

i-sp pollen-transport network for the species *Xylocopa violacea*
143x186mm (300 x 300 DPI)

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Downscaling pollen-transport networks

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to the level of individuals

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Running headline: Downscaling from species to individuals.

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21 **Summary**

22

23 **1.** Most plant-pollinator network studies are conducted at species level whereas little is
24 known about network patterns at the individual level. In fact, nodes in traditional
25 species-based interaction networks are aggregates of individuals establishing the actual
26 links observed in nature. Thus, emergent properties of interaction networks might be the
27 result of mechanisms acting at the individual level.

28

29 **2.** Pollen loads carried by insect flower-visitors from two mountain communities were
30 studied to construct pollen-transport networks. For the first time, these community-wide
31 pollen-transport networks were downscaled from species-species (*sp-sp*) to individuals-
32 species (*i-sp*) in order to explore specialization, network patterns and niche variation at
33 both interacting levels. We used a null model approach to account for network size
34 differences inherent to the downscaling process. Specifically, our objectives were: (i) to
35 investigate whether network structure changes with downscaling, (ii) to evaluate the
36 incidence and magnitude of individual specialization in pollen use, and (iii) to identify
37 potential ecological factors influencing the observed degree of individual specialization.

38

39 **3.** Network downscaling revealed a high specialization of pollinator individuals, which
40 was masked and unexplored in *sp-sp* networks. The average number of interactions per
41 node, connectance, interaction diversity and degree of nestedness decreased in *i-sp*
42 networks, because generalized pollinator species were composed of specialized and
43 idiosyncratic conspecific individuals. An analysis with 21 pollinator species
44 representative of two communities showed that mean individual pollen resource niche
45 was only c. 46% of the total species niche.

46

47 4. The degree of individual specialization was associated to inter- and intraspecific
48 overlap in pollen use and it was higher for abundant than for rare species. Such niche
49 heterogeneity depends on individual differences in foraging behaviour and likely has
50 implications for community dynamics and species stability.

51

52 5. Our findings highlight the importance of taking inter-individual variation into
53 account when studying higher-order structures such as interaction networks. We argue
54 that exploring individual-based networks will improve our understanding of species-
55 based networks and will enhance the link between network analysis, foraging theory
56 and evolutionary biology.

57

58 **Key-words:** species-based networks, individual-based networks, individual
59 specialization, ecology of individuals, linkage level, niche overlap, pollen-load analysis,
60 foraging behaviour, resource partition, generalization

61

62 Introduction

63

64 In the last couple of decades, community-studies of plant-animal interactions have been
65 explored with the aid of network theory (e.g. Memmott 1999; Jordano *et al.* 2003). In
66 such interaction-networks, animal and plant species are nodes, and links represent the
67 interactions between them. As each node is a different species, these networks are
68 *species-based*. However, each node in a species-based network consists of a population
69 of conspecific individuals, which are the true interacting actors in nature. Operating
70 exclusively at species level may obscure individual behaviour, resulting in loss of
71 valuable information (Ings *et al.* 2009). The relevance of scaling down species-based
72 pollination networks to *individual-based* networks has previously been stressed (e.g.
73 Olesen *et al.* 2010; Dupont *et al.* 2011), as patterns and forces acting at the individual
74 level may be important drivers of structure and dynamics at species level. Moreover,
75 relative invariance of network patterns and lack of differences found among different
76 species-based networks (e.g. Jordano *et al.* 2006; Petanidou *et al.* 2008) could be a
77 consequence of not resolving networks at the proper scale.

78 Despite the recognized importance of individual variation within natural
79 populations for many ecological processes (Bolnick *et al.* 2011; Dall *et al.* 2012; Sih *et*
80 *al.* 2012; Wolf & Weissing 2012), only a few empirical studies to date have applied
81 network theory as a tool for exploring ecological interactions at the individual level. For
82 example, individual-based networks have been used to study intrapopulation patterns of
83 resource partition (Araújo *et al.* 2010; Pires *et al.* 2011; Tinker *et al.* 2012), changes in
84 foraging preferences at increasing levels of intraspecific competition (Araújo *et al.*
85 2008), body size effects in prey-predator interactions (Woodward & Warren 2007;
86 Yvon-Durocher *et al.* 2010), patterns in roosting sites of bats (Fortuna *et al.* 2009) and

87 disease dynamics (Perkins *et al.* 2009). In the case of pollination networks, the number
88 of individual-based network studies is very scarce, all focusing on one or two species
89 (Fortuna *et al.* 2008; Dupont *et al.* 2011; Gómez *et al.* 2011, 2012). A likely explanation
90 for the scarcity of such studies is the labour-intensive sampling required to resolve
91 community-wide species networks into individual-based networks covering all species
92 present.

93 Network data at individual level may be used to test important niche breadth
94 questions, and this is a natural progression step and promising avenue for future
95 network research (Ings *et al.* 2009). It is well known that conspecific individuals vary in
96 their resource use (Van Valen 1965; Roughgarden 1972). Individual specialization
97 occurs when individuals exploit only a small subset of the total resources used by the
98 entire population, and it is a ubiquitous phenomenon in both vertebrate and invertebrate
99 populations (Bolnick *et al.* 2003). As individuals within a population vary genetically
100 and phenotypically, their resource choice may differ as well. For example, physiology,
101 criteria of optimal diet shifting, behavioural skills or social status (see Araújo, Bolnick
102 & Layman 2011 for a review on the ecological causes of individual specialization), all
103 influence individual resource use and preferences. Several indices have been developed
104 to quantify the degree of individual specialization (Bolnick *et al.* 2002), allowing
105 researchers to compare the magnitude of individual specialization across a variety of
106 ecological situations in nature. Indeed, intrapopulation variation in resource use has
107 been proposed to affect population dynamics and ecological interactions (Bolnick *et al.*
108 2011), whereas these in turn affect the magnitude and incidence of intrapopulation niche
109 variation in a feedback loop way (Araújo, Bolnick & Layman 2011).

110 Pollination networks are usually built based on field observations of plant and
111 flower-visitor interactions. However, some studies have used data from pollen loads

112 carried by flower visitors (e.g. Bosch *et al.* 2009; Alarcón 2010) finding that they give
113 complementary information. The analysis of pollen loads, which provides a record of
114 individual foraging patterns across time, addresses one component of pollinator
115 effectiveness and actually gives a good indication of probable pollinators of a given
116 plant species (Popic, Wardle & Davila 2013). Construction of pollen-transport networks
117 has also been useful in applied studies (e.g. Forup & Memmott 2005; Gibson *et al.*
118 2006; Lopezaraiza-Mikel *et al.* 2007). Here we used pollen-loads from insect flower-
119 visitors (pollinators hereafter) in two mountain scrublands to construct pollen-transport
120 networks at both the species level (*species-species* network; hereafter *sp-sp*), and the
121 individual level of the pollinators (*individuals-species* network; hereafter *i-sp*). Plants
122 were only analysed at species level. To our knowledge, no previous study has
123 downscaled a whole pollination network using this approach.

124 Our first goal was to investigate whether network structure changes when
125 downscaling from *sp-sp* to *i-sp* and if so, which network topological parameters change
126 in particular. The network-downscaling process inherently implies an increase in the
127 number of network nodes, because species are composed of groups of conspecific
128 individuals. Given that most network metrics are influenced by network size (Dormann
129 *et al.* 2009), we built null models that account for size-related differences. Changes in
130 network structure when downscaling might be expected due to differences in individual
131 pollen use resulting from different foraging patterns, individual behaviours and trait
132 variability among conspecifics. We defined niche of a pollinator species both
133 qualitatively (number of interactions to plant pollen types, i.e. linkage level) and
134 quantitatively (diversity of pollen types carried by insects). Given that linkage level of a
135 species (L_{sp}) expresses the sum of all links established by its individuals (L_i), we
136 hypothesize that pollinator species niche may be determined by means of two possible

137 mechanisms: (i) individuals are as generalized as their species, i.e. all individuals have
138 similar feeding niche (null hypothesis: $L_{sp} \approx L_i$), or (ii) individuals are more specialized
139 than the species (alternative hypothesis: $L_i \ll L_{sp}$). If the alternative hypothesis is true,
140 we would predict changes in topological parameters beyond those related to size
141 differences when downscaling from *sp-sp* to *i-sp* networks.

142 Our second goal was to evaluate the incidence and magnitude of individual
143 specialization in pollen use. First, we compared species and individual generalization
144 levels for all pollinators (i.e. population vs. individual niche). Moreover, for a subset of
145 abundant and representative pollinator species, we compared the mean empirical
146 linkage levels with those obtained from the null models and tested whether the
147 distribution of their species linkage level among conspecific individuals was nested, as
148 found previously in other studies (Araújo *et al.* 2010; Pires *et al.* 2011). In addition, we
149 measured quantitatively the relative degree of individual pollen specialization and
150 determined its significance.

151 Finally, our third goal was to identify potential ecological factors influencing
152 individual specialization in pollen use. Specifically, using structural equation modeling
153 we tested the effect of factors known to influence individual specialization from other
154 studies: (i) inter- and intraspecific overlap (competition, i.e. amount of resources shared
155 by individuals of different or same species), (ii) insect species abundance and (iii) insect
156 species phenophase, i.e. temporal extent of network membership. In the context of
157 Optimal Foraging Theory (Stephens & Krebs 1986), we expected a high degree of
158 individual specialization to be associated to: (i) low amounts of interspecific overlap,
159 because release from resource competition favours species niche expansion through
160 increased variation in resource use between individuals (Costa *et al.* 2008; Bolnick *et al.*
161 2010); (ii) high amounts of intraspecific overlap, because strong intraspecific

162 competition promotes resource use diversity among conspecifics (e.g. Svanbäck &
163 Bolnick 2005; Svanbäck & Bolnick 2007; Araújo *et al.* 2008); (iii) high abundance of
164 species, because at high densities of foragers the availability of preferred resources
165 decreases causing individuals to add different subsets of resources (e.g. Fontaine, Collin
166 & Dajoz 2008; Tinker, Bentall & Estes 2008; Svanbäck *et al.* 2011; Tinker *et al.* 2012);
167 and (iv) long species phenophases, because species with short phenophases might be
168 composed by short-lived individuals using similar and narrower subsets of resources
169 due to temporal restriction in resource pool compared to species with long phenophases.
170

171 **Materials and methods**

172

173 STUDY SITES AND DATA COLLECTION

174 Plant-pollinator interactions were studied at two sites on the highest mountain in
175 Mallorca (Puig Major, 1445 m): (i) *Sa Coma de n'Arbona* (CN) at 1100 m a.s.l.
176 (39°48'05" N 2°47'9" E) and (ii) *Passadis de Ses Clotades* (PC) at 1400 m a.s.l.
177 (39°48'34" N 2°47'50" E). Plant-pollinator interactions were surveyed during the entire
178 flowering season, from May to August 2010, on clear and calm days. Pollinator
179 censuses of 5 min, focusing upon randomly selected plant individuals of every species
180 in bloom, were carried out between 10 am and 5 pm three times a week. During each
181 census we recorded: (i) taxonomic identity of plant species under observation; (ii)
182 taxonomic identity of insect pollinators (species name if possible or morphospecies
183 otherwise; hereafter species), and (iii) number of individuals of each insect species
184 observed. After each census, flower-visiting insects were captured, placed separately in
185 clean vials and stored in a freezer for later pollen analysis and expert identification. We
186 carried out a total of 458 censuses at CN (38 h 10 min) and 377 at PC (31 h 25 min),
187 capturing 73 and 61 insect species, respectively. At each site, abundance and
188 phenophase of each insect species were estimated as total number of individuals
189 observed in all censuses and total number of days between first and last observation
190 date of flower-visiting individuals, respectively.

