
23 overlooking community-level dynamics. Yet species do not interact in isolation, they are  
24 embedded within larger networks whose structure can affect pollinator functional roles  
25 and, ultimately, the pollination services they deliver to plants. Here, we present one of the  
26 first efforts linking pollinator visitation to plant reproduction from a community-wide  
27 perspective using a well-replicated dataset encompassing 16 well-resolved plant-  
28 pollinator networks and data on reproductive success for 19 plant species from  
29 Mediterranean shrub ecosystems. We find that, for prediction purposes, information on  
30 simple visitation metrics is sufficient. Contrastingly, a mechanistic understanding of the  
31 pathways through which differences in pollinator diversity translate into changes in  
32 reproductive success, requires additional information on community structure,  
33 particularly that reflecting niche complementarity between pollinators.

## 34 **Introduction**

35 Pollinators provide key services to plants by facilitating pollen flow between individuals.  
36 The recent declining trends found for some pollinator species in some regions of the  
37 planet (Potts *et al.* 2010, Bartomeus *et al.* 2019) have led many researchers to focus on  
38 the functional impacts of these changes in pollinator diversity, with a major focus being  
39 placed on the consequences for plant reproductive success (Biesmeijer *et al.* 2006).

40 Many research efforts have targeted the reproductive success of individual plant  
41 species (Albrecht *et al.* 2012; Thomson 2019), and used relatively simple visitation  
42 metrics (e.g., the number of pollinator species that visit a plant or the number of visits  
43 they perform) to explain the differences observed across different plant individuals.  
44 Contrastingly, community-level analyses remain scarce (Bennett *et al.* 2018). Yet plants  
45 and pollinators do not interact in isolation, but rather are embedded within larger  
46 networks of interactions encompassing other plant and pollinator species. We are thus  
47 missing an important part of the picture, which includes the direct interactions between  
48 the whole ensemble of plants and pollinators, but also the indirect interactions between  
49 species within one guild (e.g., plants) through their shared resources (Pauw 2013;  
50 Carvalho *et al.* 2014; Lázaro *et al.* 2014; Mayfield & Stouffer 2017). Understanding  
51 how changes in pollinator diversity and interaction structure affect whole community  
52 assemblages is thus a major challenge that requires attention.

53 The few pollination studies that have analysed the effects of changing pollinator  
54 diversity for reproductive success at the community level have done so using mainly  
55 experimental setups. As an example, a study that experimentally recreated a plant  
56 community with 9 plant species and differing levels of pollinator diversity across

57 different enclosures, found that not only pollinator species diversity had an effect for  
58 average reproductive success, but also they found that community structure had an  
59 important effect (Fründ *et al.* 2013). In particular, these authors found that niche  
60 complementarity between pollinators, in terms of plant species and temperature coverage  
61 (a measure of the overlap in the use of plant resources and optimum temperature activity)  
62 had a positive effect for average seed set at the community level (Fründ *et al.* 2013). This  
63 provides added information on the effects of biodiversity for ecosystem functioning,  
64 suggesting that not only the diversity of species present, but also the diversity of roles and  
65 ways in which a community is structured, are determinant factors.

66         Indeed, theoretical research has long suggested that the structure of multitrophic  
67 communities has an effect for ecosystem functioning (reviewed in Thompson *et al.*  
68 2012). This line of research, primarily driven by food-web studies, has greatly advanced  
69 theory, but these ideas have not yet been tested using empirical data (but see Poisot *et al.*  
70 2013). Specifically, a major knowledge gap resides in understanding which aspects of  
71 structure determine which aspects of function (Thompson *et al.* 2012). We are now at a  
72 point in which there is considerable understanding on the attributes characterizing  
73 mutualistic interaction networks (Bascompte & Jordano 2007) and we have a substantial  
74 understanding of how these attributes vary along different types of gradients (Tylianakis  
75 & Morris 2016; Pellissier *et al.* 2017). Especially, in the case of pollination, we have  
76 ample knowledge on the attributes that shape these mutualistic interactions at the  
77 community level, such as a prevalence of nested structures (Bascompte *et al.* 2003) or the  
78 presence of asymmetric specialization as a pervasive feature (Vázquez & Aizen 2004).  
79 However, the pathways by which the structure of these networks of interactions affect

80 key ecosystem functions such as plant reproduction remain to be understood (Winfree  
81 2013). The time is thus ripe to use this knowledge to explore relationships between  
82 community structure and ecosystem functioning, with special emphasis being placed on  
83 the underlying mechanisms that drive these relationships.

84 Here, we present one of the first efforts linking pollinator visitation and plant  
85 reproductive success at the community level. To this end, we use a well-replicated dataset  
86 encompassing 16 well-resolved plant-pollinator interaction networks coupled with data  
87 on the reproductive success of 19 plant species recorded at Mediterranean shrub  
88 ecosystems within the area of influence of Doñana National Park in SW Spain. Our study  
89 focuses on understanding whether adding information on the structure of the community  
90 to previously used simple visitation metrics (e.g., the number and diversity of pollinator  
91 species visiting a plant species) aids in better explaining the differences observed in  
92 community-wide reproductive success. In doing so, we conducted our analyses focusing  
93 on reproductive success at two different levels: (i) at the species level by considering the  
94 effect of the position of a focal species within the larger network and its impact on its  
95 individual reproductive success, and (ii) at the community level, by evaluating how  
96 attributes that describe the whole community might affect average values of reproductive  
97 success. In addition to average values, we also evaluate whether community structure  
98 helps us explain differences in equity in reproductive success across species within a  
99 community, as a measure of evenness in the pollination service delivered.

100 Our results suggest that for prediction purposes, information on simple visitation  
101 metrics, particularly regarding the diversity of pollinators that visit a plant species, is  
102 sufficient. However, we find that a mechanistic understanding of the pathways through

103 which differences in pollinator diversity translate into changes in reproductive success  
104 requires additional information on network structure, notably information on the  
105 complementarity between the functions performed and the niches occupied by different  
106 pollinator species.

