

1 **Niche complementarity between pollinators increases**
2 **community-level plant reproductive success**

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5 Short running title: Network structure effects on ecosystem functioning

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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 models including information on simple
30 visitation metrics alone are good in explaining the variability in reproductive success
31 observed. However, insights into the mechanisms through which differences in pollinator
32 diversity translate into changes in reproductive success require additional information on
33 network structure, particularly that reflecting niche complementarity between pollinators.
34 Specifically, we find a positive effect of increasing niche complementarity between
35 pollinators on plant reproductive success.

36 **Introduction**

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

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

56 The few pollination studies that have analysed the effects of changing pollinator
57 diversity for reproductive success at the community level have done so using mainly
58 experimental setups. As an example, a study that experimentally recreated a plant

59 community with 9 plant species and differing levels of pollinator diversity across
60 different enclosures, found that not only pollinator species diversity had an effect for
61 average reproductive success, but that plant-pollinator interaction structure also had an
62 important effect (Fründ *et al.* 2013). In particular, these authors found that niche
63 complementarity between pollinators, in terms of plant species and temperature coverage
64 (a measure of the overlap in the use of plant resources and optimum temperature activity)
65 had a positive effect for average seed set at the community level (Fründ *et al.* 2013). This
66 provides added information on the effects of biodiversity for ecosystem functioning,
67 suggesting that not only the diversity of species present, but also the diversity of roles and
68 ways in which a community is structured, are determinant factors.

69 Indeed, theoretical research has long suggested that the structure of multitrophic
70 communities has an effect for ecosystem functioning (reviewed in Thompson *et al.*
71 2012). This line of research, rooted in niche theory and revamped by food-web studies
72 (MacArthur & Levins 1967; May & MacArthur 1972, Tilman 1982, Godoy *et al* 2018),
73 has greatly advanced theory, but these ideas have not yet been tested using empirical data
74 (but see Poisot *et al.* 2013). Specifically, a major knowledge gap resides in understanding
75 which aspects of structure determine which aspects of function (Thompson *et al.* 2012).
76 This is because although a network perspective has promised to encapsulate complex
77 ecological mechanisms occurring at the community level – such as indirect interactions
78 (Holt 1977, Abrams *et al* 1998) or niche overlap (Woodward & Hildrew 2002)- less
79 attention has been given to the ways in which these mechanisms relate to observed
80 ecosystem processes (Blüthgen 2010). In contrast, we are now at a point in which there is
81 considerable understanding on the attributes characterizing mutualistic interaction

82 networks (Bascompte & Jordano 2007). Especially, in the case of pollination, we have
83 ample knowledge on the attributes that shape these mutualistic interactions at the
84 community level. Amongst them is the prevalence of nested structures, i.e., arrangements
85 where specialist species interact with a subset of the species that generalists interact with
86 (Bascompte *et al* 2003) and which is thought to promote species diversity (Bastolla *et al*
87 2009); or the relatively high extent of complementary specialization at the community
88 scale, which may be directly related to key ecosystem functions (Blüthgen & Klein
89 2011). However, the mechanisms by which these potential pathways affect plant
90 reproduction remain to be understood (Winfree 2013). The time is thus ripe to use the
91 existing knowledge around plant-pollinator network structures to explore the relationship
92 between network structure and ecosystem functioning empirically, with special emphasis
93 being placed on the underlying ecological mechanisms that drive these relationships.

94 Here, we present one of the first efforts linking pollinator visitation and plant
95 reproductive success at the community level using empirical data on plant-pollinator
96 interaction networks and plant reproductive success. To this end, we use a well-replicated
97 dataset encompassing 16 well-resolved plant-pollinator interaction networks coupled with
98 data on the reproductive success of 19 plant species recorded in Mediterranean shrub
99 ecosystems. Our study focuses on understanding whether adding information on selected
100 interaction network structure indices to previously used simple visitation metrics (e.g.,
101 the number and diversity of pollinator species visiting a plant species) aids in better
102 explaining the differences observed in community-wide reproductive success. In doing
103 so, we conducted our analyses focusing on reproductive success at two different levels:
104 (i) at the species level by considering the effect of the position of a focal species within

105 the larger network and its impact on its individual reproductive success, and (ii) at the site
106 level, by evaluating how attributes that describe the whole site might affect average
107 values of reproductive success. Specifically, our study focuses on how the interplay
108 between niche complementarity and redundancy determines reproductive success. Plant
109 reproductive success requires of the delivery of conspecific pollen and thus of a certain
110 degree of niche complementarity (Blüthgen & Klein 2011). Yet, greater values of
111 nestedness, which imply redundancy in species functions, are thought to promote species
112 diversity (Bastolla *et al.* 2009) and stability (Thébault & Fontaine 2010) within plant-
113 pollinator networks. At present, we do not know how either of these network
114 characteristics affects the functions performed by pollinators. Finally, in addition to
115 average values, we also evaluate whether network structure helps explain differences in
116 equity in reproductive success across species within a community, as a measure of
117 evenness in the pollination service delivered.

118 Our results suggest that models including information on simple visitation metrics
119 alone are good in explaining the variability observed in reproductive success. However,
120 insights into the mechanisms through which differences in pollinator diversity translate
121 into changes in reproductive success require additional information on network structure,
122 notably information on the complementarity between the functions performed and the
123 niches occupied by different pollinator species. Specifically, we find a positive effect of
124 increasing niche complementarity between pollinators on plant reproductive success.

