

Increasing modularity when downscaling networks from species to individuals

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Downscaling networks from species to individuals is a useful approach to incorporate inter-individual variation and to investigate whether topology of species-based networks results from processes acting at the scale of individuals, such as foraging behaviour. Here, we analyzed pollen-transport networks at two scales, i.e. pollinator species–plant species (sp–sp) and pollinator individuals–plant species (i–sp), and assessed whether modularity – a prevalent pattern in most pollination networks – is consistent across both scales. To test this we use three different algorithms developed for the calculation of modularity (unipartite, bipartite and weighted bipartite modularity) and compare the results obtained. Downscaling networks revealed a higher modular structure in i–sp networks than in sp–sp networks, regardless of the modular metric used. Using a null model approach, we show that modularity at the individual scale is originated by the existence of a high heterogeneity and specialization in the partition of pollen resources among conspecific individuals, a pattern which obviously cannot be observed at the species level. Modules in i–sp networks consisted of individuals sometimes neither taxonomically nor functionally related, but sharing common pollen resources at different moments of the flowering season. Interestingly, conspecific individuals may belong to different modules. Both plant and insect phenologies were important drivers of the modularity detected in individual-based networks, even determining the topological roles of nodes in the networks. A temporal turnover of modules was identified, i.e. modules of individuals assembled and disassembled over time as species modify their foraging choices throughout the flowering season adjusting to ecological conditions. Downscaling from species to individual-based networks is a promising approach to study the interplay among structural patterns and processes at different, but interdependent organizational levels.

Interactions between plants and their pollinators can be represented at the community level using complex networks. Such real networks have topological features, which differ from randomly constructed networks (Bascompte and Jordano 2007). Detection of community structure within these networks is important in order to further identify the underlying ecological and evolutionary processes causing them (Lewinsohn et al. 2006) and to determine the potential consequences of such patterns for network stability and dynamics (Tylianakis et al. 2010). Nestedness and modularity are two of the patterns most frequently investigated in plant–pollinator mutualistic networks (Bascompte et al. 2003, Olesen et al. 2007). Both can coexist in the same network, being complementary rather than exclusive; even single modules are often nested (Lewinsohn et al. 2006, Olesen et al. 2007), although the correlation between modularity and nestedness depends on network connectance (Fortuna et al. 2010).

A species–species network has a nested link pattern if specialist species interact with proper subsets of the species interacting with the more generalist ones (Bascompte et al. 2003). On the other hand, a modular pattern consists of densely connected groups of species with sparse connections

to species in other groups (Olesen et al. 2007). These strongly linked subgroups are called modules or compartments. Complex algorithms are needed to identify them (Guimerà and Amaral 2005b). Depending on the pattern of within and between-module connections, species can be classified into different topological roles (Guimerà and Amaral 2005a, Olesen et al. 2007). Especially, regarding their species composition, modules have been viewed as potentially co-evolutionary units of biological significance (Olesen et al. 2007, Dupont and Olesen 2009, Donatti et al. 2011).

A modular structure is derived from constraints in the interactions. Modularity in different kinds of network is indeed associated with a variety of ecological factors and explanatory processes (Bascompte and Olesen in press), such as: 1) convergence in pollination syndromes (Danieli-Silva et al. 2012); 2) phylogeny and body mass in food webs (Rezende et al. 2009); 3) trophic specialization and host range selection in plant–herbivore interactions (Prado and Lewinsohn 2004); 4) species phenology in plant–pollinator networks (Bosch et al. 2009, Martín González et al. 2012); 5) species niche organization and diet in food webs (Guimerà et al. 2010) and 6) spatial or habitat segregation (Fortuna et al. 2009, Dupont et al.

2014). However, the degree of modularity and the number of modules in a network can be constant over time-cumulative periods (Dupont and Olesen 2012).

Modularity is a topological property important for network robustness. It may increase overall network stability because the spreading of perturbations across weakly connected modules occurs slowly so that effects stay embedded within modules (Fortuna et al. 2009, Stouffer and Bascompte 2011). The relationship between modularity and stability, however, may depend on whether the interaction is mutualistic or antagonistic (Thébault and Fontaine 2010) as well as on the specific type of perturbation.

