

# **SEASONAL VARIATION IN FLORAL RESOURCES AND THEIR POTENTIAL CONSEQUENCES ON PLANT- POLLINATOR NETWORK STRUCTURE**

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My contribution to this study started in February 2017. I conducted the following tasks: 1) Design of the specific objectives (with help from my supervisors); 2) Literature search and preparation of theoretical background; 3) Preparation of the data base and calculation of the variables needed; 4) Design of statistical analysis (with help from my supervisors) and execution; 5) Interpretation of results and preparation of manuscript (with help from my supervisors).

This manuscript follows the instructions of Ecology.

## 1 **Abstract**

2 Seasonality defines the variation in environmental conditions occurring at specific intervals  
3 within a year. Because seasonality follows a recurrent pattern, associated changes in community  
4 structure are relatively well understood. However, little is known about how seasonality affects  
5 the structure of ecological interactions. Mediterranean plant-pollinator communities experience  
6 strong seasonal declines in floral resource availability from spring to summer. We contemplate  
7 two possible, not mutually exclusive, pollinator responses to this seasonal decline. First, based on  
8 optimal foraging theory, pollinators might be able to restrict their visits to their preferred flower  
9 hosts in spring, while being forced to widen their trophic niche in summer (“ecological  
10 response”). Under this scenario, we would expect plant-pollinator networks to become more  
11 generalized in summer. Second, based on niche segregation theory, and provided the seasonal  
12 pattern in resource availability is consistent through the years, pollinators active in summer might  
13 have evolutionarily segregated their floral niches to mitigate interspecific competition  
14 (“evolutionary response”). Under this scenario, we would expect plant-pollinator networks to  
15 become more specialized in summer. Here, we describe seasonal changes in visitation rate (a  
16 proxy for floral resource availability) in a Mediterranean scrubland, and analyze whether these  
17 changes affect plant-pollinator network structure (seven network metrics related to  
18 specialization). We use data from a 3-year study in which plant-pollinator interactions were  
19 surveyed weekly from March to June. We find that weekly floral resource availability  
20 consistently decreases from spring to summer. Conversely, network structure variation does not  
21 follow a seasonal pattern. We also find that the weekly network structure is mostly dependent on  
22 network size. The effect of visitation rate is small and restricted to one of the seven network  
23 metrics (pollinator generality). We suggest two possible explanations for these results. First, the

24 seasonal reduction in floral resource availability may be insufficient for resources to become  
25 limiting in our community. Pollinators would then receive insufficient pressure (ecological or  
26 evolutionary) to alter their trophic niche. Second, the two proposed responses (ecological and  
27 evolutionary) may cancel each other out, resulting in few changes in network structure. Overall,  
28 our results support the idea that the macroscopic topology of interaction network is highly  
29 consistent.

30

31

32 **Key-words:** *seasonality, mutualistic network, network structure, niche overlap, plant-pollinator*  
33 *community, resource availability.*

34

## 35 **Introduction**

36 Seasonality can be defined as the variation in environmental conditions, including climatic  
37 factors and resource availability, occurring at specific regular intervals within a year. These  
38 periodic variations regulate the timing of the life-cycle of organisms (Visser et al. 2010), and  
39 therefore seasonality is believed to play a fundamental role in the evolution of the phenology of  
40 biological events. Ultimately, because different organisms schedule their activities differently  
41 over the course of the year, seasonality has a strong effect on the composition of animal and plant  
42 communities (Olesen et al. 2008, Valverde et al. 2014). In turn, these changes in species  
43 composition may bring about seasonal changes in community structure, including richness,  
44 abundance and diversity (Rotenberry et al. 1979, Gasith et al. 1999, Thompson et al. 1999,  
45 Tonkin et al. 2016), as well as in community's functional structure (McNamara & Houston 2008,  
46 Osorio et al. 2016).

47 Because seasonality follows a recurrent pattern, seasonal changes in community structure and  
48 composition are more or less predictable and relatively well understood. However, we know  
49 much less about how seasonality may affect the structure of species interactions within  
50 communities. Interaction networks are typically analyzed over entire year cycles, thus providing  
51 a complete view of the interactions occurring at a given site or geographical area. However, to  
52 analyze seasonal changes, year-long interaction networks need to be spliced into shorter intervals.  
53 This approach accounts for species turnover (Alarcón et al. 2008, CaraDonna et al. 2017), thus  
54 avoiding the inclusion of “temporal forbidden links” (interactions that cannot occur due  
55 phenological mismatch between two species; Jordano et al. 2003) in the calculation of network  
56 metrics. In addition, this approach accounts for potential variation in pollinator foraging  
57 behaviour (Kaiser-Bunbury et al. 2010) and resource consumption rates (Price et al. 2005), thus

58 helping to unveil interaction patterns that are usually hidden due to temporal data accumulation  
59 (Levin 1992, Baldock et al. 2011, Rasmussen et al. 2013, Simanonok et al. 2014, Valverde et al.  
60 2014).

61 Seasonal changes in community structure have been well-documented in plant-pollinator systems  
62 (Bosch et al. 1997, Basilio et al. 2006, Valverde et al. 2014, Kemp et al. 2016). Studies in  
63 Mediterranean environments, in particular, report a strong seasonal shift in flower availability  
64 and pollinator visitation rates from spring to summer. A situation of high flower production and  
65 low visitation rates in spring is followed by a scenario of low flower production and high  
66 visitation rates in summer (Herrera 1988, Cohen & Shmida 1993, Petanidou et al. 1995, Bosch et  
67 al. 1997, 2009, Filella et al. 2013, Flo et al. submitted). This imbalance is the basis for the  
68 changing floral market theoretical model of Cohen & Shmida (1993), whereby the spring market  
69 is regulated by pollinators and the summer market by plants.

