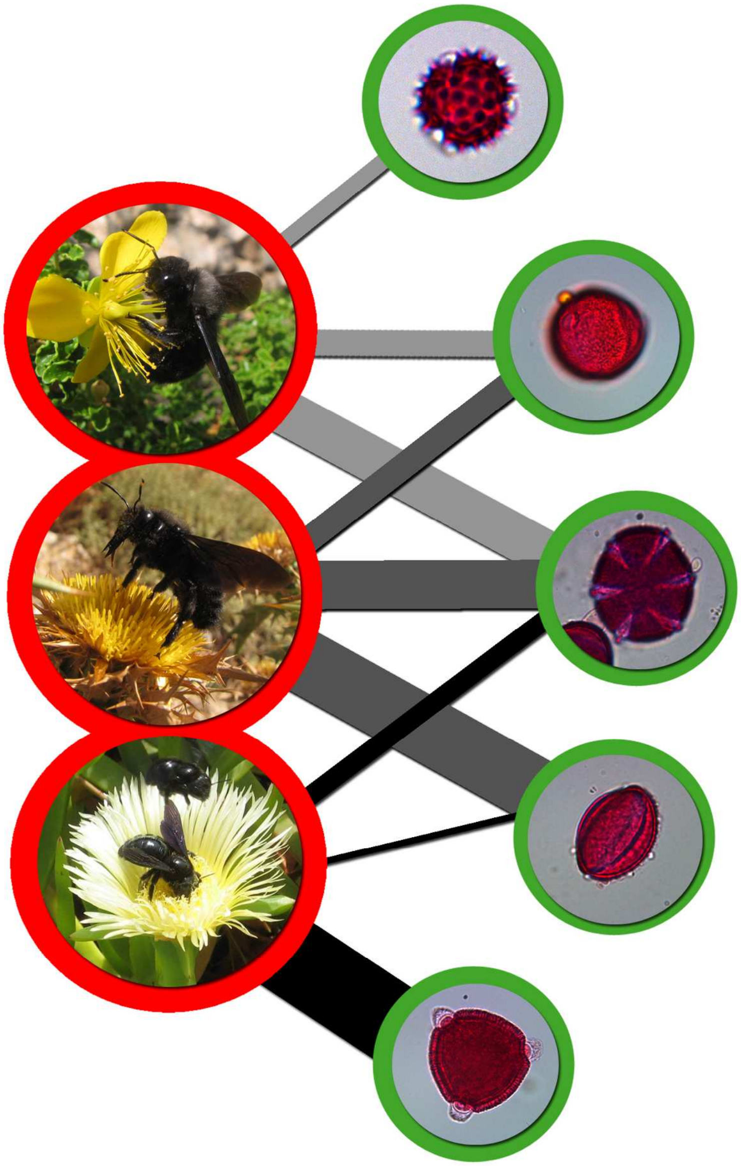

i-sp pollen-transport network for the species Xylocopa violacea
143x186mm (300 x 300 DPI)

Downscaling pollen-transport networks to the level of individuals

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Running headline: Downscaling from species to individuals.

Summary

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

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

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

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

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

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

Introduction

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

Despite the recognized importance of individual variation within natural populations for many ecological processes (Bolnick *et al.* 2011; Dall *et al.* 2012; Sih *et al.* 2012; Wolf & Weissing 2012), only a few empirical studies to date have applied network theory as a tool for exploring ecological interactions at the individual level. For example, individual-based networks have been used to study intrapopulation patterns of resource partition (Araújo *et al.* 2010; Pires *et al.* 2011; Tinker *et al.* 2012), changes in foraging preferences at increasing levels of intraspecific competition (Araújo *et al.* 2008), body size effects in prey-predator interactions (Woodward & Warren 2007; Yvon-Durocher *et al.* 2010), patterns in roosting sites of bats (Fortuna *et al.* 2009) and disease dynamics (Perkins *et al.* 2009). In the case of pollination networks, the number of individual-based network studies is very scarce, all focusing on one or two species (Fortuna *et al.* 2008; Dupont *et al.* 2011; Gómez *et al.* 2011, 2012). A likely explanation for the scarcity of such studies is the labour-intensive sampling required to resolve community-wide species networks into individual-based networks covering all species present.

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

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

Our first goal was to investigate whether network structure changes when downscaling from *sp-sp* to *i-sp* and if so, which network topological parameters change in particular. The network-downscaling process inherently implies an increase in the number of network nodes, because species are composed of groups of conspecific individuals. Given that most network metrics are influenced by network size (Dormann *et al.* 2009), we built null models that account for size-related differences. Changes in network structure when downscaling might be expected due to differences in individual pollen use resulting from different foraging patterns, individual behaviours and trait variability among conspecifics. We defined niche of a pollinator species both qualitatively (number of interactions to plant pollen types, i.e. linkage level) and quantitatively (diversity of pollen types carried by insects). Given that linkage level of a species (L_{sp}) expresses the sum of all links established by its individuals (L_i), we hypothesize that pollinator species niche may be determined by means of two possible mechanisms: (i) individuals are as generalized as their species, i.e. all individuals have similar feeding niche (null hypothesis: $L_{sp} \approx L_i$), or (ii) individuals are more specialized than the species (alternative hypothesis: $L_i << L_{sp}$). If the alternative hypothesis is true, we would predict changes in topological parameters beyond those related to size differences when downscaling from *sp-sp* to *i-sp* networks.

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

Finally, our third goal was to identify potential ecological factors influencing individual specialization in pollen use. Specifically, using structural equation modeling we tested the effect of factors known to influence individual specialization from other studies: (i) inter- and intraspecific overlap (competition, i.e. amount of resources shared by individuals of different or same species), (ii) insect species abundance and (iii) insect species phenophase, i.e. temporal extent of network membership. In the context of Optimal Foraging Theory (Stephens & Krebs 1986), we expected a high degree of individual specialization to be associated to: (i) low amounts of interspecific overlap, because release from resource competition favours species niche expansion through increased variation in resource use between individuals (Costa *et al.* 2008; Bolnick *et al.* 2010); (ii) high amounts of intraspecific overlap, because strong intraspecific competition promotes resource use diversity among conspecifics (e.g. Svanbäck & Bolnick 2005; Svanbäck & Bolnick 2007; Araújo *et al.* 2008); (iii) high abundance of species, because at high densities of foragers the availability of preferred resources decreases causing individuals to add different subsets of resources (e.g. Fontaine, Collin & Dajoz 2008; Tinker, Bentall & Estes 2008; Svanbäck *et al.* 2011; Tinker *et al.* 2012); and (iv) long species phenophases, because species with short phenophases might be composed by short-lived individuals using similar and narrower subsets of resources due to temporal restriction in resource pool compared to species with long phenophases.