## 107 **Methods**

### 108 *Plant pollinator interactions*

109 Our study was conducted in SW Spain within the area of influence of Doñana National  
110 Park (Fig. 1). Here, we surveyed 16 Mediterranean woodland patches with an average  
111 distance of 7 km between them (min= 3 km, max= 46.5 km). Each site was surveyed 7  
112 times during the flowering season of 2015 (from February to May) following a 100-m x 2  
113 m transect for 30 mins. Along each transect, we identified all plant species and recorded  
114 all the flower visitors that legitimately visited them during each 30-min period. In  
115 addition, at each round we conducted 3 minutes of focal observations on 3 individuals per  
116 species belonging to the 19 most common species across the study area ( $6.25 \pm 1.73$   
117 species per site). Furthermore, we included some interactions between plant and  
118 pollinator individuals that were not observed during the sampling but that were  
119 opportunistically recorded immediately before or after the sampling periods, as some of  
120 these interactions are difficult to document and might be important to define network  
121 structure (Jordano 2016). Floral visitors (from now on referred to as pollinators) that  
122 could not be identified in the field were captured, stored and identified in the laboratory  
123 by FPM with the aid of experts in the different taxonomic groups (see

124 acknowledgements). All surveys were done under similar weather conditions, avoiding  
125 windy or rainy days.

### 126 *Plant reproductive success*

127 Within each site, we marked between 3 and 12 individuals ( $6.49 \pm 2.37$ ) belonging to 1  
128 to 6 plant species ( $4.06 \pm 1.69$ ), depending on the availability and presence of flowers  
129 during the sampling events. For each individual, at the end of the season, we recorded  
130 fruit set (i.e. the proportion of flowers that set fruit), the average number of seeds per fruit  
131 and the average seed weight per fruit (1-36 fruits subsampled; mean =  $11.17 \pm 6.85$ ). Our  
132 survey included a total of 19 different plant species across our 16 sites.

### 133 *Data analyses*

134 In order to evaluate the completeness of our sampling of the pollinator and plant  
135 community as well as that of their interactions, we estimated the asymptotic number of  
136 species present, including non-detected species, and calculated the proportion detected  
137 with our original sampling data. We used Chao 1 asymptotic species richness estimators  
138 (Chao *et al.* 2009) and estimated the richness of pollinators, plants and plant–pollinator  
139 links accumulated as sampling effort increased up to 100% sampling coverage using  
140 package iNEXT (Hsieh *et al.* 2016) within the R environment (R Development Core  
141 Team 2011). We then extracted the values covered by our sampling.

142 In order to analyse how differences in community structure might affect plant  
143 reproductive success, we constructed weighted plant-pollinator interaction networks by  
144 pooling the data for the 7 rounds of sampling. We thus obtained one weighted interaction  
145 network per site, representing the frequency of visits by different pollinator species to

146 different plant species. For each network, we then proceeded to extract a series of  
147 relevant network metrics at the species and community levels.

#### 148 *Species-level network analysis*

149 At the species level, we focused on attributes defining the position of a focal plant species  
150 within the larger community. As such, we considered two metrics providing  
151 complementary non-redundant information: (i) average niche overlap in terms of  
152 pollinators between a focal plant species and other plant species in the community, which  
153 covers the potential indirect interactions between different plant species through shared  
154 resources (in this case pollinators), and (ii) centrality, which depicts the importance of the  
155 role played by a plant species within the larger community (as resource for a large  
156 number of pollinator species) and its contribution to network cohesiveness.

157 Niche overlap was calculated as the average overlap in pollinator species visiting  
158 a focal plant and each of the other plants in the community using the Morisita index  
159 (Zhang 2016). As a measure of centrality we used weighted closeness centrality, which  
160 represents the number of shortest paths going through a focal plant based on a unipartite  
161 projection of the bipartite plant-pollinator network using a weighted representation of the  
162 network (Dormann *et al.* 2009). Here, links between plant species represent shared  
163 pollinator species.

#### 164 *Community-level network analysis*

165 At the community level, we followed the same logic as the one presented at the species  
166 level. Thus, we also calculated two network metrics providing complementary non-



167 redundant information. In this case we focused on (i) nestedness and (ii) niche  
168 complementarity.

169         Nestedness is the property by which specialists interact with a subset of the  
170 species that generalists interact with (Bascompte *et al.* 2003). Although there is an  
171 ongoing debate in the literature, some studies have found that nested networks are more  
172 stable and resilient to perturbations because nestedness promotes a greater diversity by  
173 minimizing competition among species in a community (Bastolla *et al.* 2009). However,  
174 many network attributes vary with network size and complexity (Blüthgen *et al.* 2006). In  
175 the case of nestedness, we know it can be affected by network size and connectance  
176 (Song *et al.* 2017). An approach that is often used to correct for this, is to use null models  
177 and to compare null-model corrected nestedness values across different networks.  
178 However, this approach has been recently shown to present the same issues, as z-scores  
179 also change with network size and connectance (Song *et al.* 2017). We thus followed the  
180 advice provided by Song *et al.* (2017) by using a normalized value of the widely-used  
181 nestedness metric NODF (Almeida-Neto & Ulrich 2011),  $NODF_c$ . This normalized value  
182 is calculated as  $NODF_c = NODF_n / (C * \log(S))$ , where C is connectance, S is network  
183 size and  $NODF_n = NODF / \max(NODF)$ , which is independent of network size and thus  
184 comparable across different networks (Song *et al.* 2017).

185         Niche complementarity metrics are important because plant reproductive success  
186 depends on the delivery of conspecific pollen and thus of a certain level of specialization  
187 or niche divergence (reviewed in Brosi 2016). To calculate niche complementarity, we  
188 used a community-level measure defined as the total branch length of a functional  
189 dendrogram based on qualitative differences measured using a Euclidean distance in

190 visitor assemblages between plants (Petchey & Gaston 2007; Devoto *et al.* 2012). All  
191 network metrics were calculated using package bipartite (Dormann *et al.* 2009).

192 All of these metrics were calculated using all the data as well as for the subset of  
193 the data excluding interactions observed outside of sampling periods. Differences  
194 between results are minimal for both and thus we will only present results for the analysis  
195 using the full dataset.

### 196 *Statistical analyses*

197 In order to evaluate whether adding information on community structure improves our  
198 ability to explain differences in reproductive success - both at the species and the  
199 community level - we used general linear (GLMs) and general linear mixed models  
200 (GLMMs). In both cases (species and community-level models) we fit two types of  
201 models: (i) model 1, that only included simple visitation metrics and (ii) model 2 that  
202 additionally included information on community structure. All response variables were  
203 previously scaled for each species to allow meaningful comparisons across species with  
204 contrasting life histories.