Most networks studied to date are constructed at the species level, i.e. they represent interactions among species. However, a species is in fact a population of phenotypically diverse individuals, so species-based networks overlook the existing intraspecific variation. Individual variation within natural populations is a fundamental factor in ecological and evolutionary processes (Darwin 1859, Bolnick et al. 2011, Dall et al. 2012, Wolf and Weissing 2012). Ecologically, variation in traits (e.g. size, sex, age, social status) determines differences in foraging behaviours and resource use among individuals (Bolnick et al. 2003, Araújo et al. 2011), which in turn might affect structure, dynamics and stability of ecological interactions at a community scale (Beckerman et al. 2006, Bolnick et al. 2011). Therefore, downscaling networks from species-level to individual-level is a fundamental step for linking individuals to population dynamics and community structure (Ings et al. 2009, Beckerman et al. 2010), but also a way to link community biology to natural selection. For instance, further research is needed to investigate whether the structural properties described in species-based networks are maintained in individual-based networks or not (Tur et al. 2014), and which are the drivers behind patterns detected at the individual level.

Here, we investigate consistency of the modular pattern to network downscaling from species to individuals. We constructed pollen-transport networks from two mountain habitats at both species level (pollinator species–plant species network; hereafter sp–sp) and individual level (individual pollinator–plant species network; hereafter i–sp) by studying the pollen loads of insect flower-visitors. First, we explore modularity at both levels (i.e. species and individuals) using different modularity metrics – unipartite modularity (Newman and Girvan 2004, Guimerà and Amaral 2005a, Olesen et al. 2007), bipartite modularity (Barber 2007) and weighted bipartite modularity (Dormann and Strauss 2014) – and we address whether the pattern found is consistent across levels. We expect to detect modularity in i–sp networks if the pattern is already present in sp–sp networks, but we predict a stronger modularity in the former due to a high degree of individual specialization in the use of pollen resources (Tur et al. 2014) and the potential existence of individuals or groups with alternative foraging preferences within a species (Araújo et al. 2008, Tinker et al. 2012). To test this prediction, 100 null i–sp networks of same size and species composition as the empirical ones were constructed, but in which all conspecific individuals act as generalized as their species (i.e. there is no degree of individual specialization). The comparison of null and empirical i–sp networks allows identifying how much information is lost

when intraspecific variation is not considered in interaction networks. Given that results may vary depending upon the modularity metric used, particularly in the identification of modules (Thébault 2013), we compare the different metrics. Second, we analyze how conspecific individuals are organized into modules. Conspecific individuals with similar interaction patterns are likely to aggregate in the same module. Alternatively, conspecific individuals specialized on different pollen resources might belong to different modules and thus the degree of individual specialization would in turn affect the degree of heterogeneity in module membership within species, i.e. species with a higher degree of individual specialization might have conspecific individuals spread into a higher number of modules than species with a low degree of individual specialization. Third, we discuss the drivers of modularity in i–sp networks and the underlying mechanisms influencing the distribution of individuals across modules. As only a few pollination networks have been studied at the individual level (see Dupont et al. 2011, 2014 and Gómez and Perfectti 2012 for single species network approaches), the ecological factors causing modularity at this level are poorly known. Specifically, we focus upon pollen resource affinity among individuals and phenology as drivers of module composition. Finally, we identify the topological roles of insect individuals and plant species in i–sp modules, and explore the influence of abundance, phenophase and linkage level upon topological role assignment. As far as we know, our study is the first to investigate the interplay between two organizational levels in modularity pattern of pollination networks and to assess whether modularity is driven by the same or different factors at the two levels.

Material and methods

Data sampling and network construction

We studied interactions between plants and insect flower-visitors at two locations from the highest mountain in Mallorca (Puig Major, 1445 m): 1) Sa Coma de n'Arbona (CN) at 1100 m a.s.l. (39°48'05"N, 2°47'9"E) and 2) Passadís de Ses Clotades (PC) at 1400 m a.s.l. (39°48'34"N, 2°47'50"E). Fieldwork was conducted throughout the flowering season (May to August 2010). Observations of pollinators (i.e. insects visiting flowers and touching the reproductive parts of these) were carried out on randomly selected single plants or patches during 5-min surveys. We recorded identity and number of observed pollinator individuals. When possible, these pollinators were captured at the end of the survey and stored separately in clean vials for later taxonomical identification and pollen load analysis. All plant species in bloom in the area were surveyed three times a week, on calm and sunny days, between 10 a.m. and 5 p.m. Flower abundance (flowers m⁻²) of each plant species was estimated every two weeks by counting the number of open flowers in fixed transects (nine in CN and three in PC).