Materials and methods

STUDY SITES AND DATA COLLECTION

Plant-pollinator interactions were studied at two sites on the highest mountain in Mallorca (Puig Major, 1445 m): (i) *Sa Coma de n'Arbona* (*CN*) at 1100 m a.s.l. (39º48'05" N 2º47'9" E) and (ii) *Passadís de Ses Clotades* (*PC*) at 1400 m a.s.l. (39º48'34" N 2º47'50" E). Plant-pollinator interactions were surveyed during the entire flowering season, from May to August 2010, on clear and calm days. Pollinator censuses of 5 min, focusing upon randomly selected plant individuals of every species in bloom, were carried out between 10 am and 5 pm three times a week. During each census we recorded: (i) taxonomic identity of plant species under observation; (ii) taxonomic identity of insect pollinators (species name if possible or morphospecies otherwise; hereafter species), and (iii) number of individuals of each insect species observed. After each census, flower-visiting insects were captured, placed separately in clean vials and stored in a freezer for later pollen analysis and expert identification. We carried out a total of 458 censuses at *CN* (38 h 10 min) and 377 at *PC* (31 h 25 min), capturing 73 and 61 insect species, respectively. At each site, abundance and phenophase of each insect species were estimated as total number of individuals observed in all censuses and total number of days between first and last observation date of flower-visiting individuals, respectively.

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

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

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

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

We selected the following parameters to describe *sp-sp* and *i-sp* network structure: number of pollinator nodes (A), number of pollen type nodes (P), total number of nodes (T), total number of interactions (I), linkage level (L), network size (N), linkage density (LD), connectance *(C)*, nestedness ($NODF$), interaction diversity (H_2) and interaction evenness (E_2) (see Table S1 in Supporting Information for definitions). The significance of the *NODF* metric was assessed against 1,000 randomizations using the fixed row and column totals constrained model, i.e. node linkage level was fixed. We calculated the probability of randomly obtaining higher *NODF* values than that of the empirical matrix with a one-tailed Z-test. All network metrics were obtained with the *bipartite* (version 1.17, Dormann, Gruber & Fründ 2008) and *vegan* (version 2.0-6, Oksanen *et al.* 2012) packages implemented in the *R* statistical software version 2.15.0 (*R* Development Core Team 2012).

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

EVALUATION OF INCIDENCE AND MAGNITUDE OF INDIVIDUAL SPECIALIZATION

We compared linkage level of each insect species (L_{sp}) with those of their individuals (L_i) to explore specialization at both levels. For species with ≥ 5 sampled individuals (14 spp. at *CN,* 7 spp. at *PC*), we calculated average $\overline{L_i}$ of a given species, and compared it to the $\overline{L_i}$ obtained in null networks. We concluded that a species was composed of individuals being significantly more specialized than the species when empirical $\overline{L_i}$ < 95% of 1,000 null $\overline{L_i}$. Within a species, both generalist and specialist individuals were frequently found, so we evaluated the presence of a nested pattern in species linkage level partition among conspecifics. We followed the same procedure explained above for *NODF* calculation with a set of 21 *i-sp* submatrices (matrices for species with ≥ 5 sampled individuals) (see Fig. 3 for an example).

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

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

ANALYSIS OF ECOLOGICAL FACTORS AFFECTING THE DEGREE OF INDIVIDUAL SPECIALIZATION

Interspecific overlap

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

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

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

Intraspecific overlap

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

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

where $\sum_i \sum_j w_{ij}$ is the total overlap among all conspecific individuals in the subnetwork of S (sum of the link weights for all individuals of S) and the denominator is the maximum overlap for the subnetwork of S, i.e. when all the conspecific individuals share all pollen types used by the species (*n* = total number of pollen types used by *S* and *a* = total number of conspecific individuals of species *S*). See Appendix S4 for an illustrative example of the detailed calculation method of intraspecific overlap. It is important to note that our estimates of inter- and intraspecific overlap in pollen use are only a ‘proxy’ of competition, as either individuals or species, respectively, might share the same flower species but use a different resource (e.g. pollen or nectar). We thus prefer to use the neutral term ‘overlap’ instead of competition because the real sign of the interaction is unknown.

Statistical analysis

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

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

SAMPLING LIMITATIONS AND STUDY CAVEATS

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

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

Results

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

Downscaling from *sp-sp* to *i-sp* modified most network topological parameters studied (Table 1). The direction and magnitude of the observed changes depended on the foraging behaviour of insect individuals, as shown by the contrasting results obtained between null models and empirical networks. Empirical *i-sp* networks were obviously larger in size than *sp-sp*, as most species were resolved into several individuals except singleton observations (i.e. insect species observed only once and therefore consisting of one individual). Consequently, at both study sites, downscaling increased total number of interactions (I) 1.5-fold (Fig. 1), although significantly less than the expected with null *i-sp* networks. Linkage density (LD) and network connectance (C) in empirical *i-sp* networks was nearly half the expected compared to the null hypothesis. Therefore, such differences between *sp-sp* and *i-sp* can be attributed to a significant decrease in the number of links per pollinator node in empirical *i-sp* networks (Table 1), rather than to an effect of increasing network size. Single individuals had a narrower foraging niche than their corresponding species. Mean pollinator linkage level (L_A) in *i-sp* networks was c. 50% lower than that predicted by the null model. Mean interaction diversity for pollinators (H_A) was also significantly smaller when downscaling, because individuals transported fewer and a more variable load of pollen types than their corresponding species. Because of this idiosyncratic and heterogeneous individual behaviour, changes in network nestedness were also observed. Both *sp-sp* and *i-sp* networks were significantly nested; however, $NODF$ values were consistently lower in empirical *i-sp* than in null *i-sp* networks. Furthermore, minor but statistically significant decreases of interaction diversity (H_2) were observed in empirical *i-sp* networks compared to null models, due to differences in the number of interactions, whereas interaction evenness (E_2) increased showing a reduction in the skewness in the distribution of link frequencies.

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

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

On average, an individual niche represented c. 46% of total species niche (mean *WIC/TNW* ± sd; *CN* = 0.45 ± 0.25, *PC* = 0.48 ± 0.27; empirical *WIC/TNW* < null *WIC/TNW* for all species) (Fig. 4, Table S2). At both sites, a large fraction of individuals (63.5% in *CN* and 54% in PC) had a niche which differed strongly from their species' niche, i.e. $PS_i < 0.5$ (Fig. S2). However, the intraspecific variability of PS_i was high (average coefficient of variance in mean PS_i of species was 59% at *CN* and 86% at *PC*). Thus, most species consisted of both generalist and specialist individuals (examples in Fig. 3).