125 **Methods**

126 *Plant pollinator interactions*

127 Our study was conducted in SW Spain within the area of influence of Doñana National
128 Park, i.e., within the limits of the Natural Space of Doñana as defined by the local
129 government (Junta de Andalucía, Fig. 1). All sites were located within similar elevations
130 (ranging from 50 to 150 m a.s.l.), similar habitat and soil types, and presented similar
131 plant composition (plant mean Sørensen beta-diversity among sites = 0.41), reducing
132 potential confounding factors. Here, we surveyed 16 Mediterranean woodland patches
133 with an average distance of 7 km between them (min= 3 km, max= 46.5 km). Each site
134 was surveyed 7 times during the flowering season of 2015 (from February to May)
135 following a 100-m x 2 m transect for 30 mins. Along each transect, we identified all plant
136 species and recorded all the floral visitors that landed on their flowers and touched the
137 plant's reproductive parts during each 30-min period. Only floral visitors (from now on
138 referred to as pollinators) that could not be identified in the field were captured, stored
139 and identified in the laboratory by FPM and experts in the different taxonomic groups
140 (see acknowledgements). In addition, at each round we conducted 3 minutes of focal
141 observations recording all floral visitors observed on 3 plant individuals per species
142 belonging to the 19 most common (based on previous surveys) plant species across the
143 study area (mean \pm SD: 6.25 \pm 1.73 species per site). Furthermore, we included some
144 interactions between plant and pollinator individuals that were not observed during the
145 sampling but that were opportunistically recorded immediately before or after the
146 sampling periods, as some of these interactions are difficult to document and might be
147 important to define network structure (Jordano 2016). These opportunistic interactions
148 represented 22.96% of all interactions recorded. All surveys were done under similar

149 weather conditions, avoiding windy or rainy days. Surveys were done during mornings
150 and afternoons with the sampling order being established randomly.

151 *Plant reproductive success*

152 Within each site, we marked between 3 and 12 individuals (mean \pm SD: 6.49 \pm 2.37,
153 Table S2) belonging to 1 to 6 plant species (mean \pm SD: 4.06 \pm 1.69, Table S1),
154 depending on the availability and presence of flowers during the sampling events. For
155 each individual, at the end of the season, we recorded fruit set (i.e. the proportion of
156 flowers that set fruit), the average number of seeds per fruit and the average fruit and
157 seed weight per fruit (1-36 fruits subsampled; mean \pm SD: 11.17 \pm 6.85, Table S3). Our
158 survey included a total of 19 different plant species across our 16 sites. Plants species
159 were selected based on their availability, with sampling being focused on the most
160 abundant plant species. The values at the species level were then averaged per site to
161 calculate unique reproductive success measures at the site level. All plant species depend
162 on pollinators to maximize their reproduction (Table S4).

163 *Data analyses*

164 In order to evaluate the completeness of our sampling of the pollinator and plant
165 community as well as that of their interactions, we estimated the asymptotic number of
166 species present (Chao *et al.* 2009), a non-parametric estimator of species richness for
167 abundance data. This estimator includes non-detected species and allowed us to calculate
168 the proportion detected with our original sampling data. We used Chao 1 asymptotic
169 species richness estimators (Chao *et al.* 2009) and estimated the richness of pollinators,
170 plants and plant–pollinator links accumulated as sampling effort increased up to 100%

171 sampling coverage using package iNEXT (Hsieh *et al.* 2016) within the R environment
172 (R Development Core Team 2011). We then extracted the values covered by our
173 sampling.

174 In order to analyse how differences in network structure might affect plant
175 reproductive success, we constructed plant-pollinator interaction networks by pooling the
176 data for the 7 rounds of sampling. We thus obtained one interaction network per site,
177 representing the number of individuals of different pollinator species recorded visiting
178 each different plant species. For each network, we then proceeded to extract a series of
179 relevant network metrics at the species and site levels.

180 In addition, we checked for potential spatial autocorrelation in our data by means
181 of Mantel correlograms. Autocorrelation values were low for all variables included in our
182 analyses (Figure S1) and hence we treat each site as independent in our analysis.

183 *Species-level network analysis*

184 At the species level, we focused on attributes defining the position of a focal plant species
185 within the larger community. As such, we considered two metrics providing
186 complementary non-redundant information: (i) average niche overlap in terms of
187 pollinators between a focal plant species and each of the other plant species in the
188 community, which estimates the potential indirect interactions between different plant
189 species through shared resources (in this case pollinators), and (ii) centrality, which
190 depicts the importance of the role played by a plant species within the larger community
191 (as resource for a large number of pollinator species) and its contribution to network
192 cohesiveness.

193 Niche overlap was calculated as the average overlap in pollinator species visiting
194 a focal plant and each of the other plants in the community using the Morisita overlap
195 index, a measure of similarity between two sets of data (Zhang 2016). As a measure of
196 centrality, we used weighted closeness centrality, which represents the number of shortest
197 paths going through a focal plant based on a unipartite projection of the bipartite plant-
198 pollinator network using a weighted representation of the network (Dormann *et al.* 2009).
199 Here, links between plant species represent shared pollinator species.

200 Site-level network analysis

201 At the site level, we followed the same logic as the one presented at the species level.
202 Thus, we also calculated two network metrics providing complementary non-redundant
203 information. In this case we focused on (i) nestedness and (ii) pollinator niche
204 complementarity.