205 At the species level, model 1 included as explanatory variables the diversity of  
206 pollinator species visiting a focal plant (i.e. pollinator richness), and the total number of  
207 visits received by that plant species; while model 2 added the two network attributes  
208 calculated at the species level: average niche overlap and centrality. In this case, we  
209 included plant species nested within site as a random effect to account for the non-  
210 independence of several individuals measured for the same plant species within each site.  
211 Response variables included fruit set for different individuals of each species analyzed

212 using a binomial distribution, the average number of seeds per fruit analyzed using a  
213 normal distribution and the average values of fruit and seed weight fitted to poisson  
214 distributions.

215 At the community level, we upscaled our species-level analyses. In this case,  
216 model 1 included total pollinator richness and total pollinator abundance (i.e. number of  
217 visits received by all plants within the community) as explanatory variables. Model 2, in  
218 turn, added information on community structure by including nestedness and niche  
219 complementarity as explanatory variables. As response variable we had the average  
220 reproductive success for the whole community (i.e., average fruit set analyzed using a  
221 binomial distribution, average number of seeds per fruit and average fruit and seed  
222 weight using a normal distribution). We thus had a single value per site and no random  
223 effects are needed in this case.

224 Average values of reproductive success at the community level can be driven to a  
225 large extent by a single plant species. Yet, what will determine the persistence of a  
226 diverse plant community, is the presence of some sort of “equity” or evenness in  
227 reproductive success across the whole community. We therefore calculated a measure of  
228 equity in reproductive success at the community level as the proportion of species within  
229 a community with normalized (between 0 and 1) average fruit set values that were above  
230 0.5. We repeated this using 0.25 and 0.75 thresholds. We then used the same framework  
231 as that used for species and community-level analyses and fit the same models 1 and 2  
232 GLMs, but using equity in reproductive success as the response variable fitting a  
233 binomial distribution. In all cases, we used information criterion methods to find the best  
234 model and selected the ones with the lowest Akaike Information Criterion (AIC) value.

235 Whenever the difference between the AIC of both models was  $< 2$  ( $\Delta AIC < 2$ ), we  
236 considered that both models were equally good (Burnham *et al.* 2011). All predictor  
237 variables were centered prior to analysis.

238 Finally, we tested whether the importance of community structure in explaining  
239 differences in equity in reproductive success within communities increases with the  
240 number of plant species being considered. We expect that when only one plant species is  
241 considered, then the importance of community structure will be negligible, while we  
242 expect this importance to increase as more plant species are considered (up to a  
243 maximum number of 6 species which is the maximum we have measured in our study at  
244 a particular site).

245 To test this, we ran a simple simulation in which the number of species  
246 considered increased at each step and for each step we re-calculated equity in  
247 reproductive success. Instead of drawing plant species randomly for each step, we tested  
248 all possible combinations for each plant number level and network, as the number of  
249 combinations is low (e.g. for  $n = 3$  plant selected out of 6 there is only 20 possible  
250 combinations). Then, we tested if the relationship between equity in reproductive success  
251 and functional complementarity (given its importance in determining differences in  
252 reproductive success, see Results section) changes as a function of the number of plants  
253 considered within our simulated communities. To this end, for each level of species  
254 number considered, we randomly selected one of the generated equity values across each  
255 of the 16 communities, and regressed these 16 values against our network level predictor  
256 and extracted the model estimates. We repeated this process 1,000 times and averaged all  
257 estimates. We expect that the more plants considered, the larger the resulting average

258 estimates will be. Note that we only interpret the mean effects, as the variance among  
259 different plant number of species considered depends on the initial number of  
260 combinations.

## 261 **Results**

262 Within our sampling we recorded 1,472 pollinator individuals belonging to 57 species of  
263 plants and 277 species of pollinators. Within the pollinator community the distribution in  
264 different orders was: 87.84% Hymenoptera, 6.78% Diptera, 4.05% Coleoptera and 1.09%  
265 Lepidoptera.

266 Our sampling completeness analyses revealed that with our survey we were able  
267 to capture 18-62% of pollinator species (average = 35%), 47-98% for plant species  
268 (average = 78%) and 13-41% for plant-pollinator links (average = 27%), in line with that  
269 obtained with other studies (e.g., Chacoff *et al.* 2012, Fig. S1). Our values of sampling  
270 completeness are slightly smaller in the case of pollinators, probably as a consequence of  
271 the great diversity found in the Mediterranean region and within our study area in  
272 particular, a hotspot of insect diversity (Nieto *et al.* 2014). In addition, the fact that we  
273 include an extra effort to capture rare interactions observed outside of our main sampling  
274 might also increase the number of singletons which directly affect richness estimates.

### 275 *Species-level analyses*

276 At the species level, in the case of fruitset, our results show that model 2 is the best model  
277 explaining the variability observed. In this case, we find a positive effect of a community  
278 structure metric, the centrality of the focal plant on its fruit set (Table 1, Fig. 2A).

279 For the number of seeds per fruit, our results show again that model 2 is the best  
280 model. In this case, we find a positive effect of the niche overlap between plant species  
281 (Table 1B, Fig. 2B).

282 For all other measures of reproductive success considered (i.e., fruit and seed  
283 weight), the best model based on its AIC value was model 1, i.e., the model that only  
284 included simple visitation metrics (in this case, pollinator species diversity and the total  
285 number of visits received by a focal plant species). However, none of the variables  
286 included within our model explain the differences observed (Tables S4-S5).

### 287 *Community-level analyses*

288 At the community level, we find different patterns for fruit set and the number of seeds  
289 per fruit as compared to those for fruit and seed weight. In the case of fruit set and the  
290 number of seeds per fruit, we find that both model 1 and 2 are equally good in describing  
291 the differences observed (i.e.,  $\Delta AIC < 2$ ). Because this suggests model 2 is a good model  
292 despite its added complexity, we will comment results for this model only. In particular,  
293 we find that both fruit set and the number of seeds per fruit are positively related to niche  
294 complementarity between pollinators (Table 2, Figs. 3-4). Additionally, we find a  
295 negative effect of community-level pollinator species diversity and the total number of  
296 visits on average fruit set (Table 2A, Fig. 3), while the total number of visits positively  
297 affected the average number of seeds per fruit (Table 2B, Fig. 4). The number of visits  
298 for one of the sites was particularly large, yet this did not affect our results as removing  
299 this site from the analysis showed the same effect.