A total of 190 individuals (71 Diptera, 83 Hymenoptera, 33 Coleoptera, 3 Hemiptera) belonging to 73 distinct insect species were captured in CN and 137 individuals (43 Diptera, 64 Hymenoptera, 26 Coleoptera, 4 Hemiptera) from 61 species in PC. Number of individuals per species ranged

from 1 to 10 (mean \pm SD: 2.44 ± 1.81). In the laboratory, the pollen load of each pollinator specimen was examined. Using a pollen reference collection from the study sites, we identified the pollen types and counted all pollen grains from the body surface of each insect following the methodological procedure in Tur et al. (2014). In total, we recorded 55 pollen types on insects from CN and 49 pollen types on insects from PC. On average (mean \pm SD), $17\,982 \pm 80\,588.4$ and $18\,654 \pm 95\,421.8$ pollen grains per insect individual were counted in CN and PC, respectively.

Data from the pollen load analysis (available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.63fp5>>) were used to construct pollen-transport networks depicting the interactions between plant–pollen types and insect pollinators (see Tur et al. 2014 for details about data). We built both binary and weighted interaction matrices for each study site at two scales of resolution: 1) sp–sp, i.e. insect species and plant–pollen types and 2) i–sp, i.e. insect individuals and plant–pollen types. In binary matrices an interaction between an insect individual or species (in rows) and a flowering plant taxon (in columns) was present (i.e. corresponding cell filled with a 1), if pollen was detected on the body of the insect. In weighted matrices, interactions have an associated weight measured as the specific number of pollen grains from each pollen type identified on the body of insects.

Construction of null i–sp networks

Networks at different scales differ in size, because downscaling from sp–sp to i–sp networks increases the total number of nodes as many of the pollinator species were represented by several individuals. Given that most network descriptors are affected by network size (Dormann et al. 2009), a null model is needed to carry out comparisons across scales (species and individuals) accounting for network size-related differences. Therefore, we built 100 null i–sp weighted networks for each study site with same size and species composition as the empirical i–sp networks. In these null networks each conspecific individual was reassigned the same pollen load as observed, but pollen grains were redistributed among all pollen types used by the corresponding species with a probability equal to the observed pollen type proportion used by the species (see more details in Tur et al 2014). Thus, in these null i–sp networks, individuals act as generalized as their species (i.e. there is no degree of individual specialization) and so the null i–sp weighted networks constructed for each site serve both as a control for network size and for individual specialization. A binary version of the null i–sp networks was obtained by transforming the null weighted matrices into presence–absence matrices.

Modularity analysis

For each pollen-transport network (i.e. empirical sp–sp networks and i–sp networks at both study sites), the level of modularity, number of modules and composition of modules were calculated using three different metrics: 1) unipartite modularity (Newman and Girvan 2004), 2) bipartite modularity (Barber 2007), and 3) weighted bipartite modularity (Dormann and Strauss 2014). The

difference among these metrics is that each one was designed for a particular type of network (i.e. binary unipartite, binary bipartite and weighted bipartite networks). Thus, for the first two measures, the binary interaction matrices were used for the analysis, whereas in the last one we used the weighted matrices. All three metrics measure the extent to which interactions are organized into subgroups of tightly linked nodes, so that modularity is high when within- module connectance is high and between-module is low. Modules were identified using the simulated annealing method (Guimerà and Amaral 2005a, b), a strong and accurate modularity-detection algorithm (Danon et al. 2005) which randomly rearranges nodes and modules until a maximum modularity is achieved.