205 Nestedness is the property by which specialists interact with a subset of the
206 species that generalists interact with (Bascompte *et al.* 2003). Although there is an
207 ongoing debate in the literature, some studies have found that nested networks are more
208 stable and resilient to perturbations because nestedness promotes a greater diversity by
209 minimizing competition among species in a community (Bastolla *et al.* 2009). However,
210 many network attributes vary with network size and complexity (Blüthgen *et al.* 2006). In
211 the case of nestedness, we know it can be affected by network size and connectance
212 (Song *et al.* 2017). An approach that is often used to correct for this, is to use null models
213 and to compare null-model corrected nestedness values across different networks.
214 However, this approach has been recently shown to present the same issues, as z-scores
215 also change with network size and connectance (Song *et al.* 2017). We thus followed the

216 advice provided by Song et al. (2017) by using a normalized value of the widely-used
217 nestedness metric NODF (Almeida-Neto & Ulrich 2011), $NODF_c$. This normalized value
218 is calculated as $NODF_c = NODF_n / (C * \log(S))$, where C is connectance and S is
219 network size. $NODF_n$ is calculated as $NODF / \max(NODF)$, which is independent of
220 network size and thus comparable across different networks (Song *et al* 2017). To
221 calculate $\max(NODF)$ we used a recently corrected version of the algorithm (Simmons *et*
222 *al* 2019) in all but three sites, where the condition that the number of links > number of
223 species was not met and thus precluded us from using this new version.

224 Niche complementarity metrics are important because plant reproductive success
225 depends on the delivery of conspecific pollen and thus of a certain level of specialization
226 or niche divergence (reviewed in Brosi 2016). To calculate niche complementarity, we
227 used a community-level measure defined as the total branch length of a functional
228 dendrogram based on qualitative differences measured using a Euclidean distance in
229 visitor assemblages between plants (Petchey & Gaston 2007; Devoto *et al.* 2012). All
230 network metrics were calculated using package bipartite (Dormann *et al.* 2009).

231 All of these metrics were calculated using all the data as well as for the subset of
232 the data excluding interactions observed outside of sampling periods. Differences
233 between results are minimal for both and thus we will only present results for the analysis
234 using the full dataset (see Table S12A-H for results removing observations out of
235 transect).

236 *Statistical analyses*

237 In order to evaluate whether adding information on network structure improves our
238 ability to explain differences in reproductive success - both at the species and the site
239 level - we used generalized linear (GLMs) and generalized linear mixed models
240 (GLMMs). In both cases (species and site-level models) we fit two types of models: (i)
241 model 1, that only included simple visitation metrics and (ii) model 2 that additionally
242 included information on network structure. These models are meant to be additive, so that
243 the network metrics included are intended to complement rather than substitute the
244 simple metrics traditionally used.

245 At the species level, response variables included the fruit set for different
246 individuals of each species analyzed using a binomial distribution, the average number of
247 seeds per fruit analyzed using a normal distribution, and the average values of fruit and
248 seed weight fitted to Poisson distributions. The number of seeds per fruit was centered
249 and scaled (i.e., we subtracted column means and divided by standard deviation) to allow
250 meaningful comparisons across species with contrasting life histories. As explanatory
251 variables, model 1 included pollinator richness, and the total number of visits received by
252 each plant species; while model 2 added the two network attributes calculated at the
253 species level: average plant niche overlap and centrality. For both models, we included
254 plant species nested within site and site as random effects to account for the non-
255 independence of several individuals measured per species and site.

256 _____ At the site level, we upscaled our species-level analyses. As response variables we
257 had the average reproductive success per site (i.e., average fruit set analyzed using a
258 binomial distribution, average number of seeds per fruit and average fruit and seed
259 weight using a normal distribution). We thus had a single value per site and no random

260 effects are needed. In this case, model 1 included total pollinator richness and total
261 pollinator abundance (i.e. number of visits received by all plants within the community)
262 as explanatory variables. Model 2, in turn, added information on network structure by
263 including nestedness and pollinator niche complementarity as explanatory variables.

264 Average values of reproductive success at the site level can be driven to a large
265 extent by a single plant species. Yet, what will determine the persistence of a diverse
266 plant community, is the presence of some sort of “equity” or evenness in reproductive
267 success across the whole community. We therefore calculated a measure of equity in
268 reproductive success at the site level as the proportion of species with normalized
269 (between 0 and 1) average fruit set values that were above the 50th percentile. As any
270 selected threshold is arbitrary, we repeated this using the 25th and 75th percentile
271 thresholds (Byrnes *et al* 2014). We then used the same framework as that used for species
272 and site-level analyses and fit the same models 1 and 2 GLMs but using equity in
273 reproductive success as the response variable and fitting a binomial distribution.

274 In all cases, we used variance inflation factors to check for collinearity between
275 explanatory variables. Additionally, we ran residual diagnostics to check if model
276 assumptions were met. Then, we used the Akaike Information Criterion (AIC) to
277 compare model performance and complexity. Whenever the difference between the AIC
278 of both models was < 2 ($\Delta AIC < 2$), we considered that both models were equally good
279 (Burnham *et al.* 2011). All predictor variables were standardized prior to analysis. For
280 every model we also calculate the R^2 value, using the approximation suggested for
281 generalized mixed models when necessary (Nakagawa *et al* 2017).