300           Contrastingly, in the case of weight variables (fruit and seed weight), in both  
301 cases we find that the best model is model 1, i.e., that only including simple visitation  
302 metrics. Here, we find a consistent positive effect of community-level pollinator diversity  
303 for both weight descriptors (Tables S6-S7, Figs. S2-S3).

#### 304 *Equity in fruitset*

305           When evaluating the effect of differences in community composition and structure for  
306 equity in reproductive success across the different species within a community we find  
307 that model 1 is the best model for all the thresholds considered (0.5, 0.25 and 0.75).  
308 However, we also find a significant negative relationship between equity and pollinator  
309 species diversity using the 0.75 threshold (Fig. 5, Tables S8, S9, S10).

310           Within our simulation evaluating the effect of niche complementarity on equity in  
311 reproductive success as more plants within the community are considered, we find that  
312 the effect of complementarity becomes more important as the reproductive success of  
313 more species is considered (Fig. S4). This importance seems to reach some sort of plateau  
314 at 6 species. However, this should be further evaluated, as this is the maximum number of  
315 species simultaneously observed in a community for our study, which precludes us from  
316 simulating further numbers of species.

#### 317 **Discussion**

318           The existence of a relationship between community structure and ecosystem function has  
319 been long hypothesized, yet, the specific mechanisms by which structure influences  
320 function have remained elusive until now (Thompson *et al.* 2012). Our results show that  
321 different aspects of community structure affect different dimensions of community

322 functioning. In particular, we find that the centrality of a plant species within a  
323 community, which measures the number of connections it receives from other species in  
324 the community, has a positive effect for its fruit set. At the community level, however,  
325 we find that niche complementarity between pollinators, a measure of the overlap in the  
326 niches of different species in terms of plant coverage, has an important effect for average  
327 fruit set.

328         One of the first conclusions we can extract from the fact that in most cases both of  
329 the models we considered (i.e., the simple model based on visitation metrics and the more  
330 complex one including community structure metrics) were equally good, is that for  
331 predictive purposes simple visitation metrics, such as pollinator diversity, might be  
332 enough (Garibaldi *et al.* 2013, 2015). Yet, a mechanistic understanding of the underlying  
333 processes driving these observed patterns requires that we take into account measures of  
334 community structure, and, in particular, those related to the overlap in the niches of  
335 interacting species (Fründ *et al.* 2013).

336         Consistent with previous experimental (Fontaine *et al.* 2005; Fründ *et al.* 2013),  
337 theoretical (Pauw 2013), and empirical studies (Valdovinos *et al.* 2016, Poisot *et al.*  
338 2013), we find that niche complementarity is key in determining differences in  
339 reproductive outputs. Indeed, we find that communities where there is less overlap in the  
340 niches occupied by pollinator species had greater values of reproductive success, both  
341 greater fruit set values and larger numbers of seeds per fruit. This therefore reflects the  
342 fact that reproductive success in plant species requires of the delivery of conspecific  
343 pollen and thus of a certain degree of specialization amongst pollinator species on a  
344 particular plant resource in order to avoid the negative effects of inter-specific pollen



345 deposition (e.g., pollen loss, Flanagan *et al.* 2009) or interference with conspecific pollen  
346 (Morales & Traveset 2008).

347 In our study, we did not find an effect of nestedness for reproductive success in  
348 any case. This metric, widely used across network analysis, and which is deemed to  
349 stabilize (Bastolla *et al.* 2009) or destabilize (James *et al.* 2012) natural communities,  
350 does not seem to play a direct role in ecosystem function measured as plant reproductive  
351 success. However, our study is limited to a maximum of six plant species per community,  
352 and including more species might reveal different patterns, in which nestedness and the  
353 redundancy it implies might play a more important role.

354 Community-level plant reproductive success, measured as average fruit or seed  
355 set across all the species considered is an important part of the functions delivered by  
356 pollinators to plants. However, these average values might be masking a great deal of  
357 variability amongst plant species, and thus a nuanced view of the effect of pollinators on  
358 whole-plant ensembles is needed. This can be captured by the effect of pollinators on  
359 equity in reproductive success across plant species. This aspect ensures that reproductive  
360 success is equally distributed amongst a larger number of species, thus contributing to the  
361 maintenance of greater species diversity values in natural populations. Indeed, we know  
362 that plant species diversity within a community is largely driven by different types of  
363 direct and indirect interactions including those amongst plant species (e.g., resource  
364 competition, Goldberg & Barton 1992, or facilitation, Bruno *et al.* 2003), as well as those  
365 defining antagonistic (e.g., involving pathogens, Bagchi *et al.* 2010), or mutualistic  
366 interactions (e.g. pollinators, Benadi *et al.* 2013; Lanuza *et al.* 2018). However,  
367 equitability in reproductive success across species is seldom taken into account, despite

368 its importance in maintaining genetic diversity and ensuring the resilience of populations  
369 to further change.

370 In the case of equity, we did not find a significant effect of either simple visitation  
371 or community structure metrics. However, the results of our simulation on the importance  
372 of community structure as the number of plant species considered increases, shows us  
373 that this effect dramatically increases when more than four plant species are considered.  
374 This implies that if we were able to measure reproductive success for all the plant species  
375 in all the communities (which is not feasible given constraints in sampling effort), we  
376 might find that the effects of community structure on equity might be even more  
377 prevalent.

378 One of the unexpected results of our analyses is the strong negative effect of  
379 pollinator diversity for fruit set at the community level, as well as a negative effect on  
380 equity in reproductive success at the 0.75 threshold. An explanation to this might be the  
381 fact that pollinator diversity here includes all the pollinators surveyed, while fruit set and  
382 equity in fruit set refers to a subset of the plants in the community. More complex  
383 communities (with more pollinators, but also with more plant species, with a Pearson  
384 correlation value of 0.42 in our case) may require stabilizing mechanisms that reduce the  
385 competition exerted by the dominant plant species. This can be reached, for example, by  
386 a reduction in the reproductive success of the dominant species (Lanuza *et al.* 2018),  
387 which are precisely those evaluated in this study. These ideas open the door to explore  
388 the positive or negative effects of the complete pollinator community on full plant species  
389 coexistence, which may be determined by density-dependence effects (Benadi & Pauw  
390 2018). In our case, while fruit set is negatively related to pollinator richness, fruit and

391 seed weight show the opposite relationship, indicating that this density-dependent effect  
392 might only be limiting fruit quantity and not fruit quality. Thus, taking into account the  
393 co-flowering plant species densities may be the next step (Vanbergen *et al.* 2014).