70 These changes in floral resources and visitation rates are likely to have implications on the  
71 foraging decisions of pollinators and therefore to affect the structure of plant-pollinator  
72 interactions. Visitation rates (visits per flower and time unit) are a good indicator of resource use  
73 by pollinators (Inouye 1978). Low visitation rates indicate a surplus of floral resources for the  
74 available pollinator population, whereas high visitation rates imply that the resources are being  
75 more intensely exploited. We envision two possible responses to the decrease of floral resource  
76 availability from spring to summer observed in Mediterranean systems. The first response  
77 (henceforth “ecological response”) is based on optimal foraging theory (MacArthur & Pianka  
78 1966, Pyke et al. 1977, Stephen & Krebs 1986). According to this view, pollinators should  
79 concentrate their visits on their most preferred flower species in spring, but could be forced to  
80 widen their range of host plants in the summer if resources become limiting (Owen-Smith 1994,

81 Fontaine et al. 2008, Santos et al. 2014, Khadka et al. 2017). Even though most pollinators are  
82 generalists (Waser et al. 1996), at a given site they may concentrate most of their visits on one or  
83 a few preferred host plants (Goulson 1999, Petanidou et al. 2008, Fründ et al. 2010). The second  
84 response (henceforth “evolutionary response”) is based on the limiting similarity principle  
85 (MacArthur & Levins 1967, Pianka 1974). According to this view, if competition for limiting  
86 resources in summer is strong and consistent across years, then natural selection may favor niche  
87 segregation of pollinators, thus reducing resource flower use overlap (Sale 1974, Smith et al.  
88 1978, Tilman 1982). Processes of niche segregation due to seasonal variations in resource  
89 availability have been documented empirically (Smith et al. 1978, Spiller 1986, Dubowy 1988,  
90 Deus et al. 2003). Importantly, even though the two proposed responses (“ecological” and  
91 “evolutionary”) are not mutually exclusive, they point in different directions (higher  
92 generalization in summer versus higher specialization in summer, respectively).

93 In this study, we describe seasonal changes in floral resource production and visitation rates in a  
94 Mediterranean scrubland over 3 years, and analyze whether these seasonal changes affect plant-  
95 pollinator network structure. Our objectives are: (1) to confirm whether floral resources and  
96 pollinator visitation rates follow seasonal (spring-summer) patterns and if these patterns are  
97 consistent over 3 years; (2) to determine whether the structure of the plant-pollinator interaction  
98 network also changes seasonally and whether these changes are consistent over 3 years; (3) to  
99 analyze the effect of visitation rates (as a proxy of floral resource availability) on the structure of  
100 the interaction network. Increased generalization of the network when resources are scarce would  
101 support the “ecological response”, based on optimal foraging theory. The opposite outcome,  
102 increased specialization when resources are scarce would support the “evolutionary response”,  
103 based on niche segregation theory.

104 **Methods**

105

106 ***Study site***

107 Fieldwork was conducted in a 1-h plot during three consecutive years (2006, 2007, 2008) in a  
108 Mediterranean scrubland located in El Garraf Natural Park (Barcelona, NE Spain, UTM:  
109 409340.35, 4569657.08). The weather is strongly seasonal, with cool rainy springs (mean  
110 temperature: 14°C; precipitation: 39 mm), and hot dry summers (22°C, 13 mm). The vegetation is  
111 dominated by perennial shrubs (*Quercus coccifera*, *Rosmarinus officinalis* and *Thymus vulgaris*).

112 Field survey started at the beginning of March and ended at the end of June, when flowering is  
113 arrested in coincidence with summer drought. The timing of the flowering arrest was not entirely  
114 coincidental across years. As a result, the number of surveyed weeks differed between years (16  
115 in 2006, 15 in 2007 and 18 in 2008).

116

117 ***Flower transects***

118 Data on flower production and composition were obtained in weekly surveys along six  
119 permanent transects (50x1m) crisscrossing the 1-ha-plot. On each survey, all open flowers of the  
120 23 most abundant plant species (Supplementary Material Table S1) were recorded. These 23  
121 plant species account for the vast majority (99.7%) of all flowers counted in the transects (Flo et  
122 al. submitted).



123 *Floral resources*

124 Because pollinators are likely to respond to floral resource availability, rather than flower  
125 availability, in 2006-2007 we measured pollen and nectar production of the 23 plant species. To  
126 measure pollen production, we collected 10-15 flowers buds per species and kept them in vials  
127 with 70% ethanol. In the laboratory, each bud was dissected, and the number of anthers was  
128 counted under a stereomicroscope. Three selected anthers per flower (all anthers in Fabaceae)  
129 were removed, suspended in 2ml of 70% ethanol and sonicated in a water bath for 2-4 minutes to  
130 dislodge pollen grains. Anther tissue was subsequently removed and 9ml of isotonic solution  
131 were added. The number of pollen grains in the resulting suspension was then estimated using an  
132 electronic particle counter (Coulter Multisizer) with a 200 $\mu$ m aperture. Pollen length and width  
133 were measured under a microscope at 400 X on 15 grains per species. Pollen grain volume was  
134 calculated with the formula of an ellipsoid or sphere, depending on the shape of the pollen grain.  
135 The total pollen volume production per flower (expressed in mm<sup>3</sup>) was calculated as the product  
136 of the number of grains multiplied by their volume.