282 Finally, we tested whether the importance of network structure in explaining
283 differences in equity in reproductive success within communities increases with the
284 number of plant species being considered. We expect that when only one plant species is
285 considered, then the importance of network structure will be negligible, while we expect
286 this importance to increase as more plant species are considered (up to a maximum
287 number of 6 species which is the maximum we have measured in our study at a particular
288 site).

289 To test this, we ran a simple simulation in which the number of species
290 considered increased at each step and for each step we re-calculated equity in
291 reproductive success. Instead of drawing plant species randomly for each step, we tested
292 all possible combinations for each plant number level and network, as the number of
293 combinations is small (e.g. for $n = 3$ plant selected out of 6 there is only 20 possible
294 combinations). Then, we tested if the relationship between equity in reproductive success
295 and functional complementarity (given its importance in determining differences in
296 reproductive success, see Results section) changes as a function of the number of plants
297 considered within our simulated communities. To this end, for each level of species
298 number considered, we randomly selected one of the generated equity values across each
299 of the 16 communities and regressed these 16 values against our network level predictor
300 and extracted the model slope estimates. We repeated this process 1,000 times and
301 averaged all slope estimates. We expect that the more plants considered, the larger the
302 resulting average estimates will be. Note that we only interpret the mean effects, as the
303 variance among different plant number of species considered depends on the initial
304 number of possible combinations.

305 Results

306 Within our sampling we recorded 1,472 plant-pollinator interactions involving 277
307 pollinator species and 57 plant species. Within the pollinator community the distribution
308 of individuals in different orders was: 87.84% Hymenoptera, 6.78% Diptera, 4.05%
309 Coleoptera and 1.09% Lepidoptera.

310 Our sampling completeness analyses revealed that with our survey we were able
311 to capture 18-62% of pollinator species (average = 35%), 47-98% for plant species
312 (average = 78%) and 13-41% for plant-pollinator links (average = 27%), in line with that
313 obtained with other studies (e.g., Chacoff *et al.* 2012, Fig. S2). Our values of sampling
314 completeness are slightly smaller in the case of pollinators, probably as a consequence of
315 the great diversity found in the Mediterranean region and within our study area in
316 particular, a hotspot of insect diversity (Nieto *et al.* 2014). In addition, the fact that we
317 include an extra effort to capture rare interactions observed outside of our main sampling
318 might also increase the number of singletons which directly affect richness estimates.

319 *Species-level analyses*

320 At the species level, in the case of fruit_set, our results show that model 2 shows the best
321 fit to our data (lowest AIC value), and fixed effects explains 4% of the variability
322 observed. In this case, we find a positive effect of a network structure metric, the
323 centrality of a focal plant within the overall network on its fruit set (Table 1, Fig. 2A).

324 For the average number of seeds per fruit, our results show again that model 2
325 shows the best fit, with fixed effects explaining 4% of the variability observed in our

326 data. In this case, we find a positive effect of the niche overlap between plant species on
327 the number of seeds produced (Table 1B, Fig. 2B).

328 For all other measures of reproductive success considered (i.e., fruit and seed
329 weight), both models had similar fits, with $\Delta AIC = 2.2$ and 2 respectively. However,
330 none of the variables included within our model explain the differences observed (Tables
331 S5-S6).

332 Site-level analyses

333 At the site level, we find different patterns for fruit set and the number of seeds per fruit
334 as compared to those for fruit and seed weight. In the case of fruit set and the number of
335 seeds per fruit, we find that both model 1 and 2 are equally good in describing the
336 differences observed when penalizing for model complexity (i.e., $\Delta AIC < 2$; Burnham et
337 al 2011). This suggests model 2 is a good model despite its added complexity, and
338 actually shows a substantially better predictive ability than model 1 ($R^2 = 0.59$ for model
339 2 versus 0.47 for model 1 in the case of fruit set and $R^2 = 0.52$ for model 2 versus 0.31
340 for model 1 in the case of the number of seeds per fruit) and therefore we will comment
341 results for this model only. In particular, we find that both fruit set and the number of
342 seeds per fruit are positively related to niche complementarity between pollinators (Table
343 2, Fig. 3). Additionally, we find a negative effect of site-level pollinator richness on
344 average fruit set (Table 2A, Fig. 3).

345 Contrastingly, in the case of weight variables (fruit and seed weight), in both
346 cases we find that the best model is model 1, i.e., that only including simple visitation
347 metrics ($R^2 = 0.29$ in the case of fruit weight and 0.51 in the case of seed weight). Here,

348 we find a consistent positive effect of site-level pollinator richness for both weight
349 descriptors (Tables S7-S8, Fig. 4).

350 *Equity in fruitset*

351 When evaluating the effect of differences in community composition and network
352 structure for equity in reproductive success across the different species within a
353 community we find that model 1 is the best model for all the thresholds considered (50th,
354 25th and 75th percentiles). However, none of the variables considered are able to explain
355 differences observed in equity across sites (Tables S9, S10, S11).

356 Within our simulation evaluating the effect of niche complementarity on equity in
357 reproductive success as more plants within the community are considered, we find that
358 the effect of complementarity becomes more important as the reproductive success of
359 more species is considered (Fig. 5). This importance seems to reach some sort of plateau
360 at 6 species. However, this should be further evaluated, as this is the maximum number of
361 species simultaneously observed in a community for our study, which precludes us from
362 simulating further numbers of species.