FACTORS AFFECTING DEGREE OF INDIVIDUAL SPECIALIZATION

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

Discussion

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

NETWORK DOWNSCALING AND INDIVIDUAL FORAGING BEHAVIOR

Downscaling to the individual level revealed a high degree of specialization and heterogeneity hidden within *sp-sp* networks. Generalist pollinator species were actually found to be composed of specialist individuals. Results showed empirical *i-sp* networks had lower linkage density, connectance, nestedness and interaction diversity than predicted by null models, because conspecific individuals were idiosyncratic in their food plant choice and foraging behaviour. Species linkage level was usually partitioned among specialist individuals (Fig. 2), and this was true for all pollinators combined and also when separating species into orders (Hymenoptera, Diptera and Coleoptera, Fig. S1). Therefore, the most common mechanism for pollinator species to achieve a broad niche (here high L_{sp}) was to have individuals with different and narrow niches ($L_i << L_{sp}$) (Fig. 3a). Quantitative measures of individual specialization (*WIC/TNW*, PS_i) also confirmed this pattern and let us to reject the null hypothesis of individual generalist sampling from species pollen use distribution. Our average values of *WIC/TNW* were within the range reported by Araújo *et al.* (2011) for a broad array of taxa. Nevertheless, both generalist and specialist individuals were commonly found within a species. The frequency distribution of individual niche width was highly skewed, i.e. common species had only a few individuals with a wide niche. However, intraspecific partition of resources was quite overdispersed (i.e. non-nested) and the specialized individuals were not carrying a subset of the pollen types carried by more generalized conspecifics.

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

FACTORS INFLUENCING INDIVIDUAL SPECIALIZATION

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

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

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

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

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

RELEVANCE OF NETWORK DOWNSCALING

Downscaling networks from species to individuals is important in our efforts to explore mechanisms acting at the individual level, which further may upscale and shape species network structure (Olesen *et al.* 2010). Indeed, the individual-based networks reported here provide useful information to improve the understanding of species-based networks because most *sp-sp* networks contain a substantial proportion of singleton observations, which means they are based on observations of only one individual (e.g. 23% of an arctic network in Olesen *et al.* 2008 was based on singletons). Commonly, rare species in networks appear to be more specialized than they really are due to insufficient sampling of the rare interactions (Vázquez & Aizen 2003; Dorado *et al.* 2011). In concordance with this, our results suggest that a specialized behaviour of individuals compared to the species might be a possible explanation for the sampling bias in the estimation of linkage level in rare species. Similarly, most abundant species tend to be also the most generalized in pollination networks (e.g. Elberling & Olesen 1999; Olesen *et al.* 2008), but as we have shown here, this might actually cover a scenario where the conspecific individuals are specialized on different resources. Everything else being equal, individuals of abundant insect species are observed more frequently than those of rare species, and as new individuals are collected proportionally more new links are added to the species due to the specialized behaviour of the individuals. Thus, some broadly described specialization patterns in *sp-sp* pollination networks might have their origin in *i-sp* networks. Because ecological specialization is not a fixed species attribute and much variation exists within species, more studies are needed to explore ecological specialization across scales (Devictor *et al.* 2010).

Our findings highlight the importance of also taking inter-individual variation into account when studying higher–order structures such as networks, as part of our understanding of network structure and dynamics hidden on adjacent scale levels. For example, the high heterogeneity in pollen use among conspecifics enforces a high heterogeneity in interaction strength in species-based networks as well, which, so far, has been completely neglected. The strength of a *sp-sp* interaction depends on the number of individuals taking part in the interaction and the degree of their involvement. This has obviously important implications in the interpretation of community structure and dynamics (Bolnick *et al.* 2011; Sih *et al.* 2012). For instance, a pollen type is more likely to be an important resource to a species than other pollen types if a larger proportion of the population is using it. Consequently, having generalized species decomposed into dissimilar and specialized individuals might increase stability of species to the loss of a resource, because only a small proportion of the population would be affected (Wolf & Weissing 2012). By contrast, high individual specialization increases species vulnerability to the loss of individuals. A species composed of generalized individuals may lose a substantial proportion of its population before any effects are seen in the species-based network, whereas a species composed of specialized idiosyncratic individuals loses individuals and network links simultaneously. Therefore, our cross-scale level study suggests that individual foraging mode affects species persistence and, further, network stability. The demonstrated variation in individual resource use will affect the network outcome of disturbances, and information about the specific kind of disturbance will be important in our efforts to predict how network stability in detail is affected.

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

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Data Accessibility

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

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Supporting Information

The following supporting information is available for this article online:

Table S1. Definition of network parameters.

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

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

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

Appendix S1. Insect pollen load analysis.

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

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

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

Appendix S5. Evaluation of species sampling completeness.

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

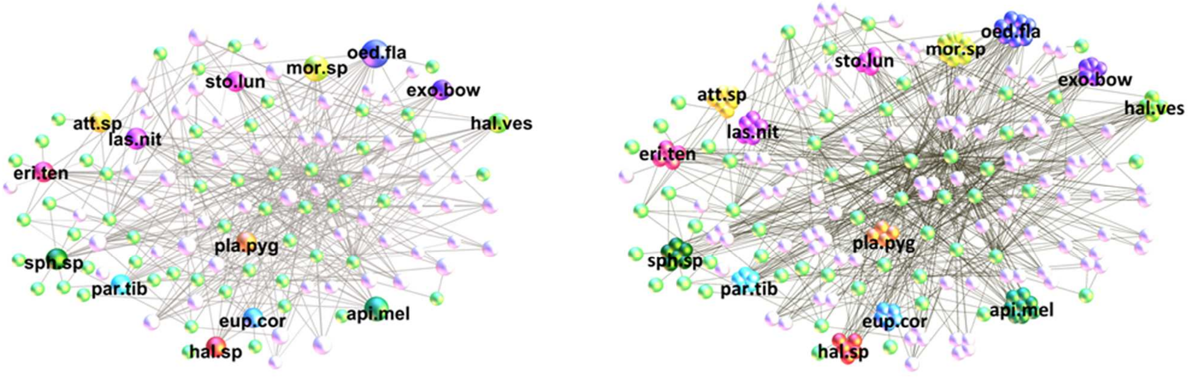
	sp-sp networks		***i-sp networks***			
	Empirical		Empirical		Null model	
Qualitative network parameters	*CN*	*PC*	*CN*	*PC*	*CN*	*PC*
Number of pollinator nodes (A)	73	61	190	137	190	137
Number of pollen type nodes (P)	55	49	55	49	55	49
Total number of nodes ($T=A+P$)	128	110	245	186	245	186
Network size ($N=AxP$)	4,015	2,989	10,450	6,713	10,450	6,713
Total number of interactions (I)	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 (*NODF*)	34.45*	38.65*	26.99*,†	29.67*,†	44.29	43.77
Quantitative network parameters						
Interaction diversity (H_2)	3.38	2.89	3.63†	3.18†	3.95	3.36
Interaction evenness ($E_2=H_2/H_{\text{máx}}$)	0.56	0.49	0.56†	0.51†	0.55	0.49
Node parameters						
Mean pollinator linkage level (L_A)	5.9	5.9†	3.5†	3.6†	7.07	6.44
Mean pollinator interaction diversity (H_A)	0.79	0.70	0.54†	0.54†	0.99	0.78
Mean pollen type linkage level (L_P)	7.89	7.35	12.38†	10.33†	24.41	18
Mean pollen type interaction diversity (H_P)	0.62	0.57	0.76†	0.69†	1.46	1.21

* Significance *p-value* < 0.001. That is the probability of getting by random a higher value of nestedness than the empirical one. See text for more details on the calculation.