191 In the laboratory, each captured insect individual was examined for pollen loads
192 by washing, identifying and counting all pollen grains from its body surface. Pollen was
193 identified at species, species cluster or morphospecies level (pollen types hereafter). See
194 Appendix S1 in Supporting Information for a detailed description of the pollen load
195 analysis procedure. At CN, a total of 190 individuals (71 Diptera, 83 Hymenoptera, 33

196 Coleoptera, 3 Hemiptera) were examined for pollen, and 55 pollen types were
197 identified. At *PC*, a total of 137 individuals (43 Diptera, 64 Hymenoptera, 26
198 Coleoptera, 4 Hemiptera) carried 49 pollen types. Lepidopterans were excluded because
199 their pollen load could not be analysed according to our quantitative methodology
200 protocol (they could not be washed).

201

202 CONSTRUCTION AND ANALYSIS OF *SP-SP* AND *I-SP* POLLEN-TRANSPORT 203 NETWORKS

204 Data from pollen load analyses were used to construct plant-pollinator interaction
205 matrices at two levels of resolution: (i) species-species (*sp-sp* network), representing
206 interactions between insect species and pollen types and (ii) individuals-species (*i-sp*
207 network), representing interactions between insect individuals and pollen types.
208 Interaction weight was the number of pollen grains of a given type carried by either the
209 insect species or the individual.

210 We selected the following parameters to describe *sp-sp* and *i-sp* network
211 structure: number of pollinator nodes (A), number of pollen type nodes (P), total
212 number of nodes (T), total number of interactions (I), linkage level (L), network size
213 (N), linkage density (LD), connectance (C), nestedness ($NODF$), interaction diversity
214 (H_2) and interaction evenness (E_2) (see Table S1 in Supporting Information for
215 definitions). The significance of the $NODF$ metric was assessed against 1,000
216 randomizations using the fixed row and column totals constrained model, i.e. node
217 linkage level was fixed. We calculated the probability of randomly obtaining higher
218 $NODF$ values than that of the empirical matrix with a one-tailed Z-test. All network
219 metrics were obtained with the *bipartite* (version 1.17, Dormann, Gruber & Fründ 2008)

220 and *vegan* (version 2.0-6, Oksanen *et al.* 2012) packages implemented in the *R*
221 statistical software version 2.15.0 (*R* Development Core Team 2012).

222 To test whether network structure changes when downscaling from *sp-sp* to *i-sp*,
223 accounting for differences in network size, we built 1,000 null *i-sp* pollen-transport
224 networks of the same size and species composition as the empirical *i-sp* networks.
225 These null networks were build combining simulated *i-sp* submatrices for each species
226 generated with the Patefield algorithm (i.e. observed marginal totals maintained for
227 matrix rows and columns). Each null *i-sp* subnetwork simulated that conspecific
228 individuals act as generalists as their species, sampling each pollen type at a rate
229 proportional to the corresponding species pollen use distribution. Thus, in null *i-sp*
230 submatrices with a rows and p columns (a was number of individuals of species S and p
231 number of plant pollen types carried by species S), each individual was reassigned the
232 same pollen load as observed but pollen grains were randomly distributed among pollen
233 types with a probability equal to the observed pollen type proportion used by the
234 species. We calculated the abovementioned parameters also for the 1,000 null *i-sp*
235 networks. When parameter values of empirical *i-sp* networks did not fall into 95%
236 confidence intervals of values for the null *i-sp* networks, differences were thus
237 attributed to individual specialization and not to a network size artifact.

238

239 EVALUATION OF INCIDENCE AND MAGNITUDE OF INDIVIDUAL 240 SPECIALIZATION

241 We compared linkage level of each insect species (L_{sp}) with those of their individuals
242 (L_i) to explore specialization at both levels. For species with ≥ 5 sampled individuals
243 (14 spp. at *CN*, 7 spp. at *PC*), we calculated average \bar{L}_i of a given species, and
244 compared it to the \bar{L}_i obtained in null networks. We concluded that a species was

245 composed of individuals being significantly more specialized than the species when
246 empirical $\bar{L}_i < 95\%$ of 1,000 null \bar{L}_i . Within a species, both generalist and specialist
247 individuals were frequently found, so we evaluated the presence of a nested pattern in
248 species linkage level partition among conspecifics. We followed the same procedure
249 explained above for *NODF* calculation with a set of 21 *i-sp* submatrices (matrices for
250 species with ≥ 5 sampled individuals) (see Fig. 3 for an example).

251 Relative degree of individual specialization in pollen use was estimated for all
252 those 21 species with ≥ 5 sampled individuals in each network. We followed the
253 intrapopulation niche width variation model suggested by Roughgarden (1972) and
254 indices developed by Bolnick *et al.* (2002, 2007). Total niche width (*TNW*) can be
255 partitioned into two components: a *within-individual component* (*WIC*) and a *between-*
256 *individual component* (*BIC*), thus $TNW = WIC + BIC$. *WIC* is the average variance in
257 the range of pollen types each conspecific individual is using, i.e. the average of
258 individuals' niche breadth. *BIC* is the variance in mean pollen use among individuals of
259 the particular species, i.e. it represents the niche variation among individuals. Relative
260 degree of individual specialization is measured as the proportion of total niche width
261 (*TNW*) explained by the within-individual component, WIC/TNW , and is thus a species-
262 level metric. This metric approaches 1 when individuals' niches include the full range of
263 pollen types used by their species, and tends to 0 when individuals use smaller, non-
264 overlapping subsets of their species' resources. We applied Monte Carlo re-sampling
265 procedures (Bolnick *et al.* 2002; Araújo *et al.* 2008, 2010) to test whether the observed
266 individual specialization was significant, i.e. observed WIC/TNW values were less than
267 95% confidence interval of WIC/TNW values obtained for the 1,000 null *i-sp*
268 submatrices of each species (null hypothesis that all individuals act as generalized as the
269 species).

270 At the individual level, we estimated specialization by calculating a proportional
271 similarity index (PS_i), which measures similarity in the use of pollen (diet overlap)
272 between an individual i and its corresponding species S . All indices were obtained using
273 R (version 2.15.0, R Development Core Team 2012), following formulae described in
274 detail in Appendix S2.

275

276 ANALYSIS OF ECOLOGICAL FACTORS AFFECTING THE DEGREE OF 277 INDIVIDUAL SPECIALIZATION

278 *Interspecific overlap*

279 To measure interspecific overlap, we transformed our two-mode pollen-transport
280 networks into one-mode networks depicting the pattern of shared pollen resources. By
281 definition, two-mode networks represent the pattern of interactions among two different
282 subsets of nodes (e.g. pollinators and pollen types), whereas one-mode networks
283 represent interactions among nodes of the same set (e.g. pollinators). We constructed
284 one-mode projections of the $sp-sp$ two-mode network matrices at each study site
285 following the co-occurrences projection method (Opsahl 2009a; Padrón, Nogales &
286 Traveset 2011), which entails counting the number of pollen types shared among each
287 pair of different insect species. We thus obtained a square symmetric matrix with a zero
288 diagonal and with s rows and s columns, where s is the number of insect species and the
289 value in each cell w_{ij} is the number of pollen types shared between them. Thus, total
290 interspecific overlap for a species s_i can be defined as the sum of all its weighted links
291 $\sum_j w_{ij}$ (degree for weighted networks in Barrat *et al.* 2004). For example, a species will
292 get a total interspecific overlap of six by sharing one pollen type with six different
293 insect species but also by sharing six different plant pollen types with one insect
294 species. In order to compare species among sites, we calculated a standardized measure

295 of interspecific overlap (species-species overlap, *SPO*), by dividing total interspecific
 296 overlap by the maximum overlap that a species can achieve in its network (i.e. when an
 297 insect species shares all pollen resources with all other insect species). Thus,

$$298 \quad SPO = \frac{\sum_j w_{ij}}{p \cdot (s-1)} \quad \text{eqn 1}$$

299 where p is total number of pollen types in the community and s is total number of insect
 300 species. *SPO* ranges from 0 (no interspecific overlap) to 1 (maximum overlap). For
 301 simplicity, we ignored phenological and size constraints and assumed all species were
 302 equally likely to share resources. *SPO* was calculated for each of the 21 selected insect
 303 species (Appendix S3 gives an example of the procedure). All one-mode network
 304 analyses were done with the *tnet* R package (version 3.0.5, Opsahl 2009b).

305 *Intraspecific overlap*

306 To estimate the degree of intraspecific overlap for each species, i.e. the amount of
 307 overlap in pollen use among its individuals, the 21 two-mode submatrices (consisting of
 308 conspecific individuals and their pollen types) were transformed into one-mode
 309 weighted networks following the same approach as above. Each one-mode matrix
 310 consisted of a rows and a columns, with a being number of conspecific individuals of
 311 species S and the cell value (w_{ij}) was number of pollen types shared by the individuals i
 312 and j . The standardized measure of intraspecific overlap (individual-individual overlap,
 313 *IO*) was calculated as

$$314 \quad IO = \frac{\sum_i \sum_j w_{ij}}{a \cdot n \cdot (a-1)} \quad \text{eqn 2}$$

315 where $\sum_i \sum_j w_{ij}$ is the total overlap among all conspecific individuals in the subnetwork
 316 of S (sum of the link weights for all individuals of S) and the denominator is the
 317 maximum overlap for the subnetwork of S , i.e. when all the conspecific individuals

318 share all pollen types used by the species (n = total number of pollen types used by S
319 and a = total number of conspecific individuals of species S). See Appendix S4 for an
320 illustrative example of the detailed calculation method of intraspecific overlap. It is
321 important to note that our estimates of inter- and intraspecific overlap in pollen use are
322 only a ‘proxy’ of competition, as either individuals or species, respectively, might share
323 the same flower species but use a different resource (e.g. pollen or nectar). We thus
324 prefer to use the neutral term ‘overlap’ instead of competition because the real sign of
325 the interaction is unknown.

326 *Statistical analysis*

327 Structural equation modeling (SEM) was used to determine the effects of inter- and
328 intraspecific overlap, insect species abundance and species phenophase on the degree of
329 individual specialization (WIC/TNW). This technique explores causal relationships
330 among ecological variables and it allows decomposing total effects into direct and
331 indirect effects (Grace 2006). We proposed a model with intra- (IO) and interspecific
332 overlap (SPO) directly influencing WIC/TNW and also abundance and phenophase
333 connected directly to WIC/TNW as well as indirectly through effects on IO and SPO
334 (see full path diagram in Fig. 5). Standardized path coefficients were estimated with
335 maximum likelihood method, significance of each one determined with a Wald test and
336 error terms expressed as $\sqrt{1-R^2}$. Indirect effects were calculated by the product of the
337 path coefficients connecting two variables of interest, and total effects were defined as
338 the sum of direct and indirect effects. To assess whether the model fits the observed data
339 we performed a Chi-square test of goodnes-of-fit (χ^2) and calculated the standardized
340 root mean residuals (SRMR). A non-significant χ^2 indicates that predicted covariance
341 among variables in the model is not distinguishable from the observed covariances,
342 while SRMR calculates deviations between observed and predicted covariances.