363 **Discussion**

364 The existence of relationships between interaction network structure and ecosystem
365 function have ve been long hypothesized, yet, the specific mechanisms by which structure
366 influences function have remained elusive until now (Thompson *et al.* 2012). Our results
367 show that different aspects of network structure affect different dimensions of ecosystem
368 functioning. In particular, we find that the centrality of a plant species within a
369 community, which measures the number of connections it receives from other species in

370 the community, has a positive effect for its fruit set. At the site level, we find that greater
371 values of niche complementarity between pollinators result in larger average fruit sets
372 and number of seeds per fruit.

373 One of the first conclusions we can extract from the fact that in most cases both of
374 the models we considered (i.e., the simple model based on visitation metrics and the more
375 complex one including network structure metrics) were equally good, is that the added
376 complexity of measuring the full network of interactions may not pay off for rapid
377 assessments. Hence, simple visitation metrics, such as pollinator richness, might be
378 enough to describe general patterns (Garibaldi *et al.* 2013, 2015). Yet, adding network
379 level information may inform us of the potential ecological mechanisms underlying the
380 processes driving the observed patterns.

381 Consistent with previous experimental (Fontaine *et al.* 2005; Fründ *et al.* 2013),
382 theoretical (Pauw 2013), and empirical studies (Valdovinos *et al.* 2016, Poisot *et al.*
383 2013), we find that niche complementarity is key in determining differences in
384 reproductive outputs. Indeed, we find that communities where there is less overlap in the
385 niches occupied by pollinator species had greater values of reproductive success, both
386 greater fruit set and larger numbers of seeds per fruit. This therefore reflects the fact that
387 reproductive success in plant species requires the delivery of conspecific pollen and thus
388 of a certain degree of specialization amongst pollinator species on a particular plant
389 resource in order to avoid the negative effects of inter-specific pollen deposition (e.g.,
390 pollen loss, Flanagan *et al.* 2009) or interference with conspecific pollen (Morales &
391 Traveset 2008). However, we also find that some level of redundancy in these functions

392 is needed as revealed by the positive effect of plant niche overlap on the number of seeds
393 per fruit at the species level.

394 In our study, we did not find an effect of nestedness for reproductive success in
395 any case. This metric, widely used across network analysis, and which is deemed to
396 stabilize natural communities (Bastolla *et al.* 2009 but see James *et al.* 2012), does not
397 seem to play a direct role in ecosystem function measured as plant reproductive success.
398 However, our study is limited to a maximum of six common plant species per
399 community, and including more species, including rare species, might reveal different
400 patterns, in which nestedness and the redundancy it implies might play a more important
401 role.

402 Site-level plant reproductive success measured as average fruit or seed set across
403 all the species considered, is an important part of the functions delivered by pollinators to
404 plants. However, these average values might be masking a great deal of variability
405 amongst plant species, and thus a nuanced view of the effect of pollinators on whole-
406 plant ensembles is needed. This can be captured by the effect of pollinators on equity in
407 reproductive success across plant species. This aspect ensures that reproductive success is
408 equally distributed amongst a larger number of species, thus contributing to the
409 maintenance of greater species diversity values in natural populations. Indeed, we know
410 that plant species diversity within a community is largely driven by different types of
411 direct and indirect interactions including those amongst plant species (e.g., resource
412 competition, Goldberg & Barton 1992, or facilitation, Bruno *et al.* 2003), as well as those
413 defining antagonistic (e.g., involving pathogens, Bagchi *et al.* 2010), or mutualistic
414 interactions (e.g, pollinators, Benadi *et al.* 2013; Lanuza *et al.* 2018). However,

415 equitability in reproductive success across species is seldom taken into account, despite
416 its importance in maintaining genetic diversity and ensuring the resilience of populations
417 to further change.

418 In the case of equity, we did not find a strong effect of either simple visitation or
419 network structure metrics. However, the results of our simulation on the importance of
420 network structure as the number of plant species considered increases, shows us that this
421 effect increases when more than four plant species are considered. This implies that if we
422 were able to measure reproductive success for all the plant species in all the communities
423 (which is not feasible given constraints in sampling effort), we might find that the effects
424 of network structure on equity might be more prevalent.

425 One of the unexpected results of our analyses is the strong negative effect of
426 pollinator richness for fruit set at the site level. An explanation to this might be the fact
427 that pollinator richness here includes all the pollinators recorded during our sampling
428 efforts, i.e., it includes species that do not pollinate some of the species whose
429 reproductive success was measured. More complex communities with more pollinators,
430 but also with more plant species (Pearson correlation between plant and pollinator
431 richness = 0.42 in our case) may require stabilizing mechanisms that reduce the
432 competition exerted by the dominant plant species. A way to reduce the competition
433 exerted by these dominant species, which are precisely those evaluated in this study, is by
434 reducing their reproductive success (Lanuza *et al* 2018, Stavert *et al* 2019). These ideas
435 open the door to exploring the positive or negative effects of the complete pollinator
436 community on full plant species coexistence, which may be determined by density-
437 dependence effects (Benadi & Pauw 2018). In our case, while fruit set is negatively

438 related to pollinator richness, it is important to note that fruit and seed weight show the
439 opposite relationship, indicating that this density-dependent effect might only be limiting
440 fruit quantity and not fruit quality. Thus, taking into account the densities of co-flowering
441 plant species may be the next step (Vanbergen *et al.* 2014).

