Downscaling pollen–transport networks to the level of individuals

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

Introduction

In the last couple of decades, community studies of plant–animal interactions have been explored with the aid of network theory (Memmott 1999; Jordano, Bascompte & Olesen 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

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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 (Olesen *et al.* 2010; Dupont, Trøjelsgaard & Olesen 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 (Jordano, Bascompte & Olesen 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.* 2011), 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, Trøjelsgaard & Olesen 2011; Gómez, Perfectti & Jordano 2011; Gómez & Perfectti 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 (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 (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, that is, all individuals have similar feeding niche (null hypothesis: $L_{sp} \approx L_i$), or (ii) individuals are more specialized than the species (alternative hypothesis: $L_i \ll L_{sp}$). 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 modelling, 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, that is, 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 with: (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 (Svanbäck & Bolnick 2005, 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. (39°48′05″ N 2°47′9″ E) and (ii) *Passadís de Ses Clotades* (PC) at 1400 m a.s.l. (39°48′34″ N 2°47′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 1000 randomizations using the fixed row and column totals constrained model, that is, 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 1000 null i–sp pollen–transport networks of the same size and species composition as the empirical i–sp networks. These null networks were built 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 was 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 above-mentioned parameters also for the 1000 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 artefact.

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 1000 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, that is, the average of individuals' niche breadth. BIC is the variance in mean pollen use among individuals of the particular species, that is, 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, nonoverlapping subsets of their species' resources. We applied Monte Carlo resampling procedures (Bolnick *et al.* 2002; Araújo *et al.* 2008, 2010) to test whether the observed individual specialization was significant, that is, observed WIC/TNW values were <95% confidence interval of WIC/TNW values obtained for the 1000 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 (Supporting information).

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 $\sum w_{ij}$ (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,

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

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 in Supporting information 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, that is, 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, that is, 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 (Supporting information) 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 modelling (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 goodness-of-fit (χ^2) and calculated the standardized root mean residuals (SRMR). A nonsignificant chi-square 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, Supporting information 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, Supporting information), 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, Hill & Westerman 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 1 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 and network connectance (C) in empirical *i–sp* networks were 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

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 | |
	CN	PC	CN	PC	CN	PC
Qualitative network parameters						
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 ($N = AxP$)	4015	2989	10 450	6713	10 450	6713
Total number of interactions (I)	434	360	681[†]	506[†]	1342·48	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 ($E_2 = H_2/H_{máx}$)	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 1000 null *i–sp* networks.

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 in 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), that is, individuals were always
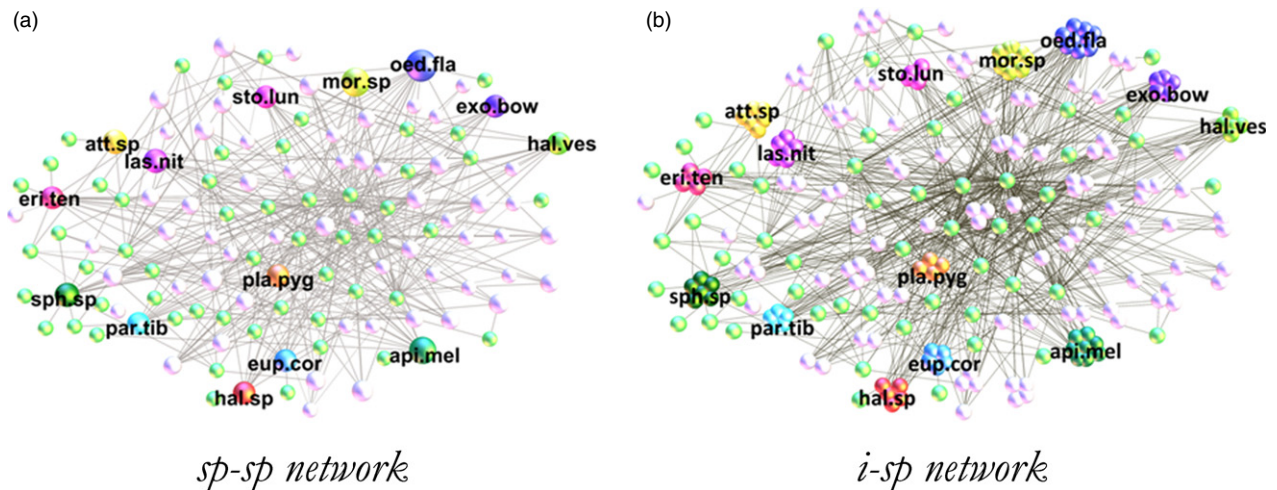