343 Variables were *log* transformed when necessary to meet the normality assumption. All
344 analyses were done in *R* version 2.15.0 (R Development Core Team 2012) with package
345 *lavaan* (Rosseel 2012).

346

347 SAMPLING LIMITATIONS AND STUDY CAVEATS

348 Downscaling a community-wide pollination network from *sp-sp* to *i-sp* is a
349 methodologically complex task, and consequently several sampling limitations must be
350 noted. First, owing to the difficulty in identifying pollen grains to species level, we
351 made ‘pollen type clusters’, referring to pollen from closely related species (see
352 Appendix S1 for details). This means specialization and overlap levels might be
353 overestimated in some cases. Downscaling may improve our understanding of
354 networks, but achieving sufficient sampling to resolve them is hard, even more than in
355 *sp-sp* networks (Chacoff *et al.* 2012). For that reason, the estimation of individual
356 specialization is restricted to a small proportion of the total number of species in the
357 networks (19% for *CN* and 11% for *PC*). The number of replicates per species is
358 relatively low (5-10 sampled individuals), mainly because quantifying pollen loads is a
359 highly time-consuming task. However, we evaluated completeness of interaction
360 detection for each species (see Appendix S5) and 69% of the expected interactions were
361 detected on average. Studies on the degree of individual specialization have not yet
362 determined the minimum number of individuals of a population needed to be sampled to
363 get reliable estimations (Araújo, Bolnick & Layman 2011). By applying Monte Carlo
364 resampling procedures, we partly overcame the problem of overestimating the measures
365 of individual specialization due to low sample sizes (Bolnick *et al.* 2002, Araújo *et al.*
366 2008).

367 Temporal consistency of the observed individual specialization is important.
368 Here, each individual pollen load sample, rather than a snapshot of the individual
369 foraging behaviour, is a picture of the extended flower visitation history of the
370 individual (Bosch *et al.* 2009). Thus, pollen loads can be reasonable estimators of
371 individual's long-term foraging patterns because pollen grains can remain attached to
372 insect bodies for long periods (Courtney *et al.* 1981). Obviously, the attachment time
373 depends upon species-specific grooming behaviour and body surface hairiness, as well
374 as pollen grain surface structure. Although we lack information about specific pollen
375 attachment times, we identified pollen grains on insects even one month after the last
376 flowering plant of a given species was blooming in the area (e.g. *Rosmarinus*
377 *officinalis*).

378

379 **Results**

380

381 STRUCTURAL PARAMETERS OF *SP-SP* AND *I-SP* NETWORKS

382 Downscaling from *sp-sp* to *i-sp* modified most network topological parameters studied
383 (Table 1). The direction and magnitude of the observed changes depended on the
384 foraging behaviour of insect individuals, as shown by the contrasting results obtained
385 between null models and empirical networks. Empirical *i-sp* networks were obviously
386 larger in size than *sp-sp*, as most species were resolved into several individuals except
387 singleton observations (i.e. insect species observed only once and therefore consisting
388 of one individual). Consequently, at both study sites, downscaling increased total
389 number of interactions (I) 1.5-fold (Fig. 1), although significantly less than the expected
390 with null *i-sp* networks. Linkage density (LD) and network connectance (C) in empirical
391 *i-sp* networks was nearly half the expected compared to the null hypothesis. Therefore,
392 such differences between *sp-sp* and *i-sp* can be attributed to a significant decrease in the
393 number of links per pollinator node in empirical *i-sp* networks (Table 1), rather than to
394 an effect of increasing network size. Single individuals had a narrower foraging niche
395 than their corresponding species. Mean pollinator linkage level (L_A) in *i-sp* networks
396 was c. 50% lower than that predicted by the null model. Mean interaction diversity for
397 pollinators (H_A) was also significantly smaller when downscaling, because individuals
398 transported fewer and a more variable load of pollen types than their corresponding
399 species. Because of this idiosyncratic and heterogeneous individual behaviour, changes
400 in network nestedness were also observed. Both *sp-sp* and *i-sp* networks were
401 significantly nested; however, $NODF$ values were consistently lower in empirical *i-sp*
402 than in null *i-sp* networks. Furthermore, minor but statistically significant decreases of
403 interaction diversity (H_2) were observed in empirical *i-sp* networks compared to null

404 models, due to differences in the number of interactions, whereas interaction evenness
405 (E_2) increased showing a reduction in the skewness in the distribution of link
406 frequencies.

407

408 PARTITION OF SPECIES LINKAGE LEVEL AMONG CONSPECIFIC 409 INDIVIDUALS AND RELATIVE DEGREE OF INDIVIDUAL SPECIALIZATION

410 In general, species' linkage level - or species' niche width - was partitioned among
411 specialized conspecific individuals. Most individuals had a much lower L_i than their
412 species (L_{sp}) (Fig. 2), i.e. individuals were always more specialized than their
413 corresponding species (average ratio $L_i/L_{sp} = 0.55$). This was also observed when insect
414 orders were treated separately (Figure S1). For the 21 species with ≥ 5 individuals, \bar{L}_i
415 was significantly lower than expected under the null hypothesis (Table S2). Therefore, a
416 generalist species was composed of specialist individuals using different resources, and
417 only in a few cases did individuals have a similar feeding niche as their corresponding
418 species (Fig. 3). When examining how resources are partitioned among individuals
419 within a species, we found a nested pattern only in five out of 14 species at CN [NODF:
420 *Halictus* spp. (*H. scabiosae* and *H. fulvipes*) = 60.39, *Halictus vestitus* = 52.71,
421 *Oedemera flavipes* = 50.29, *Paragus tibialis* = 48.77, *Stomorhina lunata* = 49.46; $P <$
422 0.001] and in one out of seven species at PC (NODF: *Halictus* spp. = 50.90, $P <$ 0.001).
423 Thus, for most species, individuals were highly heterogeneous in their use of pollen,
424 and interactions of the most specialized individuals were rarely proper subsets of those
425 of more generalized individuals.

426 On average, an individual niche represented c. 46% of total species niche (mean
427 $WIC/TNW \pm$ sd; CN = 0.45 ± 0.25 , PC = 0.48 ± 0.27 ; empirical $WIC/TNW <$ null
428 WIC/TNW for all species) (Fig. 4, Table S2). At both sites, a large fraction of

429 individuals (63.5% in *CN* and 54% in *PC*) had a niche which differed strongly from
430 their species' niche, i.e. $PS_i < 0.5$ (Fig. S2). However, the intraspecific variability of PS_i
431 was high (average coefficient of variance in mean PS_i of species was 59% at *CN* and
432 86% at *PC*). Thus, most species consisted of both generalist and specialist individuals
433 (examples in Fig. 3).

434

435 FACTORS AFFECTING DEGREE OF INDIVIDUAL SPECIALIZATION

436 Indices of inter- and intraspecific overlap in pollen use are summarized in Table S2.
437 Results for the proposed SEM model are reported in Fig. 5. Observed data fitted
438 reasonably well the proposed model ($\chi^2 = 0.198$, $d.f. = 1$, $P = 0.66$). High levels of inter-
439 and intraspecific overlap reduced individual specialization (increased *WIC/TNW*
440 values). From all ecological factors included in the model, insect species abundance
441 showed the strongest total effect on individual specialization (-0.561 , $P = 0.002$), partly
442 mediated through its significant negative association with intraspecific overlap
443 (association with interspecific overlap was non-significant). This suggests that as
444 species abundance increases, individuals use a smaller subset of the whole species
445 niche, thereby reducing overlap between conspecifics. Likewise, species phenophase
446 significantly affected intraspecific overlap, but not interspecific overlap, i.e. species
447 with short phenophases had individuals with greater overlap among conspecifics than
448 species with long phenophases. This relationship caused a negative indirect effect on
449 *WIC/TNW* (-0.358 , $P = 0.02$), although the total effect was non-significant (-0.168 , $P =$
450 0.35).

451

452 Discussion

453

454 Our analyses showed that when downscaling from *sp-sp* to *i-sp* pollen-transport
455 networks different structural parameters changed significantly, specifically linkage
456 density, connectance, nestedness and interaction diversity. The rationale for such
457 changes appears to be the high degree of individual specialization for most pollinator
458 species. This heterogeneity in pollen use and foraging behaviour among conspecific
459 individuals has been overlooked in network studies, despite the potential
460 misinterpretation of ecological dynamics and intra- and interspecific interactions
461 occurring in the community. We discuss these results suggesting possible causes and
462 implications of the main findings.

463

464 NETWORK DOWNSCALING AND INDIVIDUAL FORAGING BEHAVIOR

465 Downscaling to the individual level revealed a high degree of specialization and
466 heterogeneity hidden within *sp-sp* networks. Generalist pollinator species were actually
467 found to be composed of specialist individuals. Results showed empirical *i-sp* networks
468 had lower linkage density, connectance, nestedness and interaction diversity than
469 predicted by null models, because conspecific individuals were idiosyncratic in their
470 food plant choice and foraging behaviour. Species linkage level was usually partitioned
471 among specialist individuals (Fig. 2), and this was true for all pollinators combined and
472 also when separating species into orders (Hymenoptera, Diptera and Coleoptera, Fig.
473 S1). Therefore, the most common mechanism for pollinator species to achieve a broad
474 niche (here high L_{sp}) was to have individuals with different and narrow niches ($L_i \ll$
475 L_{sp}) (Fig. 3a). Quantitative measures of individual specialization (WIC/TNW , PS_i) also
476 confirmed this pattern and let us to reject the null hypothesis of individual generalist

477 sampling from species pollen use distribution. Our average values of WIC/TNW were
478 within the range reported by Araújo *et al.* (2011) for a broad array of taxa. Nevertheless,
479 both generalist and specialist individuals were commonly found within a species. The
480 frequency distribution of individual niche width was highly skewed, i.e. common
481 species had only a few individuals with a wide niche. However, intraspecific partition of
482 resources was quite overdispersed (i.e. non-nested) and the specialized individuals were
483 not carrying a subset of the pollen types carried by more generalized conspecifics.

484 Network downscaling from species to individuals seems a promising way to
485 connect pollination networks to pollinator foraging behaviour by further exploring
486 mechanisms underlying the observed patterns. The foraging behaviour of insect
487 pollinators is very flexible and a complex array of strategies for efficient collection of
488 pollen and nectar have been described (Goulson 1999). For instance, generalist *Apis*
489 *mellifera* individuals ($L_i/L_{sp} = 6/12$) may be scouts searching for new food resources
490 independently of each other, whereas foraging workers, which are guided to food
491 resources by specific waggle dances, only carry pollen from one or two species (Seeley
492 1983; Dupont *et al.* 2011). Furthermore, individual specialization in pollinator species
493 may reflect the individual foraging behaviour described as flower constancy (Waser
494 1986). Flower constancy occurs in many pollinators when individuals restrict their visits
495 to certain flowers, even ignoring more rewarding alternatives, although explanation of
496 this behaviour is still in debate (Chittka, Thomson & Waser 1999). This individual
497 specialization is likely to be beneficial to plants, since it might decrease heterospecific
498 pollen deposition on conspecific stigmas thus preventing stigma clogging, as well as
499 conspecific pollen loss on heterospecific flowers (Morales & Traveset 2008).