442 Our study illustrates the complexity of linking network structure to ecosystem
443 function empirically, because measuring both structure and function is challenging. For
444 example, there is an ongoing debate as to which network metrics better reflect classic
445 ecological mechanisms, such as niche partitioning or competition (Delmas *et al* 2018).
446 Here, we focus on testing two specific hypotheses, but other structural properties can be
447 explored when more data becomes available. Furthermore, the structure of plant-
448 pollinators networks is dynamic due to ecological and evolutionary reasons, but so far,
449 we are only able to characterize it for single snap-shots. Moreover, different aspects of
450 functioning may be important, such as the presence of non-linear relationships or the
451 need to consider the functioning of both trophic levels (Godoy *et al* 2018). In terms of
452 plant reproductive success and the functions performed by pollinators we can measure
453 different aspects, ranging from pollen deposition (the direct pollinator function), to its
454 final effects on plant fitness. Here, we focus on an intermediate stage including fruit
455 quantity and quality, which is of clear ecological importance.

456 In summary, our findings show that the analysis of natural communities of
457 interacting species using network analysis not only represents an ideal way of visualizing
458 and grasping the complexity present within these communities. Rather, it also represents
459 a manner of mechanistically understanding differences observed across the reproductive

460 success of individuals and/or species while linking them to potential ecological
461 mechanisms.

462 **Data accessibility**

463 All the data used is available

464 <https://zenodo.org/account/settings/github/repository/ibartomeus/BeeFunData> and the
465 code used to generate all results can be found at <https://doi.org/10.5281/zenodo.3364037>.

466

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475 access to the park.

476 **Table 1.** Results of GLMM showing the effect of simple visitation and network structure
 477 metrics on A) species-level fruit_set and B) average number of seeds per fruit based on
 478 best model selected. Bold letters indicate variables with large effects.
 479

<u>A) Fruit set</u>	<u>Estimate</u>	<u>Std.Error</u>	<u>z.value</u>
<u>(Intercept)</u>	<u>1.72</u>	<u>0.21</u>	<u>8.16</u>
<u>Pollinator richness</u>	<u>-0.01</u>	<u>0.21</u>	<u>-0.07</u>
<u>Total number of visits</u>	<u>0.14</u>	<u>0.25</u>	<u>0.57</u>
<u>Centrality</u>	<u>0.46</u>	<u>0.25</u>	<u>1.81</u>
<u>Plant niche overlap</u>	<u>0.05</u>	<u>0.24</u>	<u>0.20</u>

480
 481

<u>B) Seeds per fruit</u>	<u>Estimate</u>	<u>Std..Error</u>	<u>t.value</u>
(Intercept)	0.05	0.14	0.36
Pollinator <u>richness</u>	0.14	0.15	0.90
Total number of visits	-0.01	0.16	-0.04
Centrality	-0.15	0.15	-1.00
<u>Plant niche overlap</u>	0.22	0.17	1.32

482

483

484 **Table 2.** Results of GLM showing effect of simple visitation and network structure
 485 metrics on A) site-level average fruit set and B) site-level average number of seeds per
 486 fruit based on best model selected. Bold letters indicate variables with large effects.

A) <u>Fruit set</u>	Estimate	Std. Error	z value
(Intercept)	1.22	0.13	9.18
Pollinator richness	-0.75	0.17	-4.35
Total number of visits	-0.1 <u>6</u>	0.16	-1.0 <u>2</u>
Nestedness	0.1 <u>1</u>	0.1 <u>6</u>	0.7 <u>2</u>
<u>Pollinator niche complementarity</u>	0.2<u>9</u>	0.1<u>8</u>	1.5<u>7</u>

487

488

B) <u>Seeds per fruit</u>	Estimate	Std. Error	t value
(Intercept)	45.3 <u>7</u>	8.5 <u>5</u>	5.3 <u>1</u>
Pollinator <u>richness</u>	3.2 <u>6</u>	12.1 <u>8</u>	0.2 <u>7</u>
Total number of visits	8.3 <u>8</u>	9.9 <u>9</u>	0.8 <u>4</u>
Nestedness	-10.9 <u>4</u>	10.2 <u>1</u>	-1.0 <u>7</u>
<u>Pollinator niche complementarity</u>	29.5<u>1</u>	13.3<u>1</u>	2.2<u>1</u>

489

490

491 **Figure legends**

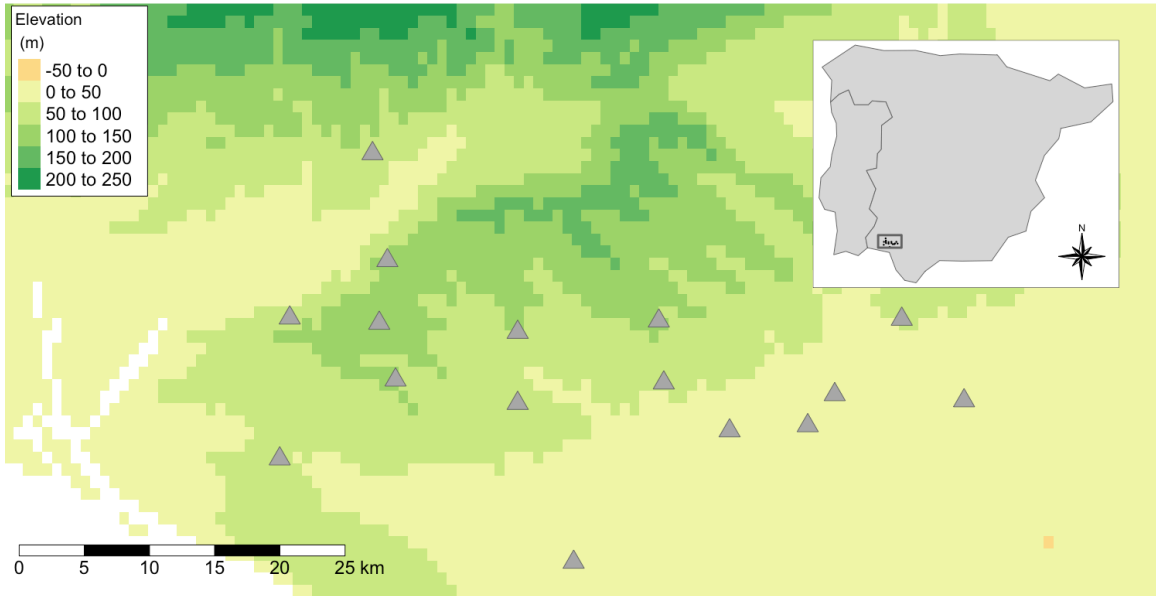
492 **Figure 1.** Map showing location of 16 study sites. Inset shows location of study area
493 within SW Spain.