Fig. 1. Pollen–transport networks at two scales of resolution: (a) species–species (*sp–sp*) and (b) individuals–species (*i–sp*). Pale green nodes are plant pollen types, whereas the rest of nodes are pollinators. Coloured and labelled nodes are pollinators with ≥5 individuals captured (see Table S2 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 0.8 beta* (Bastian, Heymann & Jacomy 2009).

more specialized than their corresponding species (average ratio L_i/L_{sp} = 0·55). This was also observed when insect orders were treated separately (Fig. S1, Supporting information). For the 21 species with ≥5 individuals, $\overline{L_i}$ was significantly lower than expected under the null hypothesis (Table S2, Supporting information). 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, Supporting information). At both sites, a large fraction of individuals (63·5% in CN and 54% in PC) had a niche
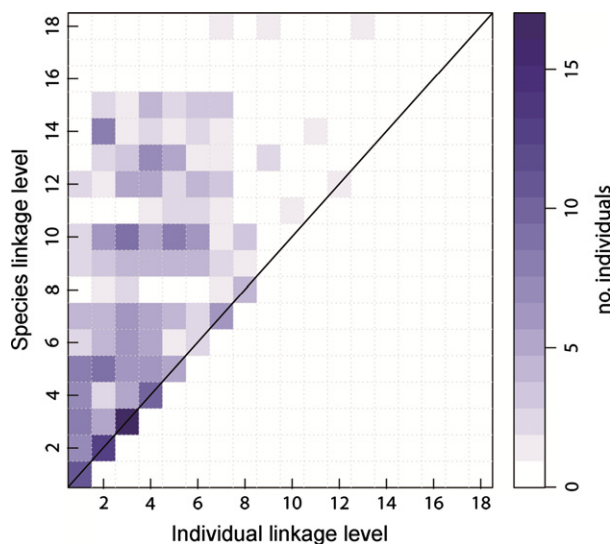
that differed strongly from their species' niche, that is, $PS_i < 0·5$ (Fig. S2, Supporting information). However, the intraspecific variability of PS_i was high (average coefficient of variance in mean PS_i of species was 59% at CN and 86% at PC). Thus, most species consisted of both generalist and 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 (Supporting information). Results for the proposed SEM model are reported in Fig. 5. Observed data fitted reasonably well the proposed model (x^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 nonsignificant). 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, that is, 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 nonsignificant ($-0·168$, 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 LD, 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 BEHAVIOUR

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 LD, connec-
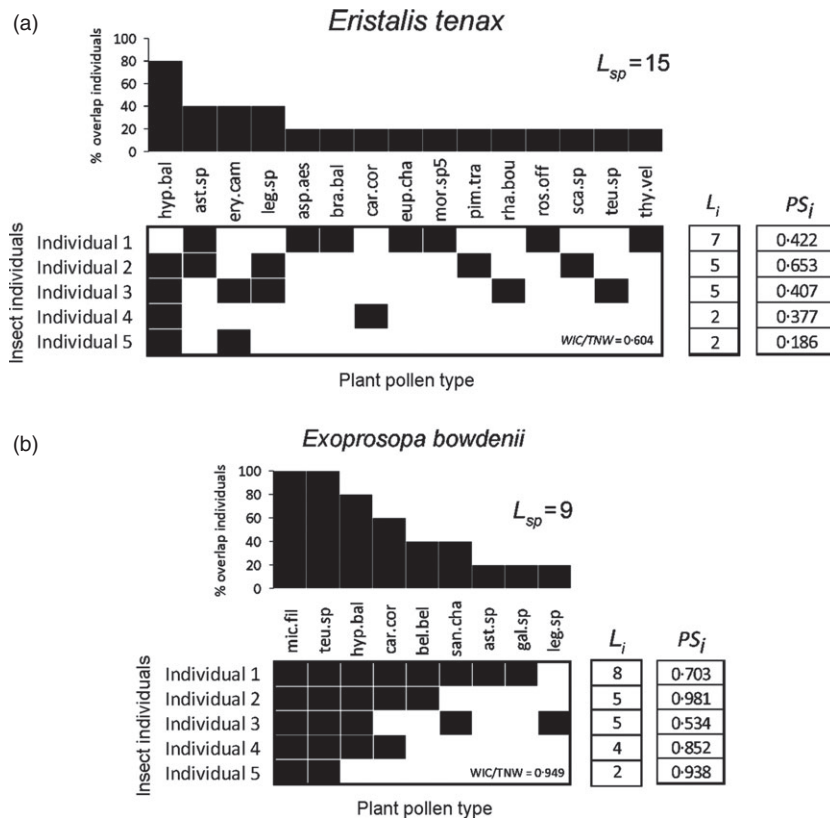