500

501 FACTORS INFLUENCING INDIVIDUAL SPECIALIZATION

502 Variation in individual specialization depends both on intrinsic (e.g. sex, age,
503 morphology, behavior and physiology) and extrinsic factors (e.g. ecological
504 interactions, population density and diversity of resources) (Bolnick *et al.* 2003; Araújo,
505 Bolnick & Layman 2011). Among the extrinsic factors explored, we found evidence of
506 a significant relationship between ecological interactions and inter-individual variation.
507 Such relationship is likely to have ecological consequences for population and
508 community dynamics (Bolnick *et al.* 2011; Wolf & Weissing 2012).

509 Low levels of interspecific overlap increased the degree of individual
510 specialization, thus supporting the notion that in the absence of competing species
511 individuals switch to different resources depending on their phenotypes (Costa *et al.*
512 2008; Bolnick *et al.* 2010). Populations can expand their diet breadth when individuals
513 expand their niche and/or specialize on different niches (Bolnick *et al.* 2007; Tinker,
514 Bentall & Estes 2008). Intraspecific competition has been documented to increase
515 individual specialization (Svanbäck & Bolnick 2007; Araújo *et al.* 2008). However, this
516 outcome depends on the type of rank preference variation among individuals, i.e.
517 whether individuals have the same or different primary and secondary preferred
518 resources (Svanbäck & Bolnick 2005; Araújo *et al.* 2011). Our results suggest a
519 scenario where at low intraspecific overlap levels individuals are using different
520 preferred resources, whereas at high levels they expand their niches adding the same
521 resources, thereby reducing individual specialization.

522 In addition, population densities affect individual foraging decisions as each
523 individual's choice depends on those made by other individuals depleting the floral
524 resources. Our SEM model suggested that as species abundance increases, conspecific
525 individuals become more specialized and heterogeneous in pollen choice, which is
526 concordant with other studies (e.g. Svanbäck & Bolnick 2007; Tinker *et al.* 2012).

527 Unexpectedly, species abundance was negatively associated to intraspecific overlap
528 level. However, this might be explained when considering insect phenologies. Two
529 species might be equally abundant by producing either a cohort with a high number of
530 individuals during a short period or several cohorts with low numbers of individuals
531 during a long period, but intraspecific competition would be stronger in the former case.

532 Finally, degree of individual specialization was not influenced by species
533 phenophase. Species with intermediate-long phenophases (range 40-100 days) showed
534 both high and low individual specialization, probably depending on whether they
535 consisted of short-lived individuals, long-lived or both. Given that species phenophase
536 was associated to intraspecific overlap (Fig. 5), we might expect species with very short
537 phenophases to consist of short-lived individuals with broad niches (relative to the
538 corresponding species). On the other hand, species with long phenophases might consist
539 of either short-lived individuals with narrow and non-overlapping niches or a
540 combination of individuals with different phenophases and degree of specialization.
541 Individual-based networks would certainly be a more informative tool to examine
542 seasonal dynamics if, for instance, individuals present at the beginning of the season
543 interact with early flowering plants whereas those present towards the end of the season
544 do it with another set of plants.

545

546 RELEVANCE OF NETWORK DOWNSCALING

547 Downscaling networks from species to individuals is important in our efforts to explore
548 mechanisms acting at the individual level, which further may upscale and shape species
549 network structure (Olesen *et al.* 2010). Indeed, the individual-based networks reported
550 here provide useful information to improve the understanding of species-based
551 networks because most *sp-sp* networks contain a substantial proportion of singleton

552 observations, which means they are based on observations of only one individual (e.g.
553 23% of an arctic network in Olesen *et al.* 2008 was based on singletons). Commonly,
554 rare species in networks appear to be more specialized than they really are due to
555 insufficient sampling of the rare interactions (Vázquez & Aizen 2003; Dorado *et al.*
556 2011). In concordance with this, our results suggest that a specialized behaviour of
557 individuals compared to the species might be a possible explanation for the sampling
558 bias in the estimation of linkage level in rare species. Similarly, most abundant species
559 tend to be also the most generalized in pollination networks (e.g. Elberling & Olesen
560 1999; Olesen *et al.* 2008), but as we have shown here, this might actually cover a
561 scenario where the conspecific individuals are specialized on different resources.
562 Everything else being equal, individuals of abundant insect species are observed more
563 frequently than those of rare species, and as new individuals are collected proportionally
564 more new links are added to the species due to the specialized behaviour of the
565 individuals. Thus, some broadly described specialization patterns in *sp-sp* pollination
566 networks might have their origin in *i-sp* networks. Because ecological specialization is
567 not a fixed species attribute and much variation exists within species, more studies are
568 needed to explore ecological specialization across scales (Devictor *et al.* 2010).

569 Our findings highlight the importance of also taking inter-individual variation
570 into account when studying higher-order structures such as networks, as part of our
571 understanding of network structure and dynamics hidden on adjacent scale levels. For
572 example, the high heterogeneity in pollen use among conspecifics enforces a high
573 heterogeneity in interaction strength in species-based networks as well, which, so far,
574 has been completely neglected. The strength of a *sp-sp* interaction depends on the
575 number of individuals taking part in the interaction and the degree of their involvement.
576 This has obviously important implications in the interpretation of community structure

577 and dynamics (Bolnick *et al.* 2011; Sih *et al.* 2012). For instance, a pollen type is more
578 likely to be an important resource to a species than other pollen types if a larger
579 proportion of the population is using it. Consequently, having generalized species
580 decomposed into dissimilar and specialized individuals might increase stability of
581 species to the loss of a resource, because only a small proportion of the population
582 would be affected (Wolf & Weissing 2012). By contrast, high individual specialization
583 increases species vulnerability to the loss of individuals. A species composed of
584 generalized individuals may lose a substantial proportion of its population before any
585 effects are seen in the species-based network, whereas a species composed of
586 specialized idiosyncratic individuals loses individuals and network links
587 simultaneously. Therefore, our cross-scale level study suggests that individual foraging
588 mode affects species persistence and, further, network stability. The demonstrated
589 variation in individual resource use will affect the network outcome of disturbances, and
590 information about the specific kind of disturbance will be important in our efforts to
591 predict how network stability in detail is affected.

592 The intraspecific heterogeneity in pollen use might be related to trait variability
593 among individuals, and most of these traits are subject to natural selection. Because
594 there are trait-matching constraints in how links are distributed in networks,
595 incorporating traits into models which predict species interactions have already helped
596 to gain more insight in network structure and properties (e.g. Petchey *et al.* 2008; Stang
597 *et al.* 2009; Ibanez 2012). Therefore, further research on individual-based networks
598 would enable us to link network theory to evolutionary biology by working at the
599 proper scale where natural selection takes place. Exploring all the potential bottom-up
600 processes determining the emergent properties of interaction networks seems a
601 promising avenue for future studies.

602

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616

617 **Data Accessibility**

618 R scripts for analysis and data can be found in: DRYAD entry doi:xx.xxxx/dryad.xxxx

619

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621

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804 and prospects. *Oikos*, **120**, 550-563.

805

806 **Supporting Information**

807 The following supporting information is available for this article online:

808 **Table S1.** Definition of network parameters.

809 **Table S2.** List of individual specialization and overlap indices calculated for the 21
810 insect species of flower-visitors selected from our networks.

811 **Fig S1.** Relation between linkage level of species (L_{sp}) and individuals (L_i) for the main
812 insect orders.

813 **Fig. S2.** Frequency histogram of the proportional similarity indices of individuals (PS_i)
814 from the 21 selected species in our networks.

815 **Appendix S1.** Insect pollen load analysis.

816 **Appendix S2.** Indices for quantifying individual specialization and niche components.

817 **Appendix S3.** Measuring interspecific overlap in one-mode weighted networks.

818 **Appendix S4.** Measuring intraspecific overlap with one-mode weighted networks.

819 **Appendix S5.** Evaluation of species sampling completeness.

820

For Review Only

821 **Table 1.** Structural properties of the empirical *sp-sp* networks, empirical *i-sp* networks
 822 and null *i-sp* networks.

823

	<i>sp-sp networks</i>		<i>i-sp networks</i>			
	Empirical		Empirical		Null model	
<i>Qualitative network parameters</i>	<i>CN</i>	<i>PC</i>	<i>CN</i>	<i>PC</i>	<i>CN</i>	<i>PC</i>
Number of pollinator nodes (<i>A</i>)	73	61	190	137	190	137
Number of pollen type nodes (<i>P</i>)	55	49	55	49	55	49
Total number of nodes ($T=A+P$)	128	110	245	186	245	186
Network size ($N=AxP$)	4,015	2,989	10,450	6,713	10,450	6,713
Total number of interactions (<i>I</i>)	434	360	681 [†]	506 [†]	1,342.48	881.78
Linkage density ($[LD=I/(A+P)]$)	3.39	3.27	2.78 [†]	2.72 [†]	5.48	4.74
Connectance ($C=I/AxP$)	0.108	0.120	0.065 [†]	0.075 [†]	0.12	0.13
Nestedness (<i>NODF</i>)	34.45 [*]	38.65 [*]	26.99 ^{*, †}	29.67 ^{*, †}	44.29	43.77
<i>Quantitative network parameters</i>						
Interaction diversity (<i>H</i> ₂)	3.38	2.89	3.63 [†]	3.18 [†]	3.95	3.36
Interaction evenness ($E_2=H_2/H_{max}$)	0.56	0.49	0.56 [†]	0.51 [†]	0.55	0.49
<i>Node parameters</i>						
Mean pollinator linkage level (<i>L</i> _A)	5.9	5.9 [†]	3.5 [†]	3.6 [†]	7.07	6.44
Mean pollinator interaction diversity (<i>H</i> _A)	0.79	0.70	0.54 [†]	0.54 [†]	0.99	0.78
Mean pollen type linkage level (<i>L</i> _P)	7.89	7.35	12.38 [†]	10.33 [†]	24.41	18
Mean pollen type interaction diversity (<i>H</i> _P)	0.62	0.57	0.76 [†]	0.69 [†]	1.46	1.21

824

825 * Significance *p*-value < 0.001. That is the probability of getting by random a higher value of

826 nestedness than the empirical one. See text for more details on the calculation.

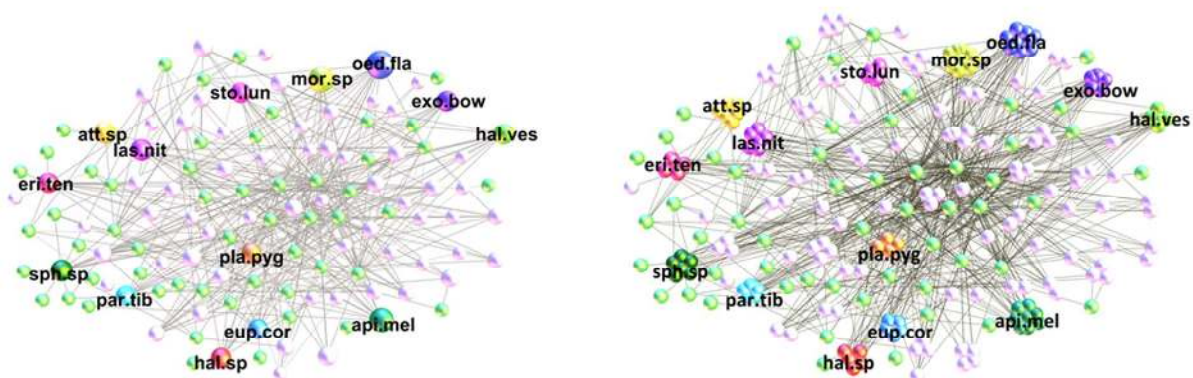
827 † Observed values were outside of 95% confidence intervals of values obtained for 1,000 null *i-*

828 *sp* networks.