494 **Figure 2.** Partial residual plot showing the effect of a single predictor for the relationship
495 between A) plant species centrality and fruit set for each of the plant species considered
496 and B) plant niche overlap and average number of seeds per fruit. Dots represent each of
497 the individuals sampled for each species within each site.

498 **Figure 3.** Partial residual plots showing the effect of A) pollinator richness, and B) niche
499 complementarity between pollinator species on site-level average fruitset and C) niche
500 complementarity between pollinator species on the average number of seeds per fruit at
501 the site level. Dots represent average values of fruit_set at the level of the community for
502 all plant species considered (N=16 sites).

503 **Figure 4.** Partial residual plots showing the effect of pollinator richness on site-level
504 average A) fruit and B) seed weight. Dots represent values for each site (N=16 sites).

505 **Figure 5.** Results of simulation evaluating the importance of niche complementarity in
506 determining differences in equity in reproductive across communities harboring from one
507 to six species. Points represent average values across 1,000 simulated combinations.

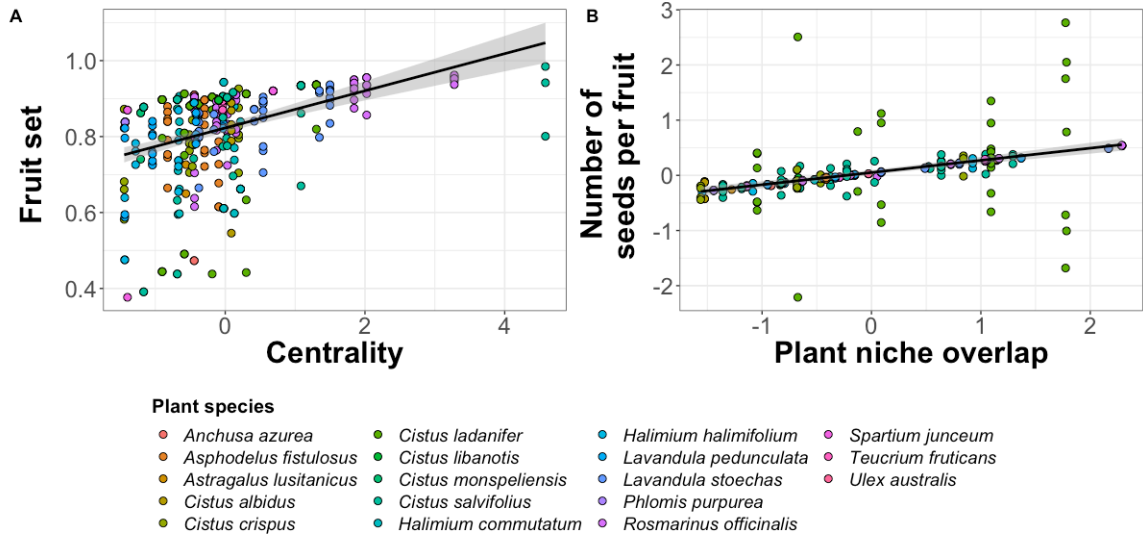


508

509 **Figure 1.**

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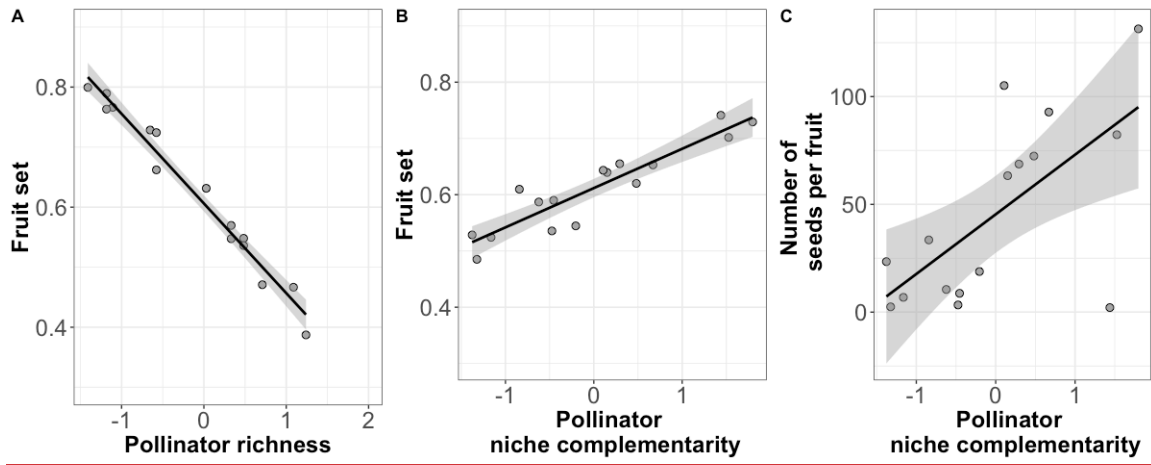
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Figure 2.