The first modularity measure calculated was unipartite modularity M_U (Newman and Girvan 2004, Guimerà and Amaral 2005a, Olesen et al. 2007) defined as

$$M_U = \sum_{m=1}^{N_M} \left[\frac{l_m}{I} - \left(\frac{d_m}{2I} \right)^2 \right] \quad (1)$$

where N_M is the number of modules in the network, I is the total number of network links, l_m is the number of links between nodes in module m (within-module links) and d_m the sum of the number of links of all nodes belonging to module m . M_U ranges from 0 to $(1 - 1/N_M)$. M_U , number of modules and composition of each one were calculated with the program NetCarto (Guimerà and Amaral 2005a, b) with the following input parameters: iteration factor = 0.95, cooling factor = 0.99 and final temperature = 0.

The second modularity metric calculated was bipartite modularity M_B defined by Barber (2007) as follows

$$M_B = \sum_{m=1}^{N_M} \left[\frac{l_m}{I} - \left(\frac{d_m^A \times d_m^B}{I^2} \right) \right] \quad (2)$$

where N_M is the number of modules in the network, I is the total number of network links, l_m is the number of links between nodes in module m (within-module links) and d_m^A and d_m^B are the sum of the number of links of the nodes within module m which belong to A -set and B -set respectively. Therefore, M_B is an extension of Newman and Girvan's measure (M_U) but taking into account bipartiteness of the network, i.e. network nodes of set A can only interact with nodes of set B . M_B , number of modules and composition of each one were calculated with the program BIPMOD (Thébault 2013).

The last modularity metric calculated was weighted bipartite modularity M_{WB} as proposed by Dormann and Strauss (2014)

$$M_{WB} = \sum_{m=1}^{N_M} \left[\frac{W_m}{W} - \left(\frac{w_m^A \times w_m^B}{W^2} \right) \right] \quad (3)$$

where N_M is the number of modules in the network, W is the total sum of link weights in the network ($W = \sum_{ij} w_{ij}$, i.e. total column and row sums), W_m is the total sum of link weights between nodes within module m ($W_m = \sum_{ij \in m} w_{ij}$)

and w_m^A and w_m^B are the sum of the link weights of the nodes within module m which belong to A -set (row sums within module m) and B -set respectively (column sums within module m). M_{WB} , number of modules and composition of each one were calculated using function `computeModules` within the *bipartite* R-package (Dormann et al. 2008). For the calculation of this measure we previously log-transformed all link weights with \log_{10} (number of pollen grains + 1) in order to avoid having very large numbers in the matrices.

For all the modularity metrics considered, significance was assessed by comparing observed values against modularity values of 100 random matrices of same size and linkage level rank distribution (null models with fixed column and row totals). We calculated Z-scores as the difference between the observed modularity and the mean modularity of randomizations divided by their standard deviation. Networks with a Z-score > 2 were considered as significantly modular.

We evaluated the differences among the three modularity metrics and the concordance of the modules identified by each metric (i.e. which individual belongs to each module) in i-sp networks at both study sites. As the simulated annealing algorithm is a stochastic optimization technique, even different runs of the algorithm can yield different classifications of nodes into modules (Guimerà and Amaral 2005a). Thus, 10 runs for each empirical i-sp network and modularity metric were performed. Concordance of modules identified, both within runs of the same metric and among runs of different metrics, was estimated with the mutual information index (Guimerà et al. 2007, Thébault 2013), which ranges from 1 (when partitions are identical) to 0 (when partitions are uncorrelated) (Supplementary material Appendix A1).

To determine whether differences in modularity among networks at both scales (species and individuals) were a result of individual specialization rather than an artifact of network size, we also calculated the above mentioned modularity metrics for the 100 null i-sp networks constructed. Modularity in empirical i-sp networks was considered as significantly higher when it ranged above 95% of modularity values obtained for these null i-sp networks.

Finally, for each pollen-transport network and for all significant modules detected inside these networks we determined: number of insect pollinator nodes (A), number of pollen type nodes (P), total number of nodes ($A + P$), total number of interactions (I), linkage level of each node (L), connectance (C) and nestedness ($NODF$). Connectance is the proportion of realized links from all possible links. $NODF$ is a measure of nestedness (Almeida-Neto et al. 2008), which ranges from 0 for non-nested matrices to 100 for perfectly nested matrices. To test whether $NODF$ was significant, values were compared with those obtained from 1000 random networks with fixed row and column totals. All these network metrics were calculated with the *bipartite* (Dormann et al. 2008) and *vegan* (Oksanen et al. 2012) packages implemented in R ver. 2.15.0 (<www.R-project.org/>).