829

830 **Figures**

831

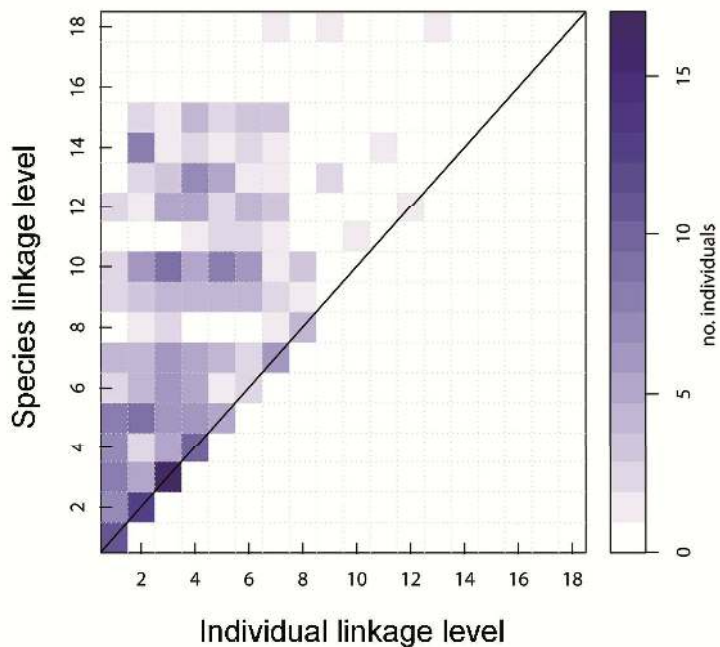
Fig.1.*(A) sp-sp network**(B) i-sp network*

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Fig. 2.

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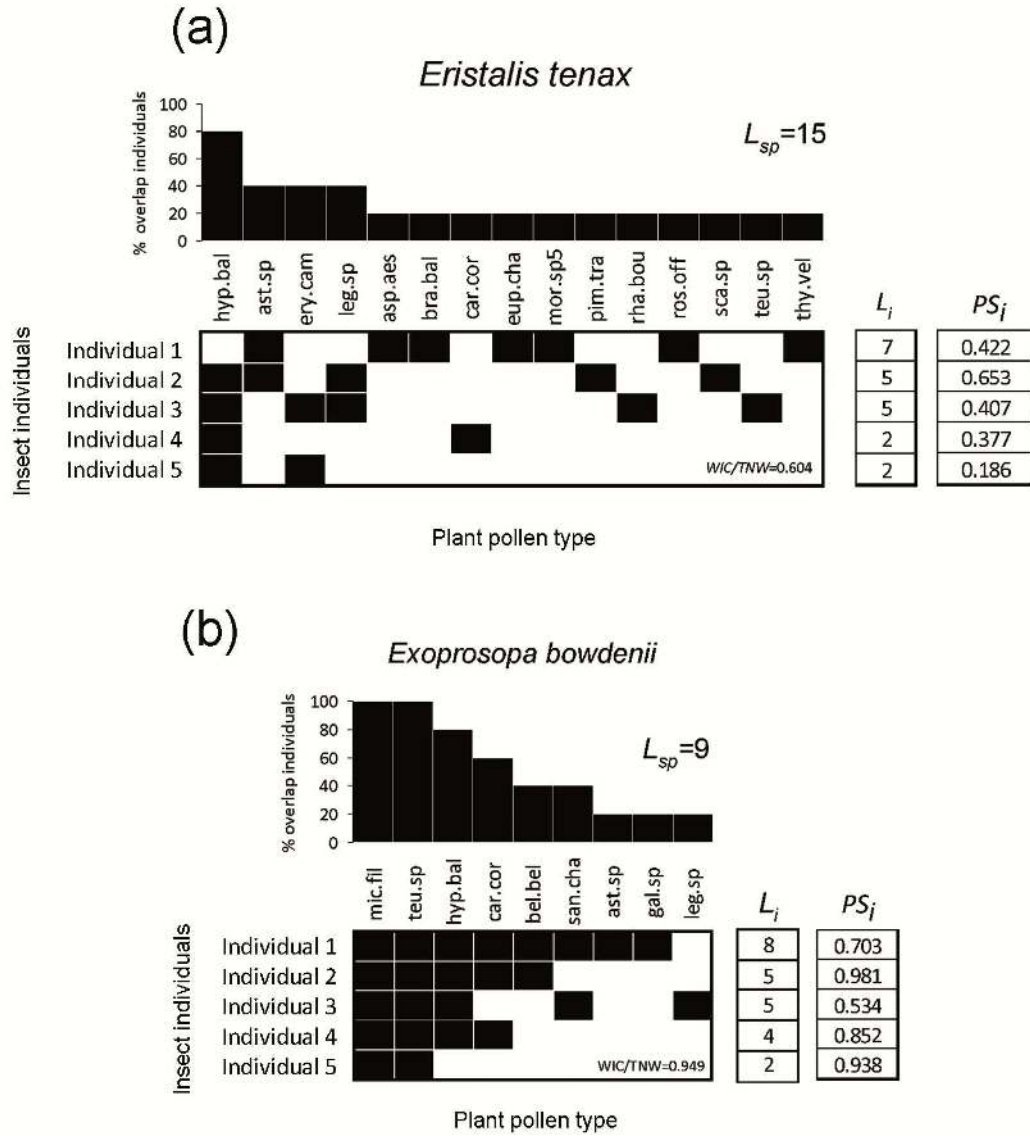
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Fig. 3.

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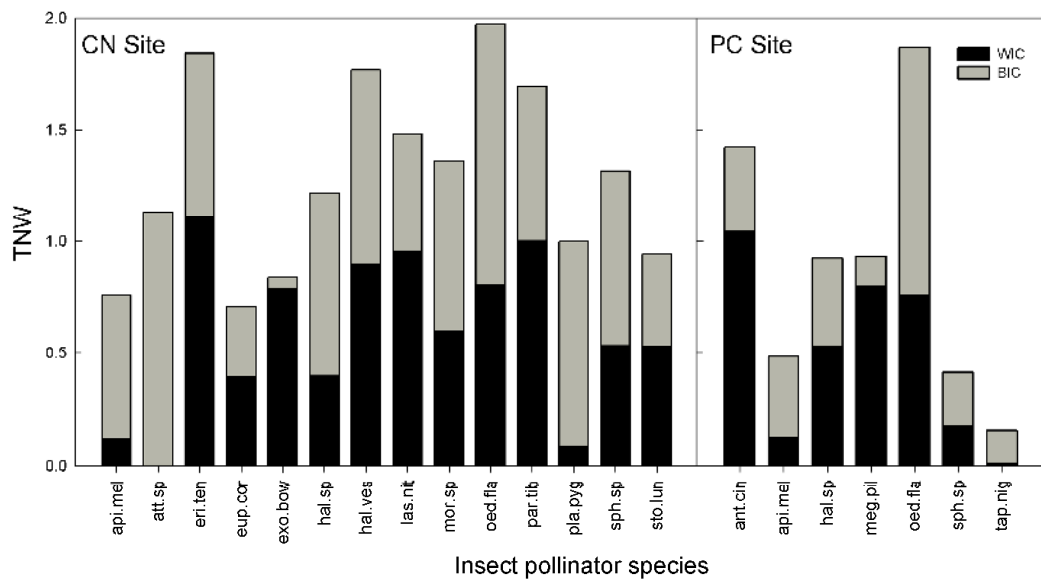
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Fig. 4

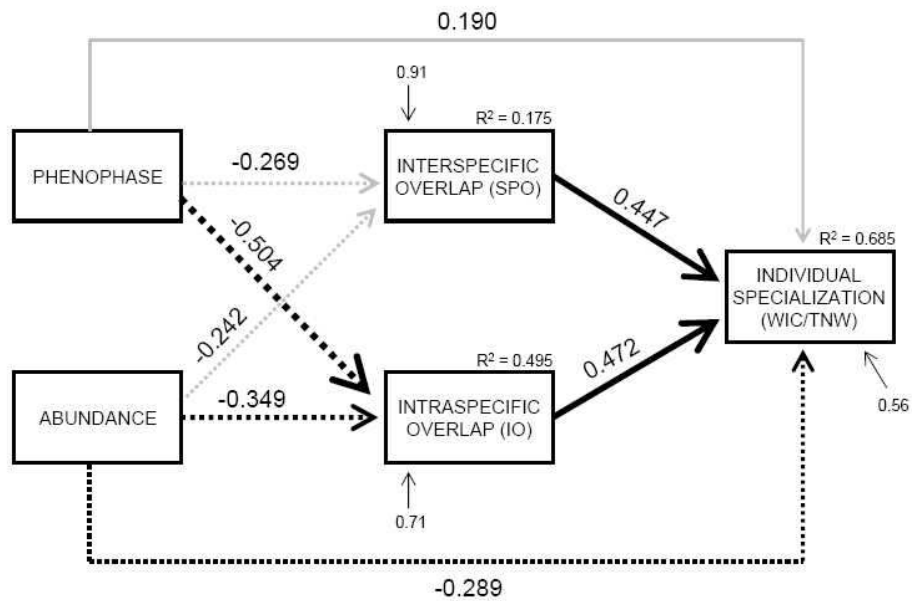


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Fig. 5.



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856 **Figure legends**

857

858 **Fig. 1.** Pollen-transport networks at two scales of resolution: (A) *species-species* (*sp-sp*)
859 and (B) *individuals-species* (*i-sp*). Pale green nodes are plant pollen types whereas the
860 rest of nodes are pollinators. Coloured and labelled nodes are pollinators with ≥ 5
861 individuals captured (see Table S2 for full species names). In network (A) each
862 pollinator node represents an insect species with a size proportional to the number of
863 individuals captured in the field. The result of decomposing each insect species node
864 into its conspecific individuals is seen in network (B), where each pollinator node
865 represents an insect individual and individuals of the same species are clumped together
866 in the graph. Networks were drawn with *Gephi 0.8beta* (Bastian *et al.* 2009).

867

868 **Fig. 2.** Comparison of species linkage level (L_{sp}) and individual linkage level (L_i). Cells
869 represent combinations of L_i and L_{sp} (data from both sites, $n = 327$) with colour intensity
870 correlating with number of individuals found at each position. Matrix diagonal is the
871 *species-individual isocline* (i.e. perfect matching of species and individuals niche width,
872 $L_i = L_{sp}$), while deviations to the left indicate individuals, being more specialized than
873 their species ($L_i < L_{sp}$). The figure shows a high density of individuals with a linkage
874 level lower than their species, although some individuals are positioned on the *species-*
875 *individual isocline* (mainly species captured one or a few times). Notice that the upper
876 right region representing highly generalized species with generalized individuals is
877 completely empty.