137 To measure nectar production, between 19 and 144 flower buds per species were covered with  
138 nylon bags. Twenty-four hours later, the accumulated nectar was measured using Drummond  
139 micropipettes (0.25, 0.50 and 1 $\mu$ l). To measure nectar concentration, we used field refractometers  
140 (Eclipse, Bellingham & Stanley). We calculated sugar content per flower (expressed in mg; Dafni  
141 1993) as a measure of nectar production. These measures were taken in 2006 and 2007 in the  
142 same study plot (sample sizes: pollen = 10-15 flowers per species; nectar = 18-144 flowers per  
143 species). The use of data from two years for our three-year study assumes that intra-specific  
144 pollen and nectar production per flower was consistent throughout the duration of the study. Even  
145 though pollen and nectar production in any given species may vary from year to year, this

146 variation is small compared to the large differences occurring across the species of our  
147 community (Flo et al. submitted)

148

#### 149 ***Interaction surveys***

150 Pollinators were surveyed two to three times per week under fair weather from 10:00 to 17:00h.  
151 On each sampling day, 5 to 10 representative individuals of each plant species in bloom were  
152 selected and their flowers counted. These plants were observed several times throughout the day  
153 for 4 minute intervals, during which time each pollinator visiting the flowers was recorded. We  
154 define visit as a contact between an individual pollinator and an individual plant, regardless of the  
155 number of flowers visited by that pollinator on that plant. Pollinators that could not be identified  
156 in the field were captured for further identification in the lab. For further sampling details, see  
157 Bosch et al. (2009). In 2007, pollinator surveys in weeks 5 (April), 6 (April) and 9 (May) could  
158 not be conducted due to prevailing bad weather conditions.

159

#### 160 ***Resource production and visitation rates***

161 Weekly pollen and nectar production were computed as the volume of pollen ( $\text{mm}^3$  of pollen/ $\text{m}^2$ ),  
162 and the quantity of nectar (mg of sugar/ $\text{m}^2$ ) produced by all plant species blooming each week,  
163 respectively. Weekly visitation rates based on pollen and nectar were computed as the number of  
164 pollinator visits recorded per volume of pollen and minute (visits/ $\text{mm}^3$  pollen and minute), and  
165 the number of pollinator visits recorded per mg of sugar and minute (visits/mg of sugar and min).  
166 Further details on the computation of these variables are provided in Supplementary Material  
167 Appendix S1. We use visitation rates as a measure of flower resource use by pollinators.

168

169 ***Interaction networks***

170 To characterize weekly interaction network structure, we built a bipartite network for every  
171 sampling week of the 3 years of study. These networks were built as adjacency matrices, with  
172 pollinator species occupying the columns and plant species the rows, and cells containing a  
173 measure of interaction strength. We computed weekly interaction strength between plant species  $i$   
174 and pollinator species  $j$  as the number of visits between the two species recorded in the  
175 interaction surveys divided by the number of surveyed flowers of species  $i$  and by 4 minutes,  
176 weighted (multiplied) by the number of flowers of species  $i$  counted in the transects in that week  
177 (Kaiser-Bunbury et al. 2009, Supplementary Material Appendix S1).

178

179 ***Network metrics***

180 Since our hypothesis links resource availability and specialization, we selected seven network  
181 metrics related to network specialization: 1) Weighted connectance; a measure of the proportion  
182 of all possible interactions that are really occurring. It is computed as the average number of  
183 pairwise interactions per species divided by the number of species in the network (Tylianakis et  
184 al. 2007). Low values of weighted connectance indicate that the network is poorly connected and  
185 therefore specialized; 2) Interaction evenness; based on Shannon's diversity Index (Tylianakis et  
186 al. 2007), it measures the uniformity of interactions between species in a network. It ranges from  
187 0 (total heterogeneity) to 1 (total homogeneity). Low values of interaction evenness denote  
188 network specialization; 3) Pollinator generality; a measure of the number of plant species that  
189 interact with each pollinator species. It is computed as the mean number of plant species

190 interacting with each pollinator species weighted by the marginal values of plant and pollinator  
191 species in the interaction matrix (Bersier et al. 2002). Low values of pollinator generality indicate  
192 that pollinators concentrate most of their visits on few plant partners and therefore are  
193 specialized; 4) Plant generality (equivalent to vulnerability in food webs) (Bersier et al. 2002).  
194 Same as above for plants; 5) Pollinator niche overlap; based on Morisita-Horn's index, it  
195 provides a measure of similarity in the identity of interactions between pollinators species  
196 (Ricklefs & Lau 1980). It ranges from 0 (no niche overlap) to 1 (perfect niche overlap). Low  
197 values of niche overlap reflect niche partitioning and therefore pollinator specialization; 6) Plant  
198 niche overlap; same as above for plants; 7)  $H_2'$ ; a measure of specialization of the entire network  
199 (Blüthgen et al. 2006). It is based on Shannon's diversity index, and calculates the extent to  
200 which realized interactions deviate from the interaction pattern expected under a neutral scenario  
201 in which species interact according to their abundances. It ranges from 0 (no specialization) to 1  
202 (maximum specialization).

203 All metrics were calculated with Bipartite v.1.16 (Dormann et al. 2009) for R (R Development  
204 Core Team 2017). A few weeks at the beginning and at the end of the flowering periods (weeks  
205 1, 2, 12, 13 in 2006; week 1 in 2007; weeks 1, 2 in 2008) were removed from the analyses  
206 because network size was too small to reliably calculate network metrics.