394 In summary, our findings show that the analysis of natural communities of  
395 interacting species using network analysis not only represents an ideal way of visualizing  
396 and grasping the complexity present within these communities, but also represents a  
397 manner of mechanistically understanding differences observed across the reproductive  
398 success of individuals and/or species. Future studies could build on this body of research  
399 by focusing on the long-lasting effects of community structure for plant fitness, by  
400 evaluating the consequences of different community structures for heritability.

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406 access to the park.

407 **Table 1.** Results of GLMM showing effect of simple visitation and community structure  
408 metrics on A) species-level fruitset and B) average number of seeds per fruit based on  
409 best model selected. Bold letters indicate significant variables.

A)	Estimate	Std..Error	z.value
(Intercept)	1.72	0.21	8.16
Pollinator species diversity	-0.01	0.21	-0.07
Total number of visits	0.14	0.25	0.57
<b>Centrality</b>	<b>0.46</b>	<b>0.25</b>	<b>1.81</b>
Niche overlap	0.05	0.24	0.20

410

B)	Estimate	Std..Error	t.value
(Intercept)	0.05	0.14	0.36
Pollinator species diversity	0.14	0.15	0.90
Total number of visits	-0.01	0.16	-0.04
Centrality	-0.15	0.15	-1.00
<b>Niche overlap</b>	<b>0.22</b>	<b>0.17</b>	<b>1.32</b>

411

412

413 **Table 2.** Results of GLM showing effect of simple visitation and community structure  
414 metrics on A) community-level average fruit set and B) community-level average number  
415 of seeds per fruit based on best model selected.

A)	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	1.22	0.13	9.08	0.00
<b>Pollinator species diversity</b>	<b>-0.76</b>	<b>0.21</b>	<b>-3.53</b>	<b>0.00</b>
<b>Total number of visits</b>	<b>-0.19</b>	<b>0.16</b>	<b>-1.24</b>	<b>0.22</b>
Nestedness	0.03	0.20	0.15	0.88
<b>Niche complementarity</b>	<b>0.36</b>	<b>0.17</b>	<b>2.13</b>	<b>0.03</b>

416

417

B)	Estimate	Std. Error	t value
(Intercept)	45.36	8.78	5.17
Pollinator species diversity	10.31	14.90	0.69
Total number of visits	8.82	10.33	0.85
Nestedness	9.71	13.56	0.72
<b>Niche complementarity</b>	<b>24.66</b>	<b>12.45</b>	<b>1.98</b>

418

419

420 **Figure legends**

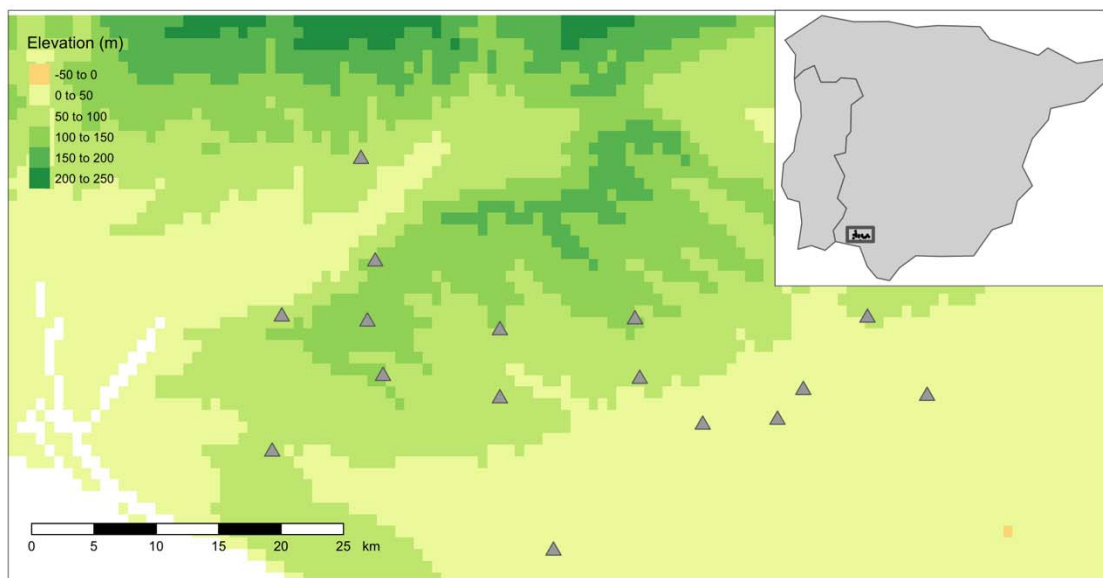
421 **Figure 1.** Map showing location of 16 study sites. Inset shows location of study area  
422 within SW Spain.

423 **Figure 2.** Partial residual plot showing the effect of A) plant species centrality on fruit set  
424 for each of the plant species considered and B) plant niche overlap on average number of  
425 seeds per fruit. Dots represent each of the individuals sampled for each species within  
426 each site.

427 **Figure 3.** Partial residual plots showing the effect of A) pollinator species diversity, B)  
428 total number of visits received and C) niche complementarity between pollinator species  
429 on community-level average fruitset. Dots represent average values of fruitset at the level  
430 of the community for all plant species considered (N=16 sites).