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

Figures

Fig.1.



(A) sp-sp network *(B) i-sp network*

Fig. 2.

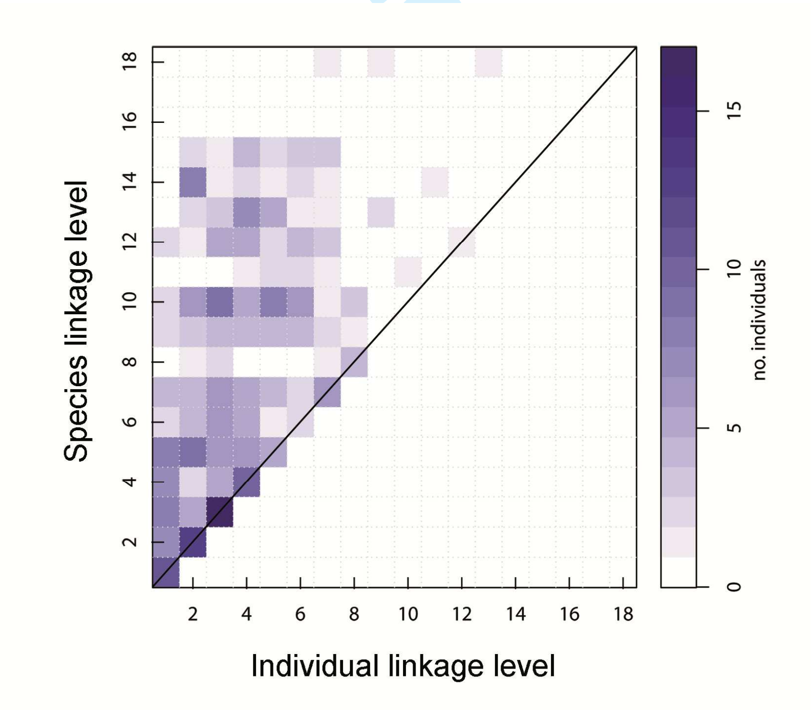


Fig. 3.

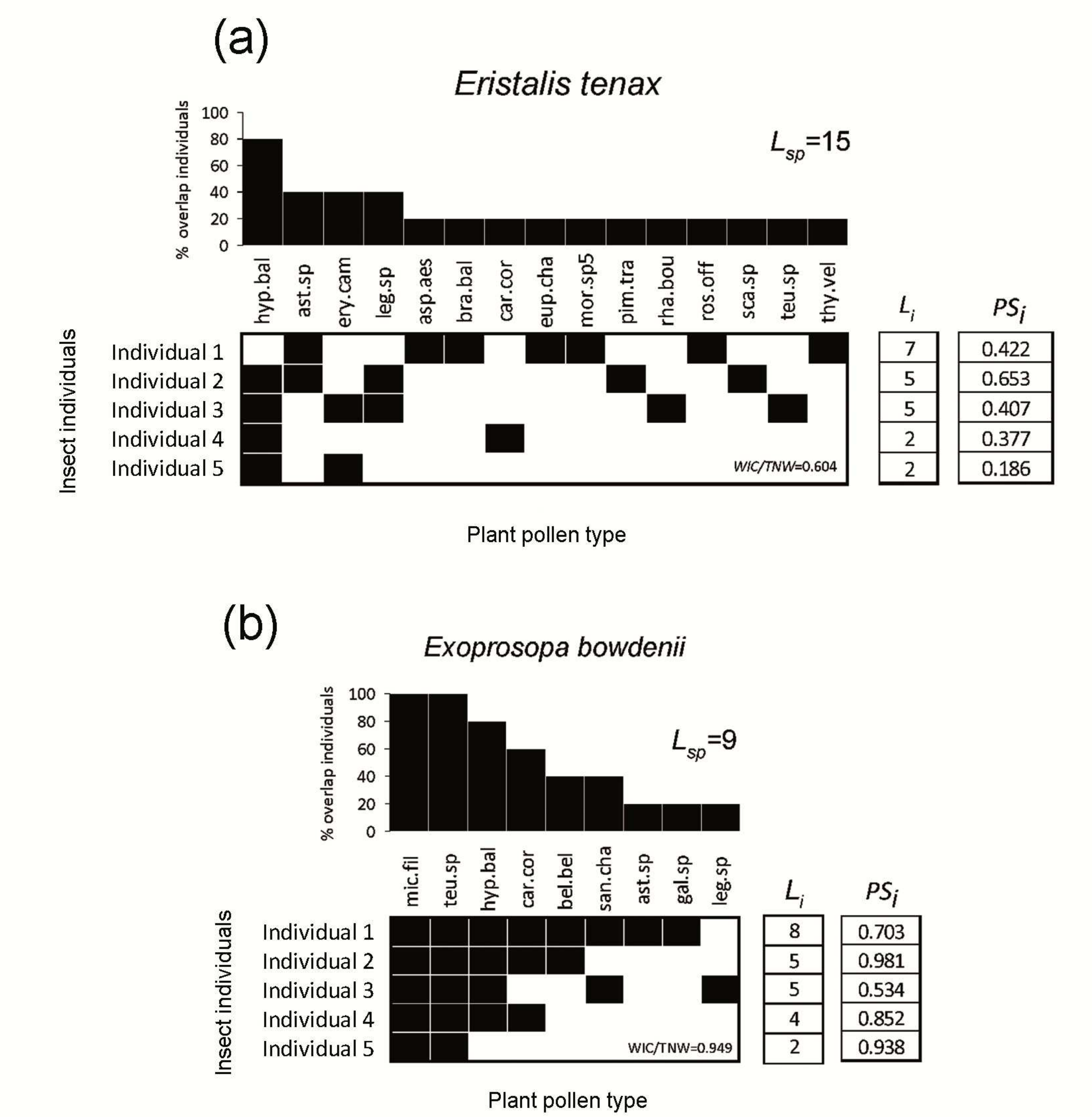

(a)
Eristalis tenax
% overlap individuals
100
80
60
40
20
0
L_{sp}=15
hyp.bal
ast.sp
ery.cam
leg.sp
asp.aes
bra.bal
car.cor
eup.cha
mor.sp5
pim.tra
rha.bou
ros.off
sca.sp
teu.sp
thy.vel
L_i
PS_i
Insect individuals
Individual 1
Individual 2
Individual 3
Individual 4
Individual 5
7
5
5
2
2
0.422
0.653
0.407
0.377
0.186
WIC/TNW=0.604
Plant pollen type
(b)
Exoprosopa bowdenii
% overlap individuals
100
80
60
40
20
0
L_{sp}=9
mic.fil
teu.sp
hyp.bal
car.cor
bel.bel
san.cha
ast.sp
gal.sp
leg.sp
L_i
PS_i
Insect individuals
Individual 1
Individual 2
Individual 3
Individual 4
Individual 5
8
5
5
4
2
0.703
0.981
0.534
0.852
0.938
WIC/TNW=0.949
Plant pollen type