207 *Statistical analysis*

208 We used Kolmogorov-Smirnov tests to analyze (for each year separately) whether the weekly  
209 distribution of visitation rates, resource production and each of the network metrics differed from  
210 a uniform distribution corresponding to the average of all weeks.

211 To test whether visitation rates had an effect on plant-pollinator network structure, we applied  
212 linear mixed-effects models (GLMMs), one for each network metric, using the “lmer” function of  
213 the lme4 package (Bates et al. 2017) in R. Weekly visitation rates based on pollen and nectar  
214 production were highly correlated (Pearson’s  $r=0.78$ ,  $p\text{-value}<0.000$ ,  $n=33$ ). For this reason, all  
215 analyses were conducted only with pollen visitation rates. Weekly pollen production was not  
216 included in the models because it was highly (and negatively) correlated to visitation rates  
217 (Pearson’s  $r=-0.76$ ,  $p<0.000$ ,  $n=35$ ), and because visitation rates provide a better measure of the  
218 amount of resource availability to pollinators. In addition to visitation rates, the models included  
219 network size (pollinator species x plant species) and the ratio of pollinator to plant species (A/P  
220 ratio), two factors well known to affect network structure (Jordano 1987, Olesen & Jordano 2002,  
221 Basilio et al. 2006, Blüthgen et al. 2007, Dormann et al. 2009), as covariates. To fulfill the  
222 assumptions of normality, pollinator niche overlap was inverse-square-transformed ( $1/x^2$ ),  
223 interaction evenness squared-transformed and visitation rates log-transformed. To account for  
224 potential yearly variation, and because we were interested in seasonal, rather than yearly patterns,  
225 year was added as a random factor in each model. In each analysis, models were constructed  
226 using all combinations of explanatory variables. We could not test for interactions between  
227 explanatory variables because some combinations of values were insufficiently represented in the  
228 data. We used the function “dredge” of the MuMIn package (Barton 2015) to select the best  
229 models based on the Akaike’s Information Criterion with a correction for small sample sizes

230 (AICc, Burnham & Anderson 2002). Models with a delta (AICc difference) < 2 were selected as  
231 the best-supported models (Burnham and Anderson 2002). Residual assumptions were checked  
232 for validation of all best-supported models. P-values for each explanatory variable within these  
233 models and the importance of the random factor were calculated using the lmerTest package  
234 (Kuznetsova et al. 2016) in R. We used the function “r.squaredGLMM” of the MuMIn package  
235 to compute marginal R<sup>2</sup> (variance explained by all the fixed factors) for each of the best-  
236 supported models.

237

## 238 **Results**

239 We recorded 14713 plant-pollinator visits corresponding to 965 interactions between 23 plant  
240 species and 237 pollinator species (Table 1). Four plant species (*Allium sphaerocephalum*,  
241 *Anagallis arvensis*, *Linum strictum* and *Scorpiurus muricatus*) did not bloom in 2006.

242

### 243 ***Seasonality of resource production and visitation rates***

244 Kolmogorov-Smirnov tests corroborated that weekly pollen production and weekly visitations  
245 rates were not uniformly distributed throughout the flowering period (Table 2). Weekly pollen  
246 production was higher in spring than in summer in all three years, while pollen visitation rates  
247 followed the opposite seasonal pattern (Fig. 1).

248 ***Seasonality of network metrics***

249 Of the seven network metrics considered, only network connectance and pollinator niche overlap  
250 showed significant temporal variation consistent across the three years of study (Table 1). The  
251 other three metrics showed significant temporal variation only in one or two years. More  
252 importantly, none of the seven metrics showed consistent patterns of seasonal (spring-summer)  
253 variability (Fig. 2).

254

255 ***Effect of visitation rates, network size and A/P ratio on network structure***

256 We used a model selection approach based on the AICc for selecting the best-supported models  
257 analyzing the effect of pollen visitation rates, network size and A/P ratio on seven network  
258 metrics.

259 The best model explaining weighted connectance included only network size, which had a  
260 negative effect (Table 3). That is, larger networks were less connected and therefore more  
261 specialized. The best model for pollinator generality included network size and pollen visitation  
262 rates (Table 3). Pollen visitation rates were negatively related to pollinator generality, indicating  
263 that pollinators were more specialized when visitation rates were higher. On the other hand,  
264 network size had a positive effect on pollinator generality, indicating that pollinators in larger  
265 weekly communities were less specialized.

266 We found two best-supported models explaining plant generality (Table 3). The first model  
267 included network size and A/P ratio. The second model included network size, A/P ratio and  
268 pollen visitation rates, although the latter variable was non-significant. In both models, network  
269 size had a positive effect, indicating that plants were more generalized in larger networks. A/P

270 ratio also had a positive effect in both models. That is, plants increased their generalization when  
271 the number of pollinator species increased in relation to the number of plant species. We also  
272 found two best-supported models for pollinator niche overlap (inverse-square-transformed)  
273 (Table 3). The first model only included network size. The second model included network size  
274 and A/P ratio, although this variable was not significant. In both models, network size had a  
275 positive effect on niche overlap. Therefore, since pollinator niche overlap was inverse-square-  
276 transformed, network size had a negative effect on pollinator niche overlap, indicating that niche  
277 segregation among pollinators increased in larger weekly communities.