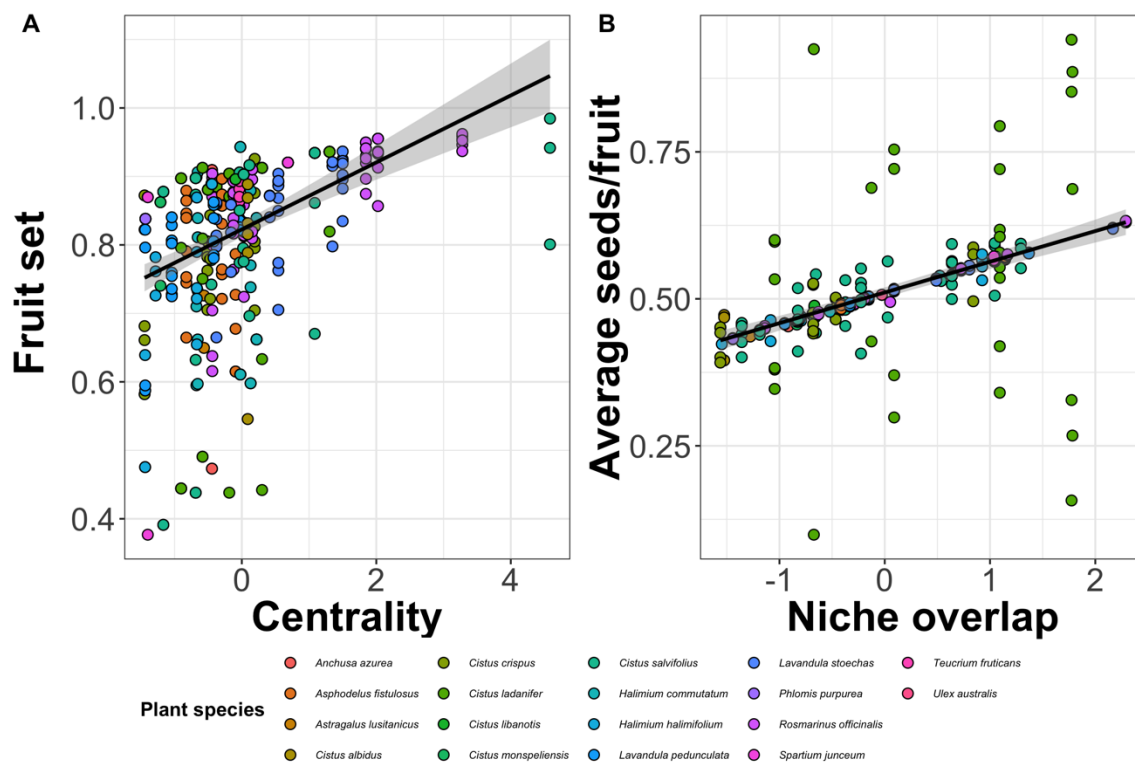
431 **Figure 4.** Partial residual plots showing the effect of A) the total number of pollinator  
432 visits received at the community level and B) niche complementarity between pollinator  
433 species on the scaled average number of seeds per fruit at the community level. Dots  
434 represent average values of previously scaled values of the number of seeds per fruit at  
435 the level of the community for all plant species considered (N=16 sites).

436 **Figure 5.** Partial residual plots showing the effect of pollinator species diversity on  
437 equity in reproductive success across species within a community (0.75 threshold). Dots  
438 represent values for each site (N=16 sites).