Fig. 4

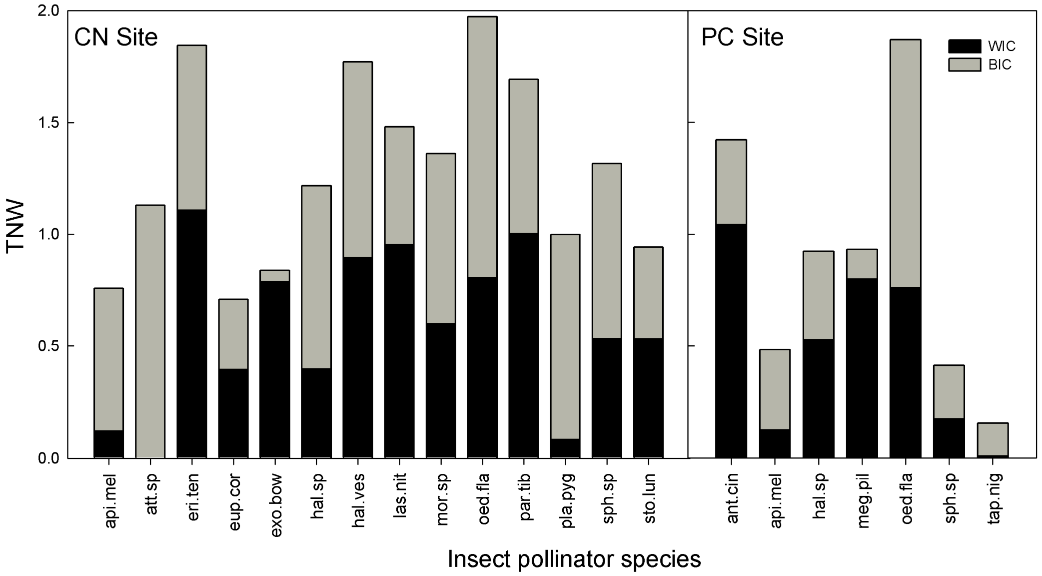

CN Site
PC Site
WIC
BIC
TNW
0.0
0.5
1.0
1.5
2.0
api.mel
att.sp
eri.ten
eup.cor
exo.bow
hal.sp
hal.ves
las.nit
mor.sp
oed.fla
par.tib
pla.pyg
sph.sp
sto.lun
ant.cin
api.mel
hal.sp
meg.pil
oed.fla
sph.sp
tap.nig
Insect pollinator species

Fig. 5.

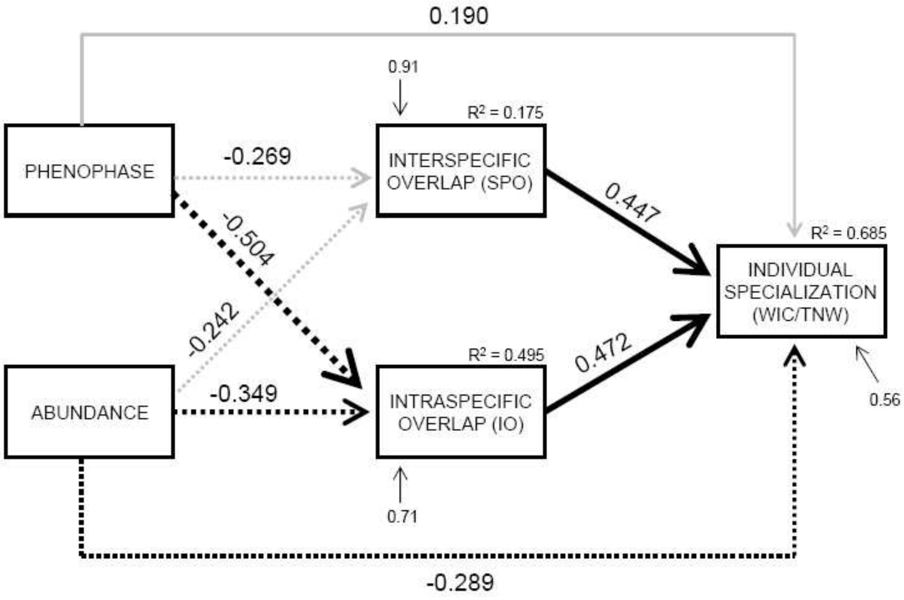

0.190
0.91
R² = 0.175
PHENOPHASE
-0.269
INTERSPECIFIC OVERLAP (SPO)
0.447
-0.504
R² = 0.685
INDIVIDUAL SPECIALIZATION (WIC/TNW)
-0.242
R² = 0.495
0.472
ABUNDANCE
-0.349
INTRASPECIFIC OVERLAP (IO)
0.56
0.71
-0.289

Figure legends

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

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

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

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

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

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

Appendix S1 *Insect pollen load analysis*

In the laboratory, we studied the pollen loads of each insect individual captured. For frequently captured species, a maximum of 10 individuals per species was included in the analysis. An isotonic water solution (1.5 ml) was added to each vial containing a specimen and shaken for 5 sec in a vortex and then washed by agitation for 15 min in an ultrasonic bath to remove pollen grains from their body surface. For honeybees, pollen clumps in the corbicula of the hind legs were removed in advance. Afterwards, insects were pinned for later identification by taxonomist experts. Vials containing the pollen load solution were centrifuged at 13.000 rpm for 15 min and inspected for any presence of a pollen pellet at the bottom. In vials with a large pollen pellet, to facilitate pollen counting, we added a *Lycopodium* spore tablet containing 18,584 spores (batch no. 177745, Lund Univ., Sweden), whereas in the other vials the supernatant was carefully removed, and the droplet with the pollen was suspended on a microscopic slide. Pollen concentrated samples were homogenized with vortex agitation in order to dissolve the spore tablets and then three drops (replicates) were mounted on slides. We added a small pink fuchsine-stained jelly cube to the pollen smear, melted it and covered the final smear with a cover slip (Kearns & Inouye 1993). To avoid any pollen contamination, laboratory instruments were cleaned with ethanol between manipulation of samples. Slides were analyzed under microscope (100-400x) to estimate total number of pollen grains from each insect individual. All pollen grains were identified to the lowest possible taxonomic level and the number of pollen grains of each species was counted (on average 60% of total slide area was inspected for pollen). In slides from pollen-dense samples, we counted the number of pollen grains and also the number of spores. In these samples, total pollen number carried by the insect was estimated as the mean of the three replicates, calculated as "number of pollen grains counted in a droplet x (18,584/number of spores counted in droplet)" (Jakobsson, Padrón & Traveset 2008). A pollen reference collection was made during the field season in order to facilitate pollen identification. Pollen grains of each species were measured and photographed under the microscope at 400x. Pollen grains of some species were indistinguishable from those of closely related species, and therefore classified into 'pollen type clusters' including more than one species: 'Galium' (including *G. cinereum*, *G. crespianum* and *G. balearicum*), 'Teucrium' (including *T. marum* and *T. asiaticum*), 'Geraniaceae' (including *Geranium colombinum*, *G. lucidum*, *G. molle*, *G. purpureum* and *Erodium cicutarium*), and 'Asteraceae' (including all Asteraceae at study sites except *Bellium bellidioides*, *Carlina corymbosa* and *Santolina chamaecyparissus*, which were identified to species). Unknown pollen grains were assigned to morphotype species.