278 The best-supported model for interaction evenness, plant niche overlap and H2' did not include  
279 any of the explanatory variables. Other models were selected for interaction evenness and H2',  
280 but none yielded a significant relationship between any of these metrics and the explanatory  
281 variables (Table 3). To establish whether the above results were influenced by strong differences  
282 among years in the relationship between the metrics and the explanatory variables, we tested  
283 whether the random factor (year) was important in our models. The variance contributed by year  
284 did not differ significantly from 0 in any of the models (Supplementary Material, Table S2).

285

## 286 **Discussion**

287 The first objective of this study was to establish whether floral resource availability followed a  
288 seasonal (spring-summer) trend in a Mediterranean scrubland, and whether this trend was  
289 consistent across years. In agreement with previous studies (Herrera 1988, Cohen & Shmida  
290 1993, Petanidou et al. 1995, Bosch et al. 1997, Filella et al. 2013, Flo et al. submitted), we found  
291 that floral resource production was higher in spring than in summer (although the trend was less



292 pronounced in 2007). In addition, we found that pollinator visitation rates followed an opposite  
293 pattern, indicating that floral resources are not only less abundant in summer but also more  
294 intensely exploited.

295 Then, we argued that seasonal variation in resource availability could affect network structure by  
296 means of two alternative responses. If, in agreement with optimal foraging theory (MacArthur &  
297 Pianka, 1966, Pyke 1977, Stephen & Krebs 1986), pollinators responded to low resource  
298 availability by increasing their range of host plants, then summer networks would be more  
299 generalized ('ecological response'). On the other hand, in a situation of chronic resource  
300 limitation in summer, natural selection could favor pollinator niche segregation, resulting in more  
301 specialized networks in summer (Sale 1974, Smith et al. 1978, Tilman 1982) ('evolutionary  
302 response'). However, none of the seven network metrics related to generalization that we studied  
303 showed a seasonal (spring-summer) pattern, indicating that the observed trend in floral resource  
304 availability did not affect network structure. This conclusion was corroborated when we analyzed  
305 the combined effects of visitation rates, network size and A/P ratio on network metrics. Of the  
306 three predictors variables, network size had the greatest influence. This result corroborates  
307 previous studies showing that network size strongly conditions network structure, including other  
308 metrics not analyzed in our study (Jordano 1987, Olesen & Jordano 2002, Basilio et al. 2006,  
309 Blüthgen et al. 2007, Dormann et al. 2009). In various studies, differences in network structure  
310 between contrasting environmental scenarios have been shown to be mediated by changes in  
311 network size (Devoto et al. 2005, Riede et al. 2010, Osorio et al. 2015). At the same time, and  
312 again in agreement with other studies (Olesen & Jordano 2002), A/P ratio was an important  
313 factor determining plant generality. Visitation rates, our variable reflecting resource availability,  
314 only had an effect on pollinator generality, and this effect was negative. This result supports the

315 hypothesis of niche segregation in pollinators (i.e., evolutionary response). However, it is  
316 important to note that we did not find an effect of visitation rate on pollinator niche overlap, and  
317 that the effect on generality was only in combination with network size.

318 We find two possible explanations for the small effects of floral resource availability on network  
319 structure. First, even if floral resource availability is clearly reduced in summer, this reduction  
320 may still be insufficient for resources to become a limiting factor in our community. Pollinators  
321 would then receive insufficient pressure (neither in ecological nor in evolutionary scale) to alter  
322 their trophic niche. Unfortunately, we do not know of any study measuring pollen-nectar levels in  
323 relation to floral resource competition in plant-pollinator systems. Second, resource availability  
324 might be a limiting factor, but the two proposed responses, ecological niche expansion and  
325 evolutionary niche segregation, could cancel each other out, resulting in few changes in network  
326 structure. Pollinators that forage in spring, when resource availability is higher, would have no  
327 selective pressure to become evolutionary specialists, but ecologically, due to the high resource  
328 availability they would be prone to behave as specialists. Instead, pollinators that forage in  
329 summer when resource availability is low, would receive selective pressure to become specialists,  
330 but ecologically they would be prone to expand their trophic niche as much as possible. Even  
331 though pollinator species vary widely in their level of specialization, extreme specialists are the  
332 exception (Waser et al. 1996). Even species that restrict pollen foraging to a plant family are  
333 known to sometimes use flowers of other families as nectar sources (Cane & Sipes 2006). In fact,  
334 pollinators are best defined as opportunistic (Waser et al. 1996, Petanidou et al. 2008), and their  
335 degree of ecological specialization has been shown to be highly labile (Goulson 1999).

336 Our study shows that floral resource abundance and pollinator visitation rates follow a strong  
337 seasonal pattern in our plant-pollinator community, but this temporal variation does not affect

338 interaction network structure. This outcome supports the idea that network structure is very  
339 consistent through time and space (Dupont et al. 2009). For example, Trøjelsgaard & Olesen  
340 (2016) reviewed 19 temporal and 22 spatial interaction networks from different parts of the  
341 world. These authors conclude that, notwithstanding high variability in microscopic features  
342 (partner affiliations, species roles) networks show a high level of consistency in their  
343 macroscopic features (connectance, nestedness). This macroscopic stability in network structure  
344 could be very important in maintaining network resilience in the face of changes in community  
345 composition and structure associated with perturbations and global change (Burkle & Alarcón  
346 2011).

347

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352

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545

546 **Table 1.** Plant, pollinator and interaction richness recorded in the three years of study.