439  
440 **Figure 1.**

441

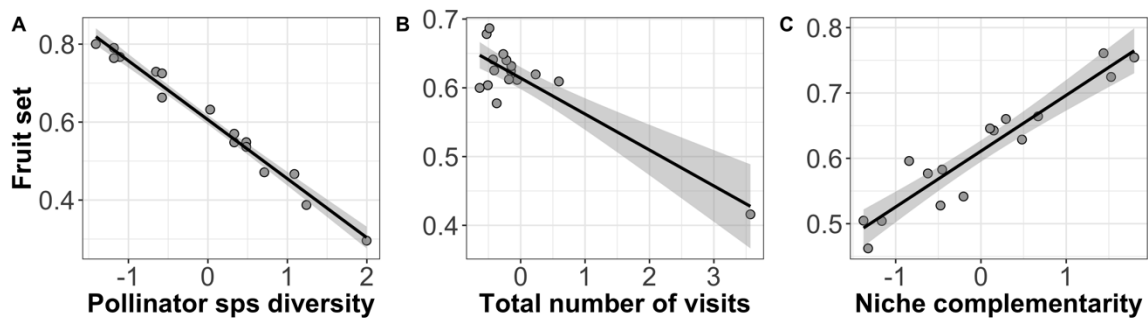


442

443 **Figure 2.**

444



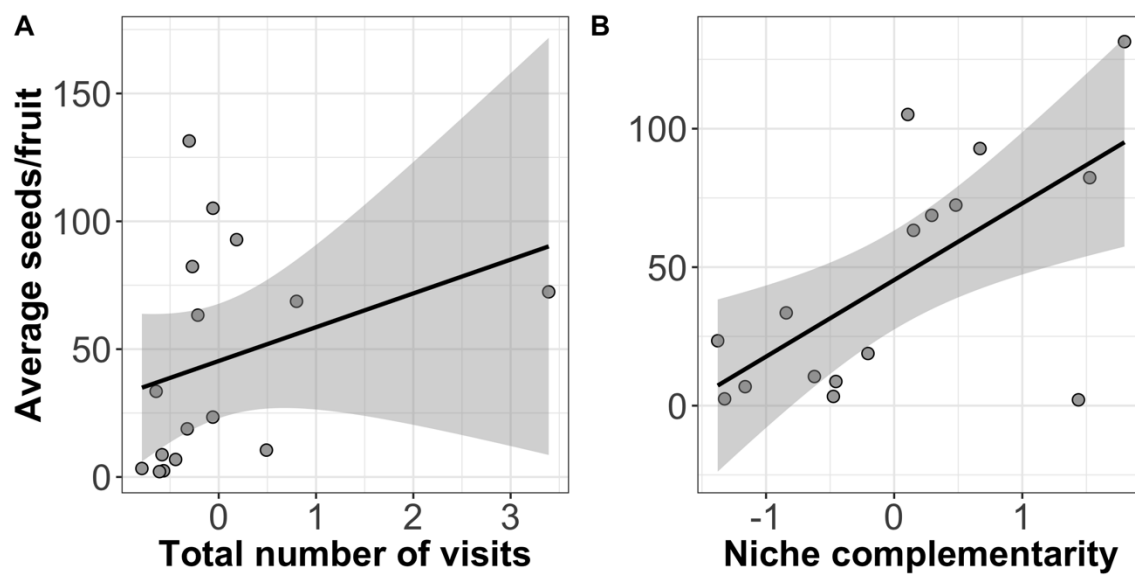


445

446 **Figure 3.**

447

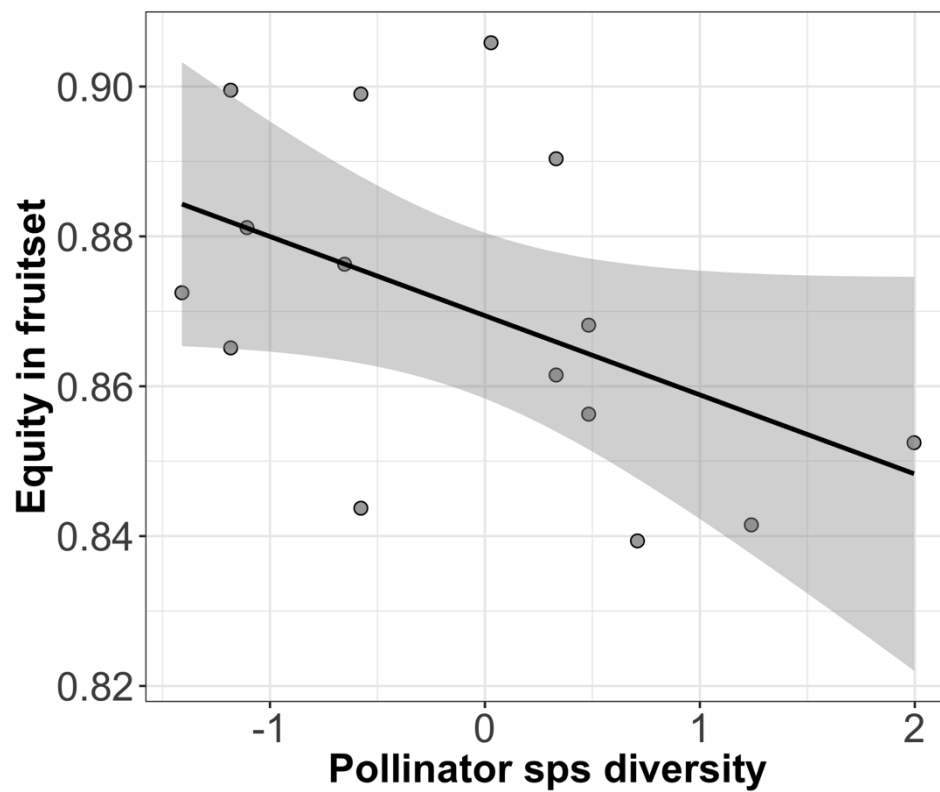
448



449

450 **Figure 4.**

451



452

453 **Figure 5.**

454

455 **References**

- 456 Albrecht, M., Schmid, B., Hautier, Y. & Müller, C.B. (2012). Diverse pollinator  
457 communities enhance plant reproductive success. *Proceedings of the Royal Society B:*  
458 *Biological Sciences*, 279, 4845 LP–4852.
- 459 Almeida-Neto, M. & Ulrich, W. (2011). A straightforward computational approach for  
460 measuring nestedness using quantitative matrices. *Environ Model Softw*, 26, 173–178.
- 461 Bagchi, R., Swinfield, T., Gallery, R.E., Lewis, O.T., Gripenberg, S. & Narayan, L. *et al.*  
462 (2010). Testing the Janzen-Connell mechanism: pathogens cause overcompensating  
463 density dependence in a tropical tree. *Ecology Letters*, 13, 1262–1269.
- 464 Bartomeus, I., Stavert, J., Ward, D. & Aguado, O. (2019). Historical collections as a tool  
465 for assessing the global pollination crisis. *Philosophical Transactions of the Royal*  
466 *Society B: Biological Sciences*, 374, 20170389.
- 467 Bascompte, J. & Jordano, P. (2007). Plant-Animal Mutualistic Networks: The  
468 Architecture of Biodiversity. *Annu Rev Ecol Evol S*, 38, 567–593.
- 469 Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). The nested assembly of  
470 plant–animal mutualistic networks. *P. Natl. Acad. Sci. USA*, 100, 9383–9387.
- 471 Bastolla, U., Fortuna, M.A., Pascual-Garcia, A., Ferrera, A., Luque, B. & Bascompte, J.  
472 (2009). The architecture of mutualistic networks minimizes competition and increases  
473 biodiversity. *Nature*, 458, 1018–1020.
- 474 Benadi, G., Blüthgen, N., Hovestadt, T. & Poethke, H.-J. (2013). When can plant-  
475 pollinator interactions promote plant diversity? *Am Nat*, 182, 131–146.

- 476 Benadi, G. & Pauw, A. (2018) Frequency dependence of pollination visitation rates  
477 suggests that pollination niches can allow plant species coexistence. *Journal of Ecology*,  
478 106, 1892-1901.
- 479 Bennett, J.M., Thompson, A., Goia, I., Feldmann, R., Ştefan, V. & Bogdan, A. *et al.*  
480 (2018). A review of European studies on pollination networks and pollen limitation, and  
481 a case study designed to fill in a gap. *AoB PLANTS*, 10, ply068–ply068.
- 482 Biesmeijer, J.C., Roberts, S.P., Reemer, M., Ohlemuller, R., Edwards, M. & Peeters, T. *et*  
483 *al.* (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the  
484 Netherlands. *Science*, 313, 351–354.
- 485 Blüthgen, N., Menzel, F. & Blüthgen, N. (2006). Measuring specialization in species  
486 interaction networks. *BMC Ecology*, 6, 1–12.
- 487 Brosi, B.J. (2016). Pollinator specialization: from the individual to the community. *New*  
488 *Phytologist*, 210, 1190–1194.
- 489 Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into  
490 ecological theory. *Trends in Ecology & Evolution*, 18, 119–125.
- 491 Burnham, K.P., Anderson, D. & Huyvaert, K.P. (2011). AIC model selection and  
492 multimodel inference in behavioral ecology: some background, observations, and  
493 comparisons. *Behav Ecol Sociobiol*, 65, 23–35.
- 494 Carvalheiro, L.G., Biesmeijer, J.C., Benadi, G., Fründ, J., Stang, M. & Bartomeus, I. *et*  
495 *al.* (2014). The potential for indirect effects between co-flowering plants via shared

496 pollinators depends on resource abundance, accessibility and relatedness. *Ecology*  
497 *Letters*, 17, 1389–1399.

498 Chacoff, N.P., Vázquez, D.P., Lomáscolo, S.B., Stevani, E.L., Dorado, J. & Padrón, B.  
499 (2012). Evaluating sampling completeness in a desert plant-pollinator network. *Journal*  
500 *of Animal Ecology*, 81, 190–200.

501 Chao, A., Colwell, R.K., Lin, C. & Gotelli, N.J. (2009). Sufficient sampling for  
502 asymptotic minimum species richness estimators. *Ecology*, 90, 1125–1133.

503 Devoto, M., Bailey, S., Craze, P. & Memmott, J. (2012). Understanding and planning  
504 ecological restoration of plant–pollinator networks. *Ecology Letters*, 15, 319–328.