Distribution of individuals among modules

In order to explore how conspecific individuals were distributed across modules in null and empirical i-sp networks, we selected species for which we sampled ≥ 5 individuals (14

spp. in CN and seven spp. in PC). For these species we quantitatively measured the dispersion of conspecific individuals between different modules, i.e. species module membership heterogeneity, with an index of qualitative variation IQV (Wilcox 1973) calculated as follows

$$IQV = \frac{N_M}{N_M - 1} \times \left(1 - \sum_{m=1}^{N_M} p_m^2 \right) \quad (4)$$

where N_M is the number of modules and p_m the proportion of individuals of species i in a module m . IQV was obtained for each of the selected species (species for which we sampled ≥ 5 individuals) and ranged from 0, when all conspecific individuals are distributed inside the same module, to 1 when conspecific individuals are evenly distributed among all modules. We calculated IQV using module membership assigned by each different metric in one of the runs of the algorithm to see whether results were consistent regardless of the modularity metric considered. In null i-sp networks species IQV is 0, as all conspecific individuals have exactly the same interactions and thus belong to the same module. However, in empirical i-sp networks we expected species with a high degree of individual specialization in the use of pollen resources (Tur et al. 2014) to be more heterogeneous in module membership than species with a low degree of individual specialization. Thus, using simple linear regression analysis, we tested if species module membership heterogeneity in empirical i-sp networks (IQV) was related to their degree of individual specialization in pollen resources measured as explained in Supplementary material Appendix A2. To identify whether IQV values calculated were associated to potential sampling biases, such as differences in the number of individuals captured per species or differences in species phenophase length, we performed Spearman correlations among IQV and these two variables.

Relationships between biological factors and modularity

We explored if pollen resource niche partitioning among individuals was associated to the modularity pattern, i.e. whether individuals within the same module were more similar in their pollen niches than individuals in different modules. For this, we used a multi-response permutation procedure MRPP (Mielke and Berry 2001) to test whether within-module pollen niche dissimilarity was less than expected by random. Pollen niche dissimilarity was calculated with pairwise Bray-Curtis distance from presence/absence i-sp matrices. The overall weighted mean of

within-module dissimilarity ($\delta = \sum_{m=1}^{N_M} \frac{n_i}{N} \times \bar{d}_m$; where N_M is

the number of modules, n_i the number of individuals within module m , N the total number of individuals in the network and \bar{d}_m the average dissimilarity among individuals within module m) was compared against δ -values obtained for 1000 permutations, which shuffled randomly individuals across modules to assess the significance level. The statistic A , which is a measure of within-module homogeneity compared to random expectation ($A = 1 - \text{observed } \delta / \text{expected } \delta$), provided an estimate of effect size. A ranges from 1 (when within-module homogeneity deviation from random

is maximum) to 0 (when it is random). MRPP was performed with R package *vegan* (Oksanen et al. 2012).

To evaluate the role of phenology as a driver of modularity, we first classified all network nodes into phenological categories: (1) May, (2) June, (3) July and (4) August. For plant pollen types, we used the date of the flowering peak, i.e. date of maximum flower abundance in the field, or date of maximum abundance of pollen grains on insects when field data were not available. For insect individuals, we used the date of field capture. We analyzed the phenological composition of each module in i-sp networks. To test whether modules were significantly associated to the phenology of nodes we performed randomization tests of independence. We generated 999 permutations of the empirical contingency tables using fixed column and row marginal sums (i.e. representing no association between variables) and then calculated χ^2 -statistic for each one. We counted the number of times (x) the χ^2 -statistic for null permutations was greater or equal to empirical χ^2 - and a p-value was calculated as $x/\text{number of permutations} + 1$.