547

Variable	2006	2007	2008	Total
548 Number of plant species	19	23	23	23
Number of pollinator species	129	148	156	237
549 Number of interactions	344	450	643	965
Number of visits	4253	3687	6773	14713

550

551

552

553 **Table 2.** Results of the Kolmogorov-Smirnov tests exploring differences between weeks in  
 554 pollen abundance, pollen visitation rates, and seven network metrics related to generalization-  
 555 specialization. Significant results are shown in bold.

		2006		2007		2008	
Variable		D	p-value	D	p-value	D	p-value
557	Pollen production	0.750	< <b>0.000</b>	0.533	<b>0.028</b>	0.647	<b>0.001</b>
	Pollen visitation rates	0.692	<b>0.003</b>	0.583	<b>0.033</b>	0.705	< <b>0.000</b>
558	Weighted connectance	0.666	<b>0.036</b>	0.634	<b>0.023</b>	0.533	<b>0.028</b>
	Interaction evenness	0.555	0.123	0.818	<b>0.001</b>	0.600	<b>0.009</b>
559	Pollinator generality	0.556	0.124	0.545	0.075	0.533	<b>0.028</b>
	Plant generality	0.777	<b>0.008</b>	0.545	0.075	0.533	<b>0.028</b>
560	Pollinator niche overlap	0.666	<b>0.036</b>	0.727	<b>0.005</b>	0.600	<b>0.009</b>
	Plant niche overlap	0.555	0.123	0.636	<b>0.023</b>	0.533	<b>0.028</b>
561	H2'	0.555	0.124	0.636	<b>0.023</b>	0.600	<b>0.009</b>

562

563 **Table 3:** Statistical outputs from the best-supported models explaining the effects of pollen  
564 visitation rates ( $\log(\text{PVR})$ ), network size and pollinator/plant ratio (A/P) on seven network  
565 metrics related to generalization-specialization.

Response Variable	Model	AICc	Weight	Marginal R <sup>2</sup>	Variables	t-value	p-value
Weighted connectance	1	-144	0.625	0.45	Network size	-5.301	<0.000
	1	-60.8	0.465	0	Intercept	11.01	0.005
(Interaction evenness) <sup>2</sup>	2	-59.1	0.69	0.03	$\log(\text{PVR})$	-0.933	0.328
	3	-58.8	0.175	0.02	Network size	-0.857	0.397
Pollinator generality	1	37.1	0.665	0.28	$\log(\text{PVR})$	-2.485	0.017
	1	144.6	0.723	0.43	Network size	2.726	0.009
Plant generality	2	146.4	0.228	0.45	A/P Ratio	3.150	0.003
	2	146.4	0.228	0.45	Network size	2.782	0.008
1/(Pollinator niche overlap) <sup>2</sup>	1	265.2	0.536	0.55	A/P Ratio	3.145	0.0003
	2	266.2	0.322	0.57	$\log(\text{PVR})$	-1.069	0.292
Plant niche overlap	1	265.2	0.536	0.55	Network size	6.393	<0.000
	2	266.2	0.322	0.57	Network size	6.629	<0.000
H2'	1	-64.4	0.536	0	A/P Ratio	-1.327	0.191
	2	-25.1	0.237	0.04	Intercept	14.37	<0.000
H2'	1	-26.5	0.49	0	Intercept	19.82	<0.000
	2	-25.1	0.237	0.04	Network size	-1.117	0.272