References in Appendix S1:

Jakobsson, A., Padrón, B. & Traveset, A. (2008) Pollen transfer from invasive *Carpobrotus* spp. to natives - A study of pollinator behaviour and reproduction success. *Biological Conservation*, **141**, 136-145.

Kearns, C.A. & Inouye, D.W. (1993) *Techniques for pollination biologists*. University Press of Colorado, Colorado, USA.

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

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

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

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

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

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

where, p_{ij} is the proportion of pollen type *j* in the total pollen load of individual *i* of species *S,* p_i is the proportion of all pollen types used by *S* that are used by individual *i*, q_j is the proportion of pollen type *j* in the total pollen load of *S,* and γ_{ij} is the proportion of total pollen type *j* used by *S* that was carried by individual *i*. Relative degree of individual specialization was obtained by dividing *WIC* by *TNW*, i.e. proportion of total niche width explained by the within-individual component.

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

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

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

References in Appendix S2:

Bolnick, D.I., Svanbäck, R., Araújo, M.S. & Persson, L. (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciencie of the United States of America,* **104**, 10075-10079.

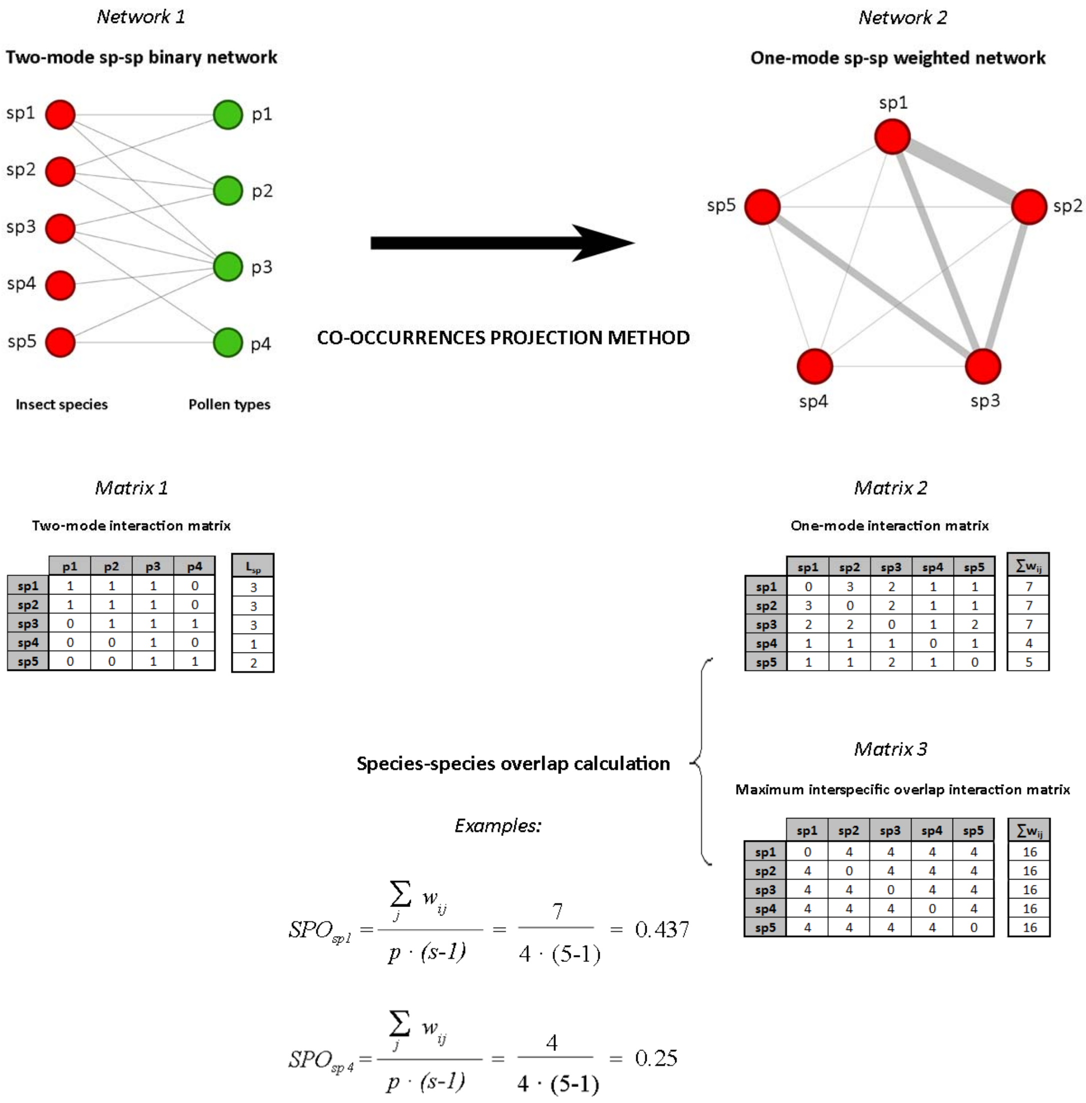
Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M. & Svanbäck, R. (2002) Measuring individual-level resource specialization. *Ecology,* **83**, 2936-2941.

Feinsinger, P., Spears, E.E. & Poole, R.W. (1981) A simple measure of niche breadth. *Ecology,* **62**, 27-32.