505 Dormann, C.F., Frund, J., Bluthgen, N. & Gruber, B. (2009). Indices, graphs and null  
506 models: analyzing bipartite ecological networks. *The Open Ecology Journal*, 2, 7–24.

507 Flanagan, R.J., Mitchell, R.J., Knutowski, D. & Karron, J.D. (2009). Interspecific  
508 pollinator movements reduce pollen deposition and seed production in *Mimulus ringens*  
509 (Phrymaceae). *American Journal of Botany*, 96, 809–815.

510 Fontaine, C., Dajoz, I., Meriguet, J. & Loreau, M. (2005). Functional Diversity of Plant–  
511 Pollinator Interaction Webs Enhances the Persistence of Plant Communities. *PLOS*  
512 *Biology*, 4, e1.

513 Fründ, J., Dormann, C.F., Holzschuh, A. & Tschardtke, T. (2013). Bee diversity effects  
514 on pollination depend on functional complementarity and niche shifts. *Ecology*, 94,  
515 2042–2054.

- 516 Garibaldi, L., Carvalheiro, L.G., Leonhardt, S.D., Aizen, M.A., Blaauw, B.R. & Isaacs,  
517 R. *et al.* (2015). From research to action: enhancing crop yield through wild pollinators.  
518 *Front Ecol Environ*, 12, 439–447.
- 519 Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R. &  
520 Cunningham, S.A. *et al.* (2013). Wild Pollinators Enhance Fruit Set of Crops Regardless  
521 of Honey Bee Abundance. *Science*, 339, 1608–1611.
- 522 Goldberg, D.E. & Barton, A.M. (1992). Patterns and Consequences of Interspecific  
523 Competition in Natural Communities: A Review of Field Experiments with Plants. *The*  
524 *American Naturalist*, 139, 771–801.
- 525 Hsieh, T.C., Ma, K.H. & Chao, A. (2016). iNEXT: iNterpolation and EXTrapolation for  
526 species diversity. R package version 2.0.8.
- 527 James, A., Pitchford, J.W. & Plank, M.J. (2012). Disentangling nestedness from models  
528 of ecological complexity. *Nature*, 487, 227–230.
- 529 Jordano, P. (2016) Sampling networks of ecological interactions. *Functional ecology*, 30,  
530 1183-1893.
- 531 Lanuza, J.B., Bartomeus, I. & Godoy, O. (2018). Opposing effects of floral visitors and  
532 soil conditions on the determinants of competitive outcomes maintain species diversity in  
533 heterogeneous landscapes. *Ecology Letters*, 21, 865–874.
- 534 Lázaro, A., Lundgren, R. & Totland, Ø. (2014). Experimental reduction of pollinator  
535 visitation modifies plant–plant interactions for pollination. *Oikos*, 123, 1037–1048.

- 536 Mayfield, M.M. & Stouffer, D.B. (2017). Higher-order interactions capture unexplained  
537 complexity in diverse communities. *Nature Ecology & Evolution*, 1, 62.
- 538 Morales, C.L. & Traveset, A. (2008). Interspecific Pollen Transfer: Magnitude,  
539 Prevalence and Consequences for Plant Fitness. *Critical Reviews in Plant Sciences*, 27,  
540 221–238.
- 541 Nieto, A., Roberts, S., Kemp, J., Rasmont, P., Kuhlmann, M. & García Criado, M. *et al.*  
542 (2014). European Red List of Bees.
- 543 Pauw, A. (2013) Can pollination niches facilitate plant coexistence? *Trends in Ecology &*  
544 *Evolution*, 28, 30-37.
- 545 Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C. & Loreau, M. *et al.*  
546 (2017). Comparing species interaction networks along environmental gradients.  
547 *Biological Reviews*, 93, 785–800.
- 548 Petchey, O.L. & Gaston, K.J. (2007). Dendrograms and measuring functional diversity.  
549 *Oikos*, 116, 1422–1426.
- 550 Poisot, T., Mouquet, N. & Gravel, D. (2013). Trophic complementarity drives the  
551 biodiversity–ecosystem functioning relationship in food webs. *Ecology Letters*, 16, 853–  
552 861.
- 553 Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E.  
554 (2010). Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol*, 25,  
555 345–353.



- 556 R Development Core Team, R. (2011). R: A Language and Environment for Statistical  
557 Computing. R foundation for statistical computing.
- 558 Song, C., Rohr, R.P. & Saavedra, S. (2017). Why are some plant–pollinator networks  
559 more nested than others? *Journal of Animal Ecology*, 86, 1417–1424.
- 560 Thompson, R.M., Brose, U., Dunne, J.A., Hall Jr., R.O., Hladyz, S. & Kitching, R.L. *et*  
561 *al.* (2012). Food webs: reconciling the structure and function of biodiversity. *Trends in*  
562 *Ecology & Evolution*, 27, 689–697.
- 563 Thomson, D.M. (n.d.). Effects of long-term variation in pollinator abundance and  
564 diversity on reproduction of a generalist plant. *Journal of Ecology*, 0.
- 565 Tylianakis, J.M. & Morris, R.J. (2016). Ecological Networks Across Environmental  
566 Gradients. *Annual Review of Ecology, Evolution, and Systematics*.
- 567 Valdovinos, F.S., Brosi, B.J., Briggs, H.M., Moisset de Espanés, P., Ramos-Jiliberto, R.  
568 & Martinez, N.D. (2016). Niche partitioning due to adaptive foraging reverses effects of  
569 nestedness and connectance on pollination network stability. *Ecology Letters*, 19, 1277–  
570 1286.
- 571 Vanbergen, A., Woodcock, B., Gray, A., Grant, F., Telford, A., Lambdon, P., Chapman,  
572 D.S., Pywell, R.F., Heard, M.S. & Cavers, S. (2014) Grazing alters insect visitation  
573 networks and plant mating systems. *Functional Ecology*, 28, 178-189.
- 574 Vázquez, D.P. & Aizen, M.A. (2004). Asymmetric specialization: a pervasive feature of  
575 plant–pollinator interactions. *Ecology*, 85, 1251–1257.

- 576 Winfree, R. (2013). Global change, biodiversity, and ecosystem services: What can we  
577 learn from studies of pollination? *Basic and Applied Ecology*, 14, 453–460.
- 578 Zhang, J. (2016). Package spaa: SPecies Association Analysis.