878

879 **Fig. 3.** *i-sp* binary pollen-transport matrices of two dipteran species representing linkage
880 level partitioning among conspecifics. There are two alternative mechanisms to evolve a

881 wide species niche: (a) generalist species composed of relatively specialized individuals
882 using different pollen types and (b) generalist species composed of relatively
883 generalized individuals using broad and similar subsets of resources. Species with high
884 heterogeneity in pollen use among conspecifics (example a) were more common. Bar
885 plots on top of the matrices show percentage of conspecific individuals carrying each
886 pollen type, so generalized species with specialized individuals have a long tail. (L_{sp} :
887 species linkage level; L_i : individual linkage level; PS_i : proportional similarity index;
888 WIC/TNW : degree of individual specialization).

889

890 **Fig. 4.** Total niche width (TNW) partition into within-individual (WIC) and between-
891 individual (BIC) components for species with ≥ 5 individuals sampled ($n = 21$, 10
892 Hymenoptera spp., 7 Diptera spp. and 4 Coleoptera spp.) at both study sites (CN =
893 *Coma de n'Arbona*, PC = *Passadís de Ses Clotades*).

894

895 **Fig. 5.** Path diagram showing the relative effect of several ecological factors (insect
896 phenophase, insect abundance, inter- and intraspecific overlap (SPO and IO
897 respectively) on the degree of individual specialization (WIC/TNW). Positive effects are
898 indicated by solid lines and negative effects by dashed lines. Thickness of arrows is
899 proportional to the standardized path coefficients indicated with numbers next to each
900 path. Significant paths are coloured in black, whereas non-significant ones are in grey.
901 R^2 and error terms are shown for each endogenous variable. Statistics of goodness of fit
902 for this model are: $\chi^2 = 0.198$, $df = 1$, $P = 0.656$; $SRMR = 0.02$.

1 **Appendix S1** *Insect pollen load analysis*

2

3 In the laboratory, we studied the pollen loads of each insect individual captured. For
4 frequently captured species, a maximum of 10 individuals per species was included in
5 the analysis. An isotonic water solution (1.5 ml) was added to each vial containing a
6 specimen and shaken for 5 sec in a vortex and then washed by agitation for 15 min in an
7 ultrasonic bath to remove pollen grains from their body surface. For honeybees, pollen
8 clumps in the corbicula of the hind legs were removed in advance. Afterwards, insects
9 were pinned for later identification by taxonomist experts. Vials containing the pollen
10 load solution were centrifuged at 13.000 rpm for 15 min and inspected for any presence
11 of a pollen pellet at the bottom. In vials with a large pollen pellet, to facilitate pollen
12 counting, we added a *Lycopodium* spore tablet containing 18,584 spores (batch no.
13 177745, Lund Univ., Sweden), whereas in the other vials the supernatant was carefully
14 removed, and the droplet with the pollen was suspended on a microscopic slide. Pollen
15 concentrated samples were homogenized with vortex agitation in order to dissolve the
16 spore tablets and then three drops (replicates) were mounted on slides. We added a
17 small pink fuchsine-stained jelly cube to the pollen smear, melted it and covered the
18 final smear with a cover slip (Kearns & Inouye 1993). To avoid any pollen
19 contamination, laboratory instruments were cleaned with ethanol between manipulation
20 of samples. Slides were analyzed under microscope (100-400x) to estimate total number
21 of pollen grains from each insect individual. All pollen grains were identified to the
22 lowest possible taxonomic level and the number of pollen grains of each species was
23 counted (on average 60% of total slide area was inspected for pollen). In slides from
24 pollen-dense samples, we counted the number of pollen grains and also the number of
25 spores. In these samples, total pollen number carried by the insect was estimated as the

26 mean of the three replicates, calculated as “number of pollen grains counted in a droplet
27 x (18,584/number of spores counted in droplet)” (Jakobsson, Padrón & Traveset 2008).

28 A pollen reference collection was made during the field season in order to facilitate
29 pollen identification. Pollen grains of each species were measured and photographed
30 under the microscope at 400x. Pollen grains of some species were indistinguishable
31 from those of closely related species, and therefore classified into ‘pollen type clusters’
32 including more than one species: ‘Galium’ (including *G. cinereum*, *G. crespianum* and
33 *G. balearicum*), ‘Teucrium’ (including *T. marum* and *T. asiaticum*), ‘Geraniaceae’
34 (including *Geranium colombinum*, *G. lucidum*, *G. molle*, *G. purpureum* and *Erodium*
35 *cicutarium*), and ‘Asteraceae’ (including all Asteraceae at study sites except *Bellium*
36 *bellidioides*, *Carlina corymbosa* and *Santolina chamaecyparissus*, which were
37 identified to species). Unknown pollen grains were assigned to morphotype species.

38

39 **References in Appendix S1:**

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45

1 **Appendix S2** *Indices for quantifying individual specialization and niche components*

2

3 We used formulae from Bolnick *et al.* (2002) to calculate each niche component (*TNW*,
 4 *WIC* and *BIC*; Roughgarden 1972, 1974) using categorical data on pollen types carried
 5 by insect specimens. Shannon diversity index is used as a proxy for variance in niche
 6 width, so the niche widens with addition of new resources and with increasing evenness
 7 in resource use. For each species with ≥ 5 individuals sampled (14 spp. at *CN*, 7 spp. at
 8 *PC*), we constructed a matrix with a rows and p columns, where a is the number of
 9 individuals of species S , p the plant pollen types found on the body of individuals of S ,
 10 and the value in each cell (n_{ij}) is the number of j 's pollen grains carried by the i th
 11 individual. Then, using those matrices for each species S , we calculated niche
 12 components as

13
$$WIC = \sum_i p_i \cdot \left(- \sum_j p_{ij} \cdot \ln(p_{ij}) \right)$$

14
$$BIC = - \left(\sum_i p_i \cdot \ln(p_i) \right) - \left[\sum_j q_j \cdot \left(- \sum_i \gamma_{ij} \cdot \ln(\gamma_{ij}) \right) \right]$$

15
$$TNW = - \sum_i q_j \cdot \ln(q_j)$$

16
$$p_{ij} = \frac{n_{ij}}{\sum_j n_{ij}} \quad p_i = \frac{\sum_j n_{ij}}{\sum_i \sum_j n_{ij}} \quad q_j = \frac{\sum_i n_{ij}}{\sum_i \sum_j n_{ij}} \quad \gamma_{ij} = \frac{n_{ij}}{\sum_i n_{ij}}$$

17

18 where, p_{ij} is the proportion of pollen type j in the total pollen load of individual i of
 19 species S , p_i is the proportion of all pollen types used by S that are used by individual i ,
 20 q_j is the proportion of pollen type j in the total pollen load of S , and γ_{ij} is the proportion
 21 of total pollen type j used by S that was carried by individual i . Relative degree of

22 individual specialization was obtained by dividing WIC by TNW , i.e. proportion of total
23 niche width explained by the within-individual component.

24 Following Bolnick *et al.* (2007) we also calculated overlap in pollen resource
25 use among each individual and the whole population as

$$26 \quad PS_i = 1 - 0.5 \cdot \sum_j |p_{ij} - q_j|$$

27 where PS_i is the proportional similarity index, measuring the similarity in pollen
28 resource use distribution of individual i and the corresponding species S (Feinsinger *et al.*
29 1981). Individuals using pollen resources in the same proportion as their species have a
30 $PS_i = 1$, whereas $PS_i = q_j$ if they are specialized in just one pollen resource j .

31

32 **References in Appendix S2:**

33 Bolnick, D.I., Svanbäck, R., Araújo, M.S. & Persson, L. (2007) Comparative support
34 for the niche variation hypothesis that more generalized populations also are more
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37 Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M. & Svanbäck, R. (2002) Measuring
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39 Feinsinger, P., Spears, E.E. & Poole, R.W. (1981) A simple measure of niche breadth.
40 *Ecology*, **62**, 27-32.

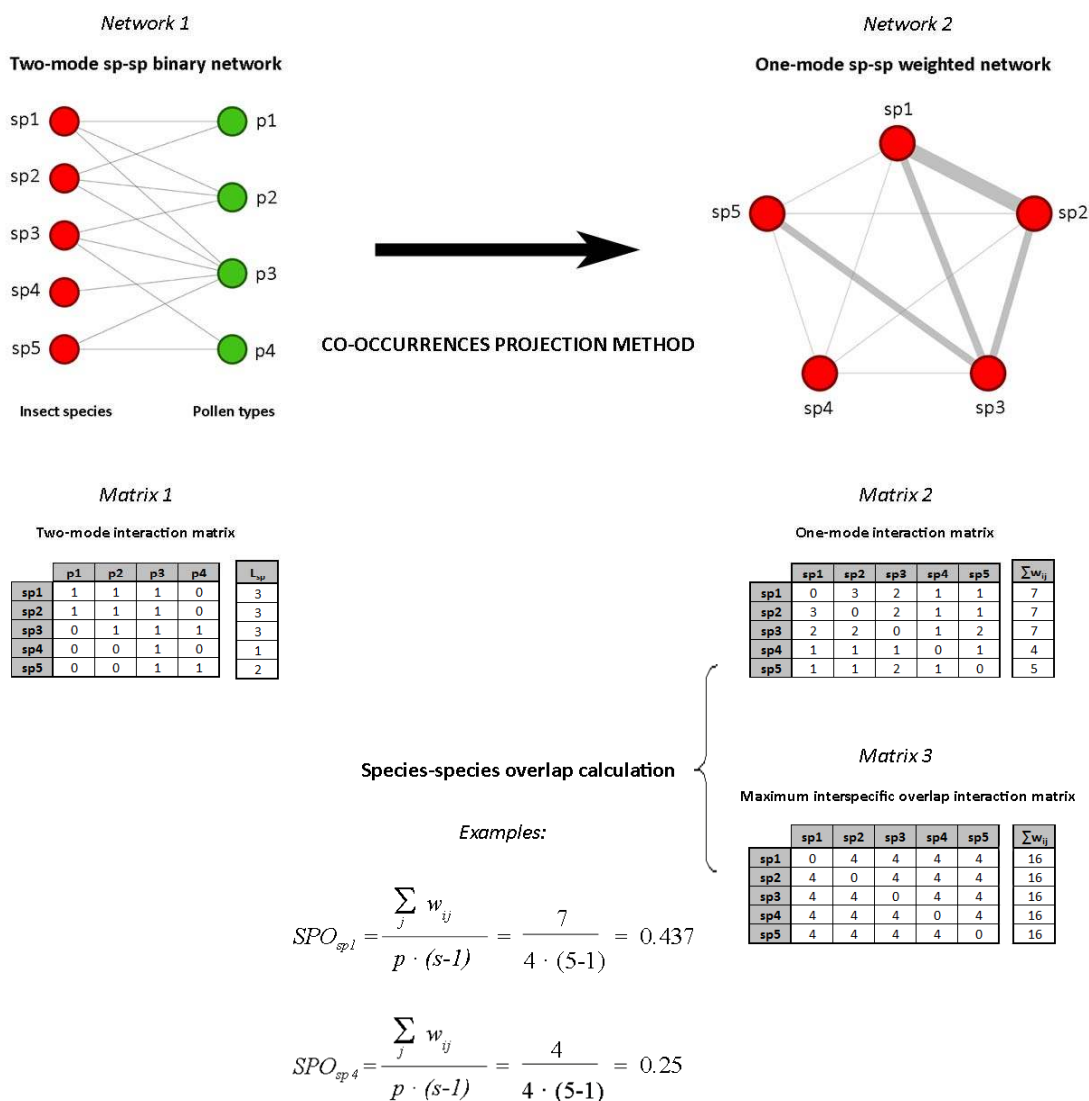
41 Roughgarden, J. (1972) Evolution of niche width. *American Naturalist*, **106**, 683-718.