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

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

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



Matrix 1

Two-mode interaction matrix

	p1	p2	p3	p4	L_{sp}
sp1	1	1	1	0	3
sp2	1	1	1	0	3
sp3	0	1	1	1	3
sp4	0	0	1	0	1
sp5	0	0	1	1	2

Matrix 2

One-mode interaction matrix

	sp1	sp2	sp3	sp4	sp5	$\sum w_{ij}$
sp1	0	3	2	1	1	7
sp2	3	0	2	1	1	7
sp3	2	2	0	1	2	7
sp4	1	1	1	0	1	4
sp5	1	1	2	1	0	5

Matrix 3

Maximum interspecific overlap interaction matrix

	sp1	sp2	sp3	sp4	sp5	$\sum w_{ij}$
sp1	0	4	4	4	4	16
sp2	4	0	4	4	4	16
sp3	4	4	0	4	4	16
sp4	4	4	4	0	4	16
sp5	4	4	4	4	0	16

$$SPO_{sp1} = \frac{\sum_j w_{ij}}{p \cdot (s\text{-}1)} = \frac{7}{4 \cdot (5\text{-}1)} = 0.437$$

$$SPO_{sp4} = \frac{\sum_j w_{ij}}{p \cdot (s\text{-}1)} = \frac{4}{4 \cdot (5\text{-}1)} = 0.25$$

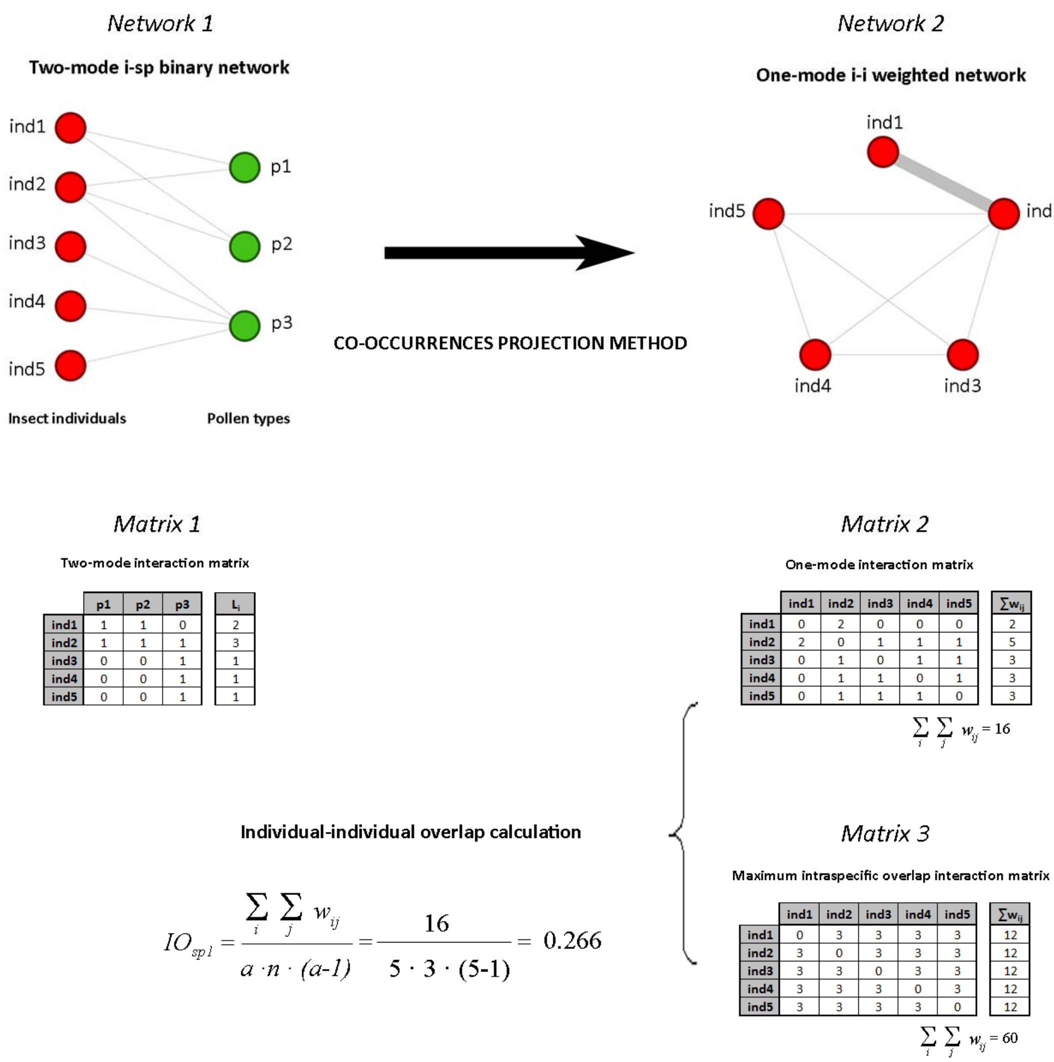
Here we present a simple hypothetical example to illustrate the procedure applied when estimating interspecific overlap (*SPO*) for insect species in our networks. *Network 1* is a two-mode binary pollen-transport network depicting interactions between five insect species (red nodes) and four plant pollen types (green nodes). Insect species are linked to plant pollen types if they carried pollen grains. *Network 1* can also be represented as an interaction matrix (*Matrix 1*) with *s* rows and *p* columns, where *s* is the number of insect species (*s* = 5), *p* is the number of plant pollen types (*p* = 4) and the value in each cell entry is 0 or 1 (i.e. absence or presence of pollen grains in insect's body, resp.). Linkage level of species (L_{sp}) is the total number of plant pollen types carried (i.e. *matrix 1* row sum). This two-mode binary network was transformed into a one-mode weighted network by counting the total number of plant pollen types shared among species (co-occurrences projection method as in Opsahl 2009 and Padrón *et al.* 2011). *Network 2* is the one-mode projection of *network 1*, where insect species are linked if pollen grains of the same plant pollen type were found on the body of both insects, and the weight of each link is the number of plant pollen types in common. For instance, *sp1* shares three pollen types with *sp2*, two pollen types with *sp3* and only one with *sp4* and *sp5*. Therefore, the maximum link weight possible in this kind of network projection is always the total number of plant pollen types present in the community (here $p = 4$). This one-mode weighted network depicting the pattern of shared pollen types among insect species can be also represented by an interaction matrix with s rows and s columns (*Matrix 2*) where the value in each cell entry (w_{ij}) is the number of plant pollen types shared. Therefore, sum of link weights ($\sum w_{ij}$, i.e. *matrix 2* row sum) is the overlap in plant pollen types among a certain species and all other species in the network. To get a standardized measure of interspecific overlap ranging from 0 to 1 (*SPO*), we divided $\sum w_{ij}$ by the maximum interspecific overlap possible for a species in the network, which was calculated as $p(s - 1)$, i.e. sum of node link weights $\sum w_{ij}$ in an hypothetical case where all insect species carried all plant pollen types from the community and therefore shared all (*Matrix 3*). We illustrate the complete calculation of species-species overlap (*SPO*) for two species in our example.

References in Appendix S3:

Opsahl, T. (2009) *Projecting two-mode networks onto weighted one-mode networks.* Available at: http://toreopsahl.com/tnet/two-mode-networks/projection/

Padrón, B., Nogales, M. & Traveset, A. (2011) Alternative approaches of transforming bimodal into unimodal mutualistic networks. The usefulness of preserving weighted information. *Basic and Applied Ecology,* **12**, 713-721.