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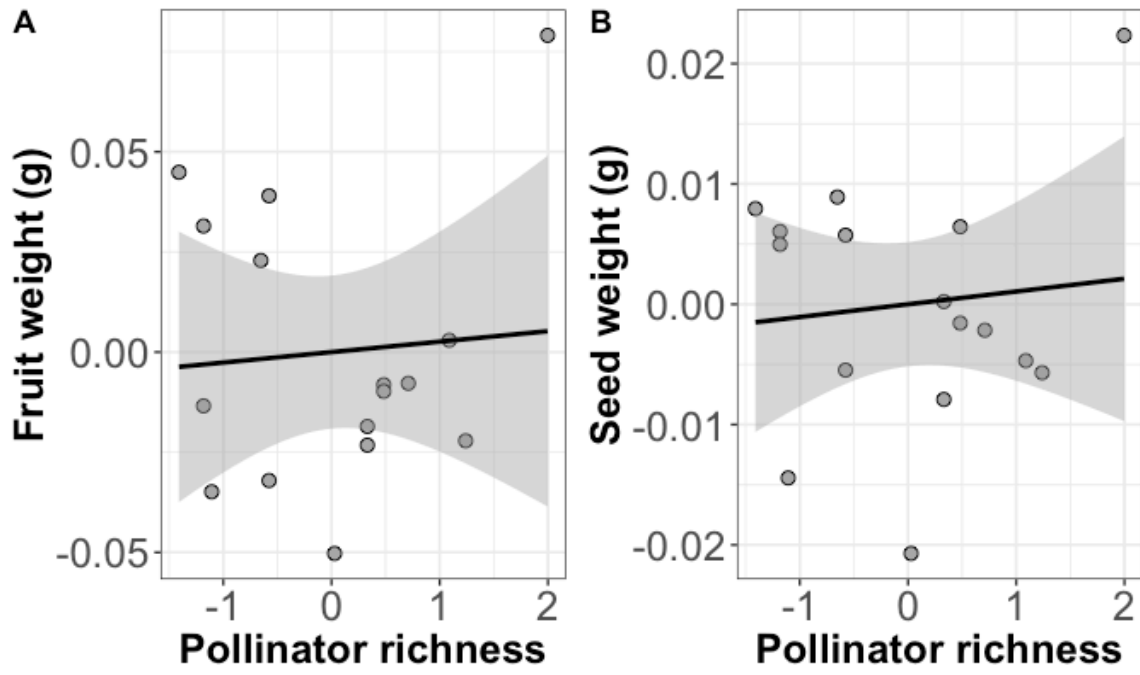
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518 **Figure 3.**

519

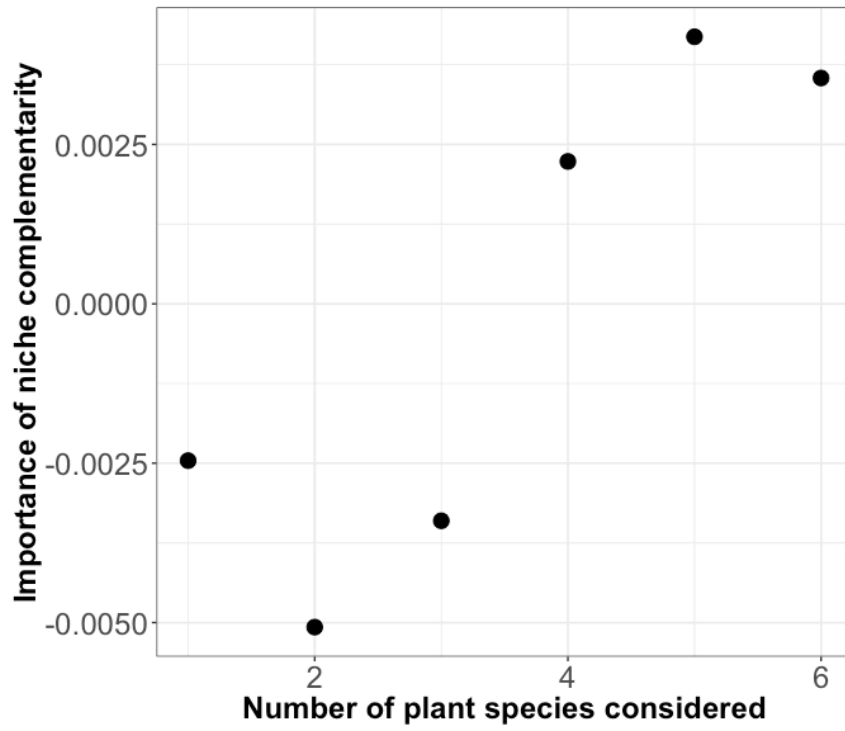
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522 **Figure 4.**

523



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Figure 5.

526

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