42 Roughgarden J. (1974) Niche width: Biogeographic patterns among lizard populations.
43 *American Naturalist*, **108**, 429-442.

44

1 **Appendix S3** *Measuring interspecific overlap in one-mode weighted networks.*

2



3

4 Here we present a simple hypothetical example to illustrate the procedure applied when
 5 estimating interspecific overlap (*SPO*) for insect species in our networks. *Network 1* is a
 6 two-mode binary pollen-transport network depicting interactions between five insect
 7 species (red nodes) and four plant pollen types (green nodes). Insect species are linked
 8 to plant pollen types if they carried pollen grains. *Network 1* can also be represented as
 9 an interaction matrix (*Matrix 1*) with *s* rows and *p* columns, where *s* is the number of
 10 insect species (*s* = 5), *p* is the number of plant pollen types (*p* = 4) and the value in each

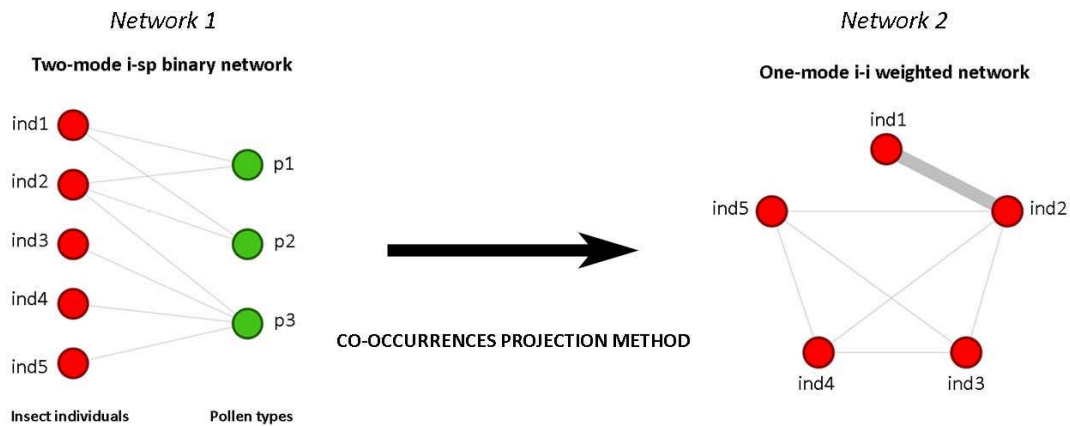
11 cell entry is 0 or 1 (i.e. absence or presence of pollen grains in insect's body, resp.).
12 Linkage level of species (L_{sp}) is the total number of plant pollen types carried (i.e.
13 *matrix 1* row sum). This two-mode binary network was transformed into a one-mode
14 weighted network by counting the total number of plant pollen types shared among
15 species (co-occurrences projection method as in Opsahl 2009 and Padrón *et al.* 2011).
16 *Network 2* is the one-mode projection of *network 1*, where insect species are linked if
17 pollen grains of the same plant pollen type were found on the body of both insects, and
18 the weight of each link is the number of plant pollen types in common. For instance, *sp1*
19 shares three pollen types with *sp2*, two pollen types with *sp3* and only one with *sp4* and
20 *sp5*. Therefore, the maximum link weight possible in this kind of network projection is
21 always the total number of plant pollen types present in the community (here $p = 4$).
22 This one-mode weighted network depicting the pattern of shared pollen types among
23 insect species can be also represented by an interaction matrix with s rows and s
24 columns (*Matrix 2*) where the value in each cell entry (w_{ij}) is the number of plant pollen
25 types shared. Therefore, sum of link weights ($\sum w_{ij}$, i.e. *matrix 2* row sum) is the overlap
26 in plant pollen types among a certain species and all other species in the network. To get
27 a standardized measure of interspecific overlap ranging from 0 to 1 (*SPO*), we divided
28 $\sum w_{ij}$ by the maximum interspecific overlap possible for a species in the network, which
29 was calculated as $p(s - 1)$, i.e. sum of node link weights $\sum w_{ij}$ in an hypothetical case
30 where all insect species carried all plant pollen types from the community and therefore
31 shared all (*Matrix 3*). We illustrate the complete calculation of species-species overlap
32 (*SPO*) for two species in our example.

33

34 **References in Appendix S3:**

- 35 Opsahl, T. (2009) *Projecting two-mode networks onto weighted one-mode networks*.
36 Available at: <http://toreopsahl.com/tnet/two-mode-networks/projection/>
37 Padrón, B., Nogales, M. & Traveset, A. (2011) Alternative approaches of
38 transforming bimodal into unimodal mutualistic networks. The usefulness of
39 preserving weighted information. *Basic and Applied Ecology*, **12**, 713-721.
40

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1 **Appendix S4** *Measuring intraspecific overlap with one-mode weighted networks.***Matrix 1**

Two-mode interaction matrix

	p1	p2	p3	L_i
ind1	1	1	0	2
ind2	1	1	1	3
ind3	0	0	1	1
ind4	0	0	1	1
ind5	0	0	1	1

Matrix 2

One-mode interaction matrix

	ind1	ind2	ind3	ind4	ind5	$\sum w_{ij}$
ind1	0	2	0	0	0	2
ind2	2	0	1	1	1	5
ind3	0	1	0	1	1	3
ind4	0	1	1	0	1	3
ind5	0	1	1	1	0	3

$$\sum_i \sum_j w_{ij} = 16$$

Individual-individual overlap calculation

$$IO_{sp1} = \frac{\sum_i \sum_j w_{ij}}{a \cdot n \cdot (a-1)} = \frac{16}{5 \cdot 3 \cdot (5-1)} = 0.266$$

Matrix 3

Maximum intraspecific overlap interaction matrix

	ind1	ind2	ind3	ind4	ind5	$\sum w_{ij}$
ind1	0	3	3	3	3	12
ind2	3	0	3	3	3	12
ind3	3	3	0	3	3	12
ind4	3	3	3	0	3	12
ind5	3	3	3	3	0	12

$$\sum_i \sum_j w_{ij} = 60$$

2

3 Here we present an example illustrating the methodology used to estimate intraspecific
 4 overlap (IO) for insect species in our networks. *Network 1* is the two-mode binary
 5 pollen-transport network for *sp1* (see previous example in Appendix S3) depicting
 6 interactions between five insect individuals (red nodes) of *sp1* and three plant pollen
 7 types (green nodes). Therefore, *network 1* represents within-species partition of pollen
 8 resources among insect individuals. Insect individuals are linked to plant pollen types if
 9 they carried pollen grains. *Network 1* can also be represented as an interaction matrix
 10 (*Matrix 1*) with a rows and n columns, where a is the number of *sp1*'s insect individuals

11 ($a = 5$), n is the number of plant pollen types visited by $sp1$ ($n = 3$, i.e. L_{sp1}) and the
 12 value in each cell entry is 0 or 1 (i.e. absence or presence of pollen grains on insect's
 13 body, respectively). Linkage level of the corresponding species (L_{sp}) is the maximum
 14 linkage level possible for conspecific insect individuals (L_i , i.e. *matrix 1* row sum). This
 15 two-mode binary network (*Network 1*) was transformed into a one-mode weighted
 16 network (*Network 2*) by counting the total number of plant pollen types shared among
 17 individuals and using it as link weight w_{ij} (co-occurrences projection method as in
 18 Opsahl 2009 and Padrón et al. 2011). In the example, $ind1$ and $ind2$ have two pollen
 19 types in common and all other individuals share a pollen type among them. This one-
 20 mode weighted network can also be represented by an interaction matrix with a rows
 21 and a columns (*Matrix 2*) where the value in each cell entry (w_{ij}) is the number of plant
 22 pollen types shared among ind_i and ind_j , so $\sum w_{ij}$ (i.e. *matrix 2* row sum) represents the
 23 total number of pollen types shared among ind_i and all other conspecific individuals.
 24 Therefore, sum of all matrix link weights ($\sum_i \sum_j w_{ij}$, i.e. *matrix 2* row and column sum)
 25 is the overlap in plant pollen types among all conspecific individuals (i.e. intraspecific
 26 overlap). To get a measure of intraspecific overlap ranging from 0 to 1 (IO), we divided
 27 by the maximum intraspecific overlap possible for the corresponding species (see
 28 *Matrix 3*). As maximum number of pollen types in common (w_{ij}) among two individuals
 29 of $sp1$ is n , maximum intraspecific overlap will occur when all conspecific individuals
 30 have the same linkage level as the species and therefore share all n pollen resources
 31 among them as represented in *Matrix 3* (i.e. $\sum w_{ij} = n \times (a - 1) = 12$ and $\sum_i \sum_j w_{ij} = a \times$
 32 $\sum w_{ij} = 12 \times 5 = 60$). Complete formulae for calculation of intraspecific overlap (i.e.
 33 individual-individual overlap, IO) is shown for $sp1$ as example.

34

35 **References in Appendix S4:**36 Opsahl, T. (2009). *Projecting two-mode networks onto weighted one-mode networks*.37 Available at: <http://toreopsahl.com/tnet/two-mode-networks/projection/>38 Padrón, B., Nogales, M. & Traveset, A. (2011) Alternative approaches of transforming
39 bimodal into unimodal mutualistic networks. The usefulness of preserving weighted
40 information. *Basic and Applied Ecology*, **12**, 713-721.

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For Review Only

1 **Appendix S5.** *Evaluation of species sampling completeness*

2

3 We aimed to determine the extent to which the number of individuals sampled per
4 species allowed for a sufficient description of species interactions (L_{sp}). To evaluate
5 completeness of our sample sizes we first computed sampled-based rarefaction curves
6 for each species (Gotelli & Colwell 2001) using the package *vegan* (version 2.0-6,
7 Oksanen *et al.* 2012) in the *R* program (version 2.15.0, R Development Core Team
8 2012). Following Chacoff *et al.* (2012), for each of the 21 species studied, we calculated
9 the percentage of estimated asymptotic richness detected as,

10

11 $\% S_{OBS} = 100 * S_{OBS} / S_E$ eqn 1

12

13 where S_{OBS} is the observed pollen type richness in the samples (i.e. species linkage
14 level, L_{sp}) and S_E is the asymptotic estimated pollen type richness (i.e. estimated species
15 linkage level). To compute S_E we used the *Chao 2* non-parametric estimator in its bias-
16 corrected form,

17

18 $S_E = S_{OBS} + [(a - 1) / a] * [u(u - 1) / 2(d + 1)]$ eqn 2

19

20 where a is the sample size (i.e. number of individuals of each species sampled for pollen
21 load analysis), u is the number of uniques (i.e. plant pollen types that occur only in one
22 sample) and d is the number of duplicates (i.e. plant pollen types that occur in two
23 samples) (Chao 2005). *Chao 2* index relies on the principle that rare species in the
24 samples carry most information on the number of un-observed species (Chao 1984) and

1 is one of the least biased estimates for small sample sizes (Colwell & Coddington
2 1994).