576

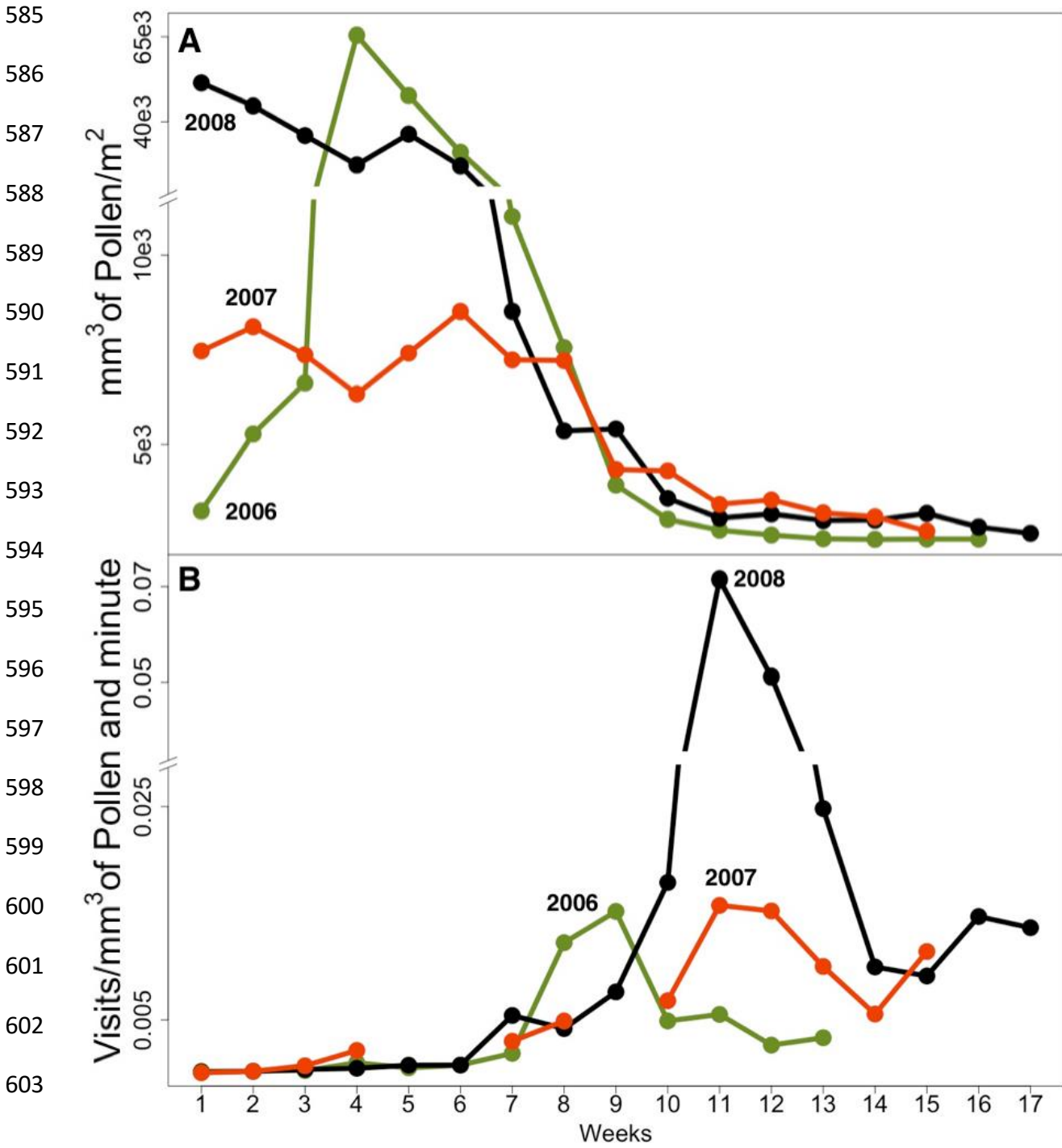
577 **Figure legends**

578 **Figure 1.** Weekly variations in (A) pollen production and (B) pollen visitation rates in the three  
579 years of study.

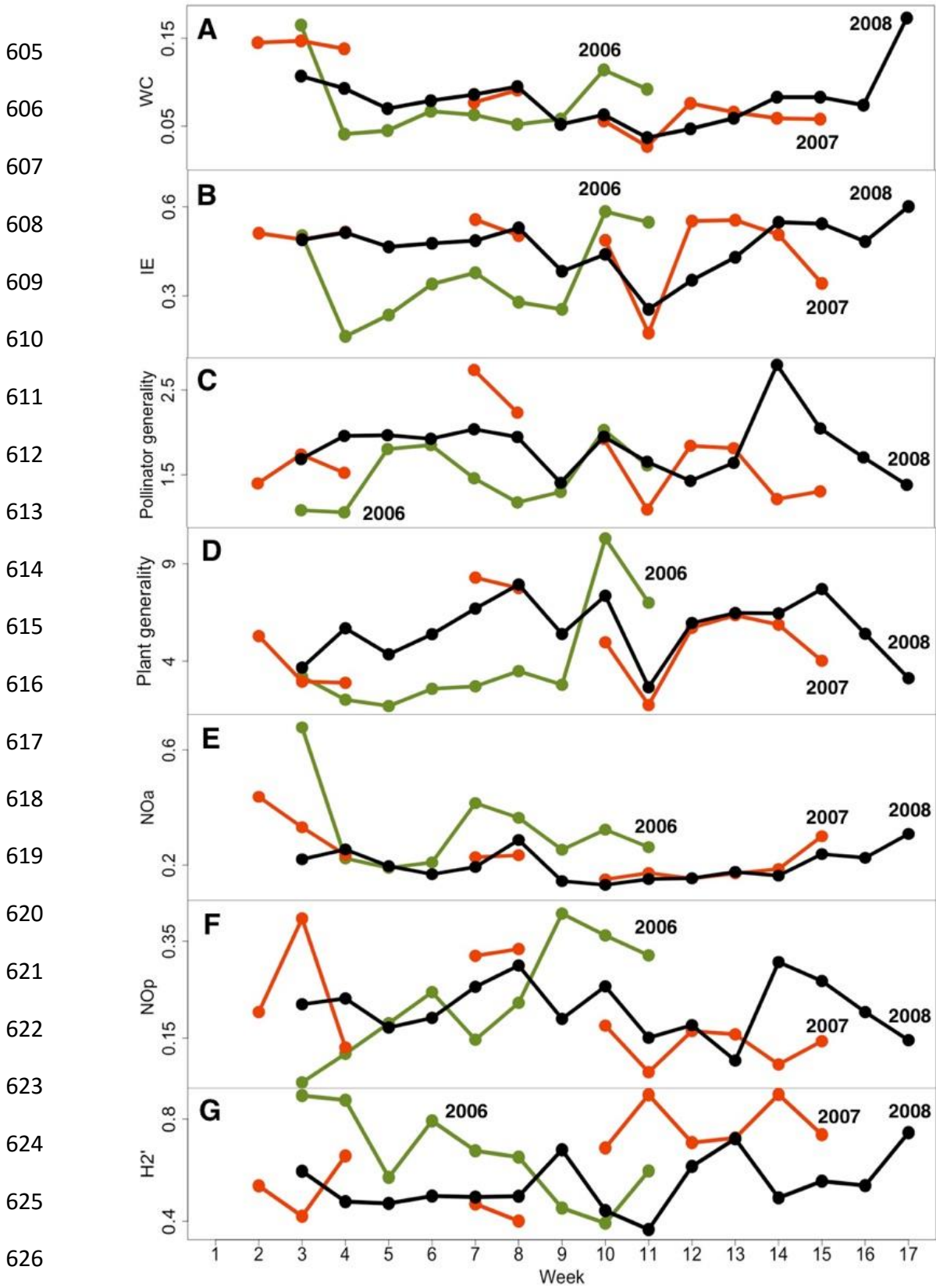
580 **Figure 2.** Weekly variation in seven network metrics related to generalization-specialization in  
581 the three years of study. (A) Weighted connectance (WC), (B) interaction evenness (IE), (C)  
582 pollinator generality, (D) plant generality, (E) pollinator niche overlap (NOa), (F) plant niche  
583 overlap (NOp) and (G) H2'.