Relationships between node features and topological roles

In empirical i-sp networks, based on the network partition into modules provided by the M_U metric, a topological role to each node was assigned depending on its connectivity. This topological role is described by two parameters: within-module degree (z , i.e. standardized number of links to other nodes in the module) and among-module connectivity (c , i.e. the level to which a node is linked to other modules) (Guimerà and Amaral 2005a, b). According to c and z , nodes (both plants and individuals) were classified into four roles (Olesen et al. 2007): 1) peripherals, which are specialists ($z \leq 2.5$ and $c \leq 0.62$); 2) connectors, which are nodes with low z and high c acting as glue among different modules ($z \leq 2.5$ and $c > 0.62$); 3) module hubs, which are highly connected nodes but mainly linked within their own module ($z > 2.5$ and $c \leq 0.62$); and 4) network hubs, which are super-generalists ($z > 2.5$ and $c > 0.62$).

Moreover, all nodes in empirical i-sp networks were also characterized by a list of biological features (linkage level, pollen abundance, flowering period length, and flowering peak for plant pollen types; individual linkage level, species abundance, species phenophase length, individual phenophase, and sex for insects) (see details in Supplementary material Appendix A3). To assess the effect of these biological features determining the role of a node in i-sp networks, we performed a multinomial logistic model for plants and a binary logistic model for insect individuals. In the multinomial logit model for the plants the response variable was 'role' coded as a factor with three levels (P = peripherals, MH = module hubs, and NH = network hubs). Connectors were excluded from this model as too few plant nodes had this role. The predictors included were: 1) flowering period length, and 2) pollen abundance (with logarithm base 10 transformation). Neither linkage level nor flowering peak were included as predictors to avoid strong collinearity in the former and because no differences were detected among roles in the latter. The model estimated the probability ratio of being assigned into a certain role based on the predictors

included, so that separate odds ratios were determined for all predictors for each role except one, which is set as a reference level and omitted from the analysis (P was selected as the base role in our model). On the other hand, for insect individual nodes we performed a binary logistic model where the response variable was 'role' coded as a factor with two levels (P and C) and the predictors included were: 1) linkage level of individuals, 2) individual phenophase (coded here as a factor with two categories: 'early season', including individuals from May–June, and 'late season' including individuals from July–August), and 3) the interaction between those two variables. For a straightforward interpretation of the models, marginal effects for each predictor and effects displays were calculated by fixing the other predictors at mean values. Analyses included in this section were performed with R packages *mlogit* (Croissant 2012), *nnet* (Venables and Ripley 2002) and *effects* (Fox and Hong 2009). R script written to perform all analyses included in this paper is deposited on figshare: <<http://dx.doi.org/10.6084/m9.figshare.1190856>>.

The downscaling approach: sampling considerations

Downscaling a whole pollination network from the species to the individual level is a challenging methodological task. Mark–reobservation of individuals (Dupont et al. 2011) or micro-radio telemetry tracking (Hagen et al. 2011) are two techniques successfully used earlier in studies of individual spatio-temporal foraging patterns in bumblebees. Despite such methods might work for sampling interactions of individuals in some pollinator species, both seem rather unfeasible for a multi-species sampling with limited human and budget resources. Instead, here pollen load analysis was used to estimate visitation patterns of insect individuals. However, several methodological issues must be considered when using this kind of data, and below we point out some of them for our particular dataset (see Tur et al. 2014 for more details). First, pollen identification to species level is sometimes uncertain for closely related species, so in these cases (four in total) we had to lump pollen from several species into one type. Second, number of individuals captured per species was low, i.e. for only 15% of all pollinator species did we sample ≥ 5 individuals, because it was not possible to capture all species whenever they were seen in the field and besides some species were rarely observed. Despite this, we calculated with rarefaction curves (following Chacoff et al. 2012) that the number of individuals captured allowed an average detection of 69% of the expected interactions per species. Interaction rarefaction curves can be saturated with fewer samples because most specimens carry pollen from more than one species (Bosch et al. 2009). Moreover, individuals collected from the same species were sampled over their entire activity period (Fig. 2), although we do not have information about the exact lifespan of each individual. Finally, pollen loads are assumed to be a reasonable proxy for the individual's interaction pattern over time. Rather than a single snapshot, pollen load analysis provides a longitudinal record of the flower visitation history of individuals (Bosch et al. 2009), because pollen grains can remain attached to the body of pollinators for long periods. Pollen from flowers visited days or weeks before insect capture might be present in low numbers, in spite of the grooming behaviour of the

insects. We detected pollen grains on insects even up to a month after the end of the flowering of a particular plant species. However it is very difficult to precise the foraging period which is represented in these insect pollen loads, as we lack information about the exact lifespan of each individual of the different species.