3

4 **References in Appendix S5:**

5 Chacoff, N.P., Vázquez, D.P., Lomáscolo, S.B., Stevani, E.L., Dorado, J. & Padrón,
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9 *Scandinavian Journal of Statistics*, **11**, 265-270.

10 Chao, A. (2005) Species richness estimation. *Encyclopedia of Statistical Sciences*
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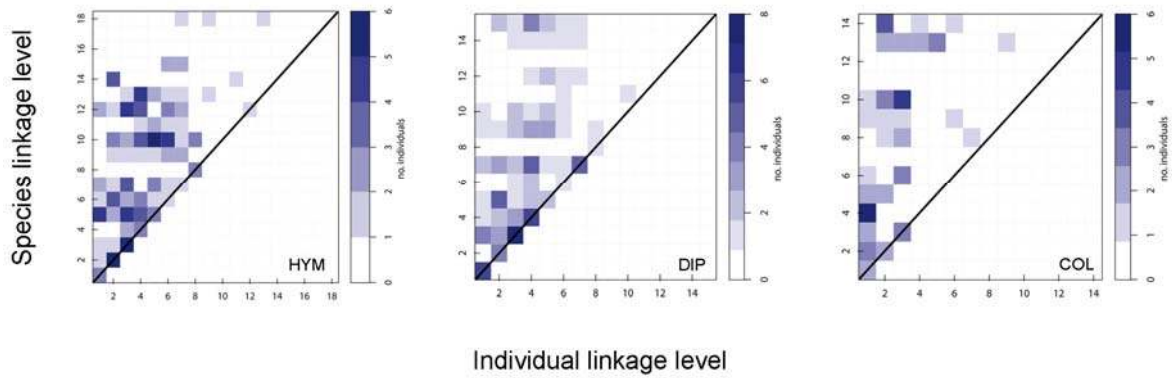
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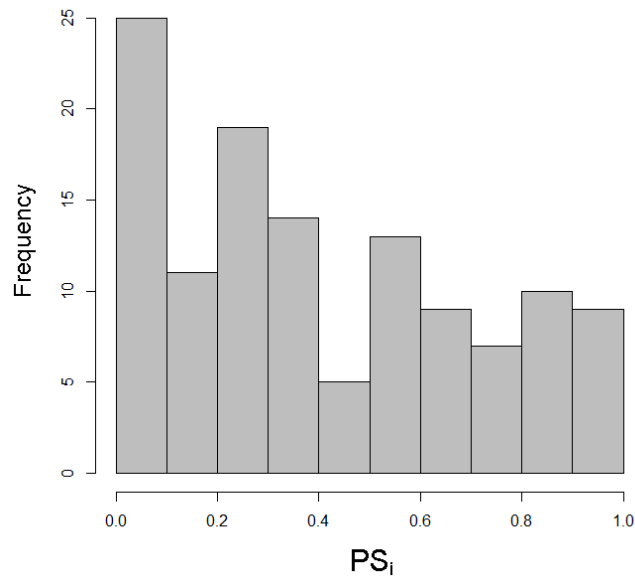


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3 **Fig. S1.** Relation between linkage level of species (L_{sp}) and individuals (L_i) for the main
 4 insect orders. Each matrix corresponds to a different insect pollinator order:
 5 Hymenoptera ($N_{HYM}=147$ individuals), Diptera ($N_{DIP}=114$) and Coleoptera ($N_{COL}=59$).
 6 Colours represent number of individuals with a given L_i and L_{sp} configuration, so figures
 7 show where the highest density of individuals is in each matrix. Matrix diagonal
 8 (*species-individual isocline*) represents perfect matching of individual niche width and
 9 species niche width ($L_i = L_{sp}$), while deviations to the left indicate individuals being
 10 more specialized than their species ($L_i < L_{sp}$). Filled cells are located in the upper region
 11 of the diagonal because of the constraint $L_i \leq L_{sp}$. For all species in the different orders,
 12 specialist individuals predominate ($L_i/L_{sp} < 1$). The trend is more marked for beetles,
 13 probably because of their lower mobility.

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3 **Fig. S2.** Frequency histogram ($N = 122$) of the proportional similarity indices of
4 individuals (PS_i) from the 21 selected species in our networks. Individuals with
5 narrower niches than their corresponding species are more frequent (60.7% individuals
6 had a $PS_i < 0.5$), although some highly generalized individuals can be found as well.

Table S1. Definitions of parameters used to describe *sp-sp* and *i-sp* networks. The first five metrics are qualitative, whereas the last two are quantitative.

Parameter	Definition
Linkage level (<i>L</i>)	Number of interactions of each network node, i.e. number of interactions per species (L_{sp}) in <i>sp-sp</i> networks and number of interactions per individual (L_i) in <i>i-sp</i> networks.
Network size (<i>N</i>)	Total number of possible interactions in the network, i.e. the number of cell entries in the interaction matrix (number of <i>i</i> rows multiplied by number of <i>j</i> columns).
Linkage density (<i>LD</i>)	Mean number of links per network node.
Connectance (<i>C</i>)	Realized proportion of all possible links (Dunne <i>et al.</i> 2002).
Nestedness (<i>NODF</i>)	Nestedness metric based on overlap and decreasing fills (Almeida-Neto <i>et al.</i> 2008). It measures to what extent the interaction pattern resembles a perfectly nested pattern where specialist species interact with a proper subsets of the species with which more generalized species interact. It ranges from 0 (non-nestedness) to 100 (perfect nestedness).
Interaction diversity (<i>H</i>)	Shannon diversity of links for a network node <i>i</i> ($H_i = -\sum_j p_{ij} \cdot \ln p_{ij}$, where $p_{ij} = \frac{n_{ij}}{\sum_j n_{ij}}$ and n_{ij} is the interaction frequency between node <i>i</i> and <i>j</i> ; here number of <i>j</i> 's pollen grains carried by insect node <i>i</i>) or Shannon diversity of links for the whole network ($H_2 = -\sum_i \sum_j q_{ij} \cdot \ln q_{ij}$, where $q_{ij} = \frac{n_{ij}}{\sum_i \sum_j n_{ij}}$) (Bersier <i>et al.</i> 2002).
Interaction evenness (E_2)	Shannon's evenness of link frequency distribution in the whole network ($E_2 = \frac{H_2}{\ln(I)}$, where <i>I</i> is the total number of links in the network and $\ln(I)$ the maximum diversity possible in the network i.e. H_{max}). It measures the heterogeneity of interaction frequencies, ranging from 0 (uneven network) to 1 (uniform network). An uneven network is one with high skewness in the distribution of link frequencies (Tylianakis <i>et al.</i> 2007).

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1 **Table S2** List of individual specialization and overlap indices calculated for the 21 insect species of flower-visitors selected from our networks.

Insect species	Label	Order	Site	a	L_{sp}	\bar{L}_i	$_{null} \bar{L}_i$	TNW	WIC	BIC	WIC/TNW*	SPO	IO
<i>Apis mellifera</i>	api.mel	HYM	CN	8	12	3.25	9.84	0.76	0.12	0.63	0.16	0.05	0.08
<i>Attalus</i> sp.	att.sp	COL	CN	6	4	1.00	3.59	1.13	0.00	1.13	0.00	0.02	0.05
<i>Eristalis tenax</i>	eri.ten	DIP	CN	5	15	4.20	13.59	1.84	1.11	0.73	0.60	0.06	0.06
<i>Eupeodes corollae</i>	eup.cor	DIP	CN	5	10	3.40	7.08	0.71	0.40	0.31	0.56	0.06	0.12
<i>Exoprosopa bowdeni</i>	exo.bow	DIP	CN	5	9	4.80	5.16	0.83	0.79	0.04	0.95	0.06	0.34
<i>Halictus</i> spp.	hal.sp	HYM	CN	5	10	4.40	9.80	1.19	0.37	0.82	0.31	0.06	0.20
<i>Halictus vestitus</i>	hal.ves	HYM	CN	5	11	5.40	11.00	1.76	0.89	0.87	0.51	0.06	0.25
<i>Lasioglossum nitidulum hammi</i>	las.nit	HYM	CN	6	12	4.00	9.09	1.41	0.89	0.52	0.63	0.06	0.16
<i>Mordellistena</i> sp.	mor.sp	COL	CN	9	10	2.44	9.10	1.35	0.60	0.75	0.44	0.06	0.09
<i>Oedemera flavipes</i>	oed fla	COL	CN	10	13	4.20	12.95	1.97	0.81	1.16	0.41	0.06	0.14
<i>Paragus tibialis</i>	par.tib	DIP	CN	5	12	5.40	11.61	1.69	1.00	0.68	0.59	0.07	0.23
<i>Plagiolepis pygmaea</i>	pla.pyg	HYM	CN	5	5	1.80	3.72	1.00	0.09	0.91	0.09	0.04	0.10
<i>Sphaerophoria</i> sp.	sph.sp	DIP	CN	6	15	4.17	12.96	1.32	0.54	0.78	0.41	0.05	0.08
<i>Stomorhina lunata</i>	sto.lun	DIP	CN	5	7	3.00	6.90	0.92	0.52	0.40	0.56	0.05	0.21
<i>Anthidium cingulatum</i>	ant.cin	HYM	PC	5	13	5.00	9.84	1.42	1.04	0.37	0.74	0.07	0.19
<i>Apis mellifera</i>	api.mel	HYM	PC	5	14	3.80	11.47	0.48	0.13	0.35	0.27	0.07	0.06
<i>Halictus</i> spp.	hal.sp	HYM	PC	5	10	4.80	9.22	0.91	0.52	0.39	0.57	0.06	0.27
<i>Megachile pilidens</i>	meg.pil	HYM	PC	6	13	5.00	8.78	0.93	0.80	0.13	0.86	0.07	0.16
<i>Oedemera flavipes</i>	oed fla	COL	PC	6	14	3.00	12.99	1.81	0.71	1.11	0.39	0.05	0.02
<i>Sphaerophoria</i> sp.	sph.sp	DIP	PC	5	14	5.00	9.84	0.40	0.17	0.23	0.42	0.08	0.12
<i>Tapinoma nigerrimum</i>	tap.nig	HYM	PC	6	7	2.00	2.80	0.14	0.01	0.14	0.05	0.05	0.06

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3 HYM: Hymenoptera; COL: Coleoptera; DIP: Diptera; CN: Coma de n'Arbona; PC: Passadís de Ses Clotades; a: number of individuals captured for pollen

4 load analysis; L_{sp} : linkage level of species; \bar{L}_i : mean linkage level of conspecific individuals; $_{null} \bar{L}_i$: mean linkage level of conspecific individuals after

5 1,000 randomizations under the null hypothesis that individuals act as generalists sampling from species pollen resource distribution proportions; TNW: total

- 1 niche width; WIC: within-individual niche component; BIC: between-individual niche component; WIC/TNW: degree of individual specialization; SPO:
2 interspecific overlap; IO: intraspecific overlap.
3 * All WIC/TNW empirical values reported were below null WIC/TNW values obtained from 1,000 randomizations.
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