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



	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

	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

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

	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

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

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

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

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

References in Appendix S4:

Opsahl, T. (2009). *Projecting two-mode networks onto weighted one-mode networks.* Available at: http://toreopsahl.com/tnet/two-mode-networks/projection/

Padrón, B., Nogales, M. & Traveset, A. (2011) Alternative approaches of transforming bimodal into unimodal mutualistic networks. The usefulness of preserving weighted information. *Basic and Applied Ecology,* **12**, 713-721.

Appendix S5. *Evaluation of species sampling completeness*

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

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

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

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

where a is the sample size (i.e. number of individuals of each species sampled for pollen load analysis), u is the number of uniques (i.e. plant pollen types that occur only in one sample) and d is the number of duplicates (i.e. plant pollen types that occur in two samples) (Chao 2005). *Chao 2* index relies on the principle that rare species in the samples carry most information on the number of un-observed species (Chao 1984) and is one of the least biased estimates for small sample sizes (Colwell & Coddington 1994).

References in Appendix S5:

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

Chao, A. (1984) Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, **11**, 265-270.

Chao, A. (2005) Species richness estimation. *Encyclopedia of Statistical Sciences* (eds. N. Balakrishnan, C. Read & B. Vidakovic) Vol. 12, pp. 7907–7916. Wiley, New York.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society (Series B)*, **345**, 101-118.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B. *et al.* (2012) *vegan*: Community Ecology Package. R package version 2.0-3. Available at: http://CRAN.R-project.org/package=vegan

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/

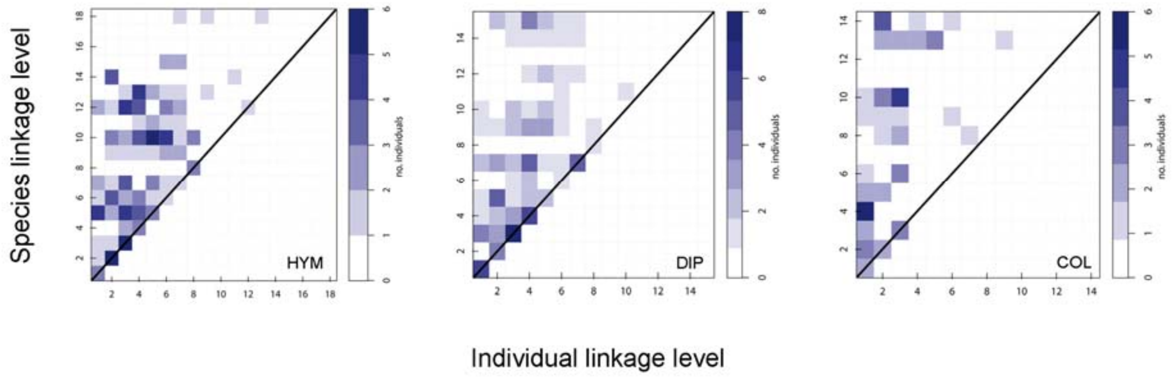


Fig. S1. Relation between linkage level of species (L_{sp}) and individuals (L_i) for the main insect orders. Each matrix corresponds to a different insect pollinator order: Hymenoptera (N_{HYM}=147 individuals), Diptera (N_{DIP}=114) and Coleoptera (N_{COL}=59). Colours represent number of individuals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

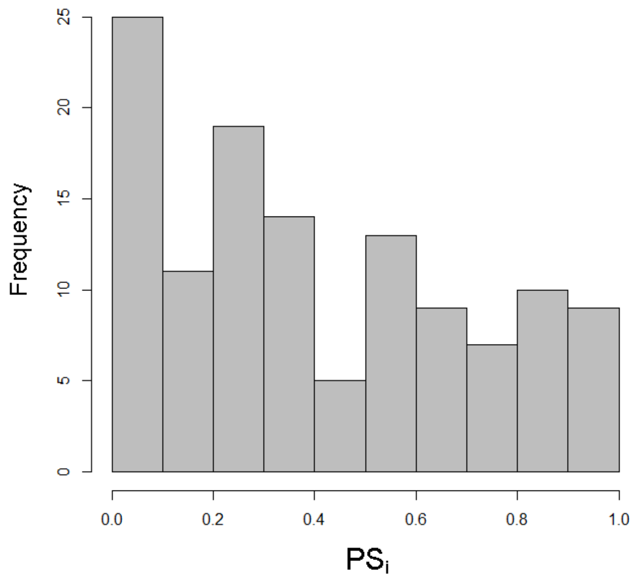


Fig. S2. Frequency histogram (N = 122) of the proportional similarity indices of individuals (PS_i) from the 21 selected species in our networks. Individuals with narrower niches than their corresponding species are more frequent (60.7% individuals had a $PS_i < 0.5$), although some highly generalized 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 (L)	Number of interactions of each network node, i.e. number of interactions per species (L_{sp}) in *sp-sp* networks and number of interactions per individual (L_i) in *i-sp* networks.
Network size (N)	Total number of possible interactions in the network, i.e. the number of cell entries in the interaction matrix (number of *i* rows multiplied by number of *j* columns).
Linkage density (LD)	Mean number of links per network node.
Connectance (C)	Realized proportion of all possible links (Dunne *et al.* 2002).
Nestedness (NODF)	Nestedness metric based on overlap and decreasing fills (Almeida-Neto *et al.* 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 (H)	Shannon diversity of links for a network node *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* and *j*; here number of *j*'s pollen grains carried by insect node *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 *et al.* 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* is the total number of links in the network and ln(*I*) the maximum diversity possible in the network i.e. $H_{máx}$). 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 *et al.* 2007).

References in Table S1:

Almeida-Neto, M., Guimarães, P., Guimarães Jr., P.R., Loyola, R.D. & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos,* **117**, 1227-1239.

Bersier, L.F., Banašek-Richter, C. & Cattin, M.F. (2002) Quantitative descriptors of food-web matrices. *Ecology*, **83**, 2394-2407.

Dunne, J.A., Williams, R.J. & Martínez, N.D. (2002) Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Science of the United States,* **99**, 12917-12922.

Tylianakis, J.M., Tscharntke, T. & Lewis, O.T. (2007) Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature*, **445**, 202-205.

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

HYM: Hymenoptera; COL: Coleoptera; DIP: Diptera; CN: Coma de n'Arbona; PC: Passadís de Ses Clotades; a: number of individuals captured for pollen load analysis; L_{sp}: linkage level of species; $\overline{L_i}$: mean linkage level of conspecific individuals; *null* $\overline{L_i}$: mean linkage level of conspecific individuals after 1,000 randomizations under the null hypothesis that individuals act as generalists sampling from species pollen resource distribution proportions; TNW: total niche width; WIC: within-individual niche component; BIC: between-individual niche component; WIC/TNW: degree of individual specialization; SPO: interspecific overlap; IO: intraspecific overlap.

* All WIC/TNW empirical values reported were below null WIC/TNW values obtained from 1,000 randomizations.