584 **Figure 1.**



604 **Figure 2.**



627 **SUPPLEMENTARY MATERIAL**628 **Table S1.** List of plant species surveyed.

629	Plant species	Family
	<i>Anagallis arvensis</i>	Primulaceae
630	<i>Allium sphaerocephalon</i>	Amaryllidaceae
	<i>Biscutella laevigata</i>	Brassicaceae
631	<i>Centaurea linifolia</i>	Asteraceae
	<i>Centaurea paniculata</i>	Asteraceae
632	<i>Cistus albidus</i>	Cistaceae
	<i>Cistus salviifolius</i>	Cistaceae
633	<i>Convolvulus althaeoides</i>	Convolvulaceae
	<i>Dorycnium hirsutum</i>	Fabaceae
634	<i>Euphorbia flavicoma</i>	Euphorbiaceae
	<i>Galium aparine</i>	Rubiaceae
635	<i>Gladiolus illyricus</i>	Iridaceae
	<i>Iris lutescens</i>	Iridaceae
636	<i>Leuzea conifera</i>	Asteraceae
	<i>Linum strictum</i>	Linaceae
637	<i>Muscari neglectum</i>	Liliaceae
	<i>Orobanche latisquama</i>	Orobanchaceae
638	<i>Phlomis lychnitis</i>	Lamiaceae
	<i>Ranunculus gramineus</i>	Ranunculaceae
639	<i>Rosmarinus officinalis</i>	Lamiaceae
	<i>Sideritis hirsuta</i>	Lamiaceae
640	<i>Scorpiurus muricatus</i>	Fabaceae
	<i>Thymus vulgaris</i>	Lamiaceae
641		
642		

643 **Table S2.** Importance of the random factor in each selected model computed with the “step”  
 644 function of the lmerTest package (Kuznetsova et al. 2016). P-values indicate whether the  
 645 variance contributed by the random factor (year) differs significantly from 0.

646	Response variable	Model	Random factor p-value
	Weighted connectance	1	0.2
647	(Interaction evenness) <sup>2</sup>	1	0.4
		2	0.2
648		3	0.2
	Pollinator generality	1	0.8
649	Plant generality	1	1
		2	1
650	1/(Pollinator niche overlap) <sup>2</sup>	1	0.6
		2	0.7
651	Plant niche overlap	1	0.6
	H2'	1	0.4
652		2	0.5

653 **APPENDIX 1**

654

655 ***Floral resource production***

656 Weekly flower production is the number of flowers produced by all the plant species blooming in  
657 a specific week (flowers/m<sup>2</sup>). Flower production of species *i* in week *w* (*FA<sub>iw</sub>*) was computed as

658

$$659 \quad FA_{iw} = \frac{ft_{iw}}{300m^2} \quad (1)$$

660 where *ft<sub>iw</sub>* is the number of flowers of species *i* recorded in the transects in week *w*. Total weekly  
661 flower production was computed as the sum of the flower production of each plant species:

662

$$663 \quad FA_w = \sum_{i=1}^n FA_{iw} \quad (2)$$

664 where *n* is the number of plant species blooming in week *w*.

665 To calculate weekly pollen and nectar production, flower production data were multiplied by the  
666 volume of pollen and the mg of sugar produced per flower by each species.

667

668 ***Flower visitation rate***

669 Weekly flower visitation rate (FVR) is the number of pollinator visits recorded per surveyed  
670 flower and minute (Visits/flower and minute). Weekly flower visitation rate was computed as:

671

672 
$$FVR_{iw} = \frac{V_{iw}}{4min \cdot fc_{iw}} \quad (3)$$

673

674 where  $V_{iw}$  is the number of visits from any pollinator recorded on plant  $i$  and  $fc_{iw}$  is the number of  
 675 flowers of species  $i$  surveyed in week  $w$ . Then, overall weekly flower visitation rate was  
 676 computed as:

677 
$$FVR_w = \sum_{i=1}^n (FVR_{iw} \cdot \frac{ft_{iw}}{ft_w}) \quad (4)$$

678

679 To calculate weekly visitation rate based on pollen and nectar, flower visitation rate was  
 680 corrected with the volume of pollen and the mg of sugar produced per flower by each species.

681

682 ***Interaction strength***

683 Weekly interaction strength between plant species  $j$  and pollinator species  $i$  was computed as the  
 684 number of visits between the two-species recorded in the interaction surveys divided by the  
 685 number of flowers of plant species  $j$  and by 4 minutes, and weighted (multiplied) by the number  
 686 of flowers of plant species  $j$  counted in the transects (Kaiser-Bunbury et al. 2009):

687 
$$S_{ijw} = \frac{V_{ijw}}{4min \cdot fc_{jw}} \cdot ft_{jw} \quad (5)$$

688

689 where  $S_{ijw}$  is the strength of the interaction between plant  $j$  and pollinator  $i$  in week  $w$ ,  $V_{ijw}$  is the  
 690 number of visits of pollinator  $i$  recorded on plant  $j$  in week  $w$ . When two species did not interact  
 691  $S_{ijw}=0$ .