Results

Comparing network modularity at the species and individual levels with different metrics

Network parameters calculated for networks at species and individual level are summarized in Table 1. Downscaling from sp-sp to i-sp networks increased total number of nodes, and also number of interactions (Table 1). However, as expected, empirical i-sp networks had less interactions and hence lower connectance values than null i-sp networks of the same size, because conspecific individuals are more specialized than their corresponding species. Moreover, sp-sp networks were significantly nested (Table 1) and remained nested when downscaling to the individual level, although NODF values for empirical i-sp networks were lower than for null i-sp networks.

The degree to which networks at the species level were modular varied depending on the modularity metric considered (Table 2). The M_U metric did not detect modules in the sp-sp networks from both sites but the other two metrics did (Table 2). By contrast, downscaling from species to individuals turned the networks more modular consistently with the three metrics. Modularity values of different metrics were quite similar, although the number and identity of modules identified in i-sp networks varied depending on the metric used (Table 2, Supplementary material Table A1). The metric showing the highest variation (% coefficient variation) among different runs of the algorithm for same network was M_{WB} , being more variable both in the modularity value returned ($M_U = 0.17\%$, $M_B = 0.25\%$, $M_{WB} = 4.71\%$) and the number of modules identified ($M_U = 2.67\%$, $M_B = 6.29\%$, $M_{WB} = 15.82\%$). Congruence of the identities of modules identified within different runs of the metrics was high (mutual information > 0.8) in the case of M_U and M_B , but not for M_{WB} which showed a concordance between runs comparable to the concordance existent among M_U and M_B (Supplementary material Table A1).

In both study sites, modularity values of empirical i-sp networks were above the range of values obtained for null

Table 2. Modularity values obtained for empirical networks at different scales (species-species and individuals-species) and number of modules identified using different metrics. Significance of modularity is shown with z-scores (> 2 is significant), calculated as the difference between observed modularity and mean modularity of 100 randomizations (fixed-fixed column and row sums null model) divided by their standard deviation.

	sp-sp networks		i-sp networks	
	CN	PC	CN	PC
Unipartite modularity				
M_U	0.31	0.31	0.37	0.38
Number of modules	5	5	6	5
Z-score	0.73	0.89	3.51	5.25
Bipartite modularity				
M_B	0.32	0.32	0.38	0.39
Number of modules	6	6	9	7
Z-score	7.39	3.69	7.95	8.34
Weighted bipartite modularity				
M_{WB}	0.32	0.33	0.33	0.39
Number of modules	6	6	13	8
Z-score	92.88	86.35	76.63	104.38

i-sp networks of the same size due to the specialization of individuals. This result was consistent regardless of the modularity metric used (Fig. 1).

Composition of modules in i-sp networks: distribution of individuals among modules

Hereafter, and unless otherwise is indicated, we only provide the results obtained with M_U because this modularity metric has been that mostly used in pollination network studies (Bosch et al. 2009, Dupont and Olesen 2009). Although the metric was originally designed for unipartite networks and makes no distinction between types of nodes, it performs well for bipartite networks and the modularity values obtained are similar to those obtained using the modularity metric designed for bipartite ones (Thébault 2013).

In the study site CN, the empirical i-sp network had six modules, with sizes ranging from 24 to 64 nodes, and two nodes disconnected from the main network (Supplementary material Fig. A1a). However, all modules were strongly connected, as shown by the relatively high numbers of between-module links compared to within-module links (Table 3). At PC, the i-sp network had five modules: two large modules (49–65 nodes) with a high number of within-module links, two medium-sized modules (ca 30 nodes) with more between-module links than within-module links and finally, a small module of only two plants and

Table 1. Parameters describing the structure of the empirical networks at the different scales studied (sp-sp = species – species and i-sp = individuals – species) and the null i-sp networks constructed for comparison. Mean \pm SD values ($n = 100$) of the null networks are shown.

	sp-sp Empirical		i-sp networks Null		i-