Fig. 2. Comparison of species linkage level (L_{sp}) and individual linkage level (L_i). Cells represent combinations of L_i and L_{sp} (data from both sites, n = 327) with colour intensity correlating with number of individuals found at each position. Matrix diagonal is the *species–individual isocline* (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).

tance, 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, Supporting information). 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 ($L_i \ll L_{sp}$) (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, Bolnick & Layman (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, that is, 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, Trøjelsgaard & Olesen 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, behaviour 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
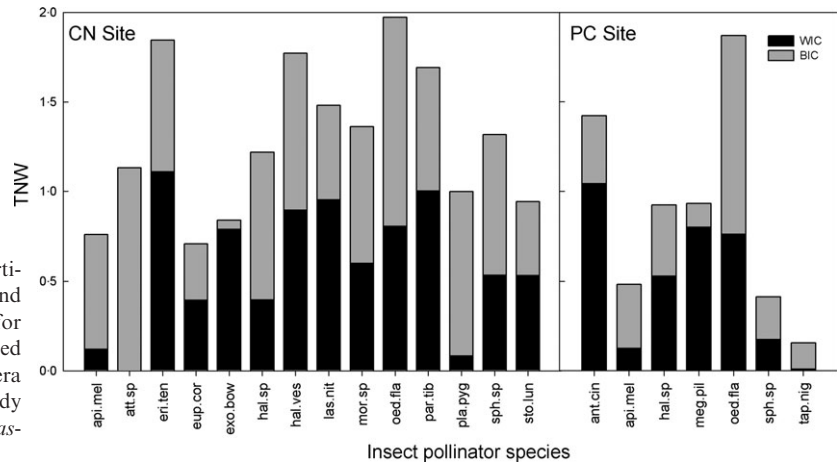
Fig. 4. Total niche width (TNW) partition into within-individual (WIC) and between-individual (BIC) components for species with ≥5 individuals sampled (*n* = 21, 10 Hymenoptera spp., 7 Diptera spp. and 4 Coleoptera spp.) at both study sites (CN = *Coma de n'Arbona*, PC = *Passadís de Ses Clotades*).
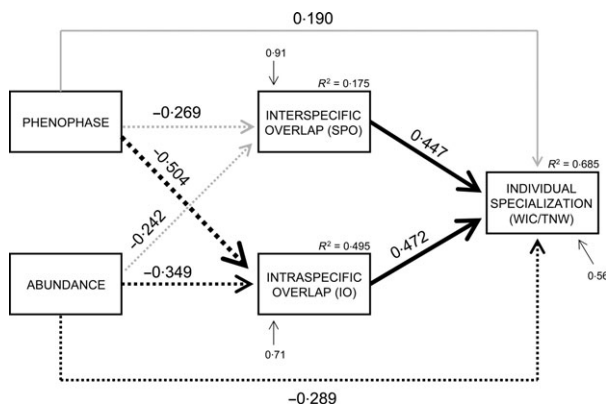

Fig. 5. Path diagram showing the relative effect of several ecological factors insect phenophase, insect abundance, inter- and intraspecific overlap (SPO and IO respectively) on the degree of individual specialization (WIC/TNW). Positive effects are indicated by solid lines and negative effects by dashed 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 nonsignificant 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.

and interindividual 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, that is, whether individuals have the same or different primary

and secondary preferred resources (Svanbäck & Bolnick 2005; Araújo, Bolnick & Layman, 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 with 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 nonoverlapping 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 interindividual 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 are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.63fp5.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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.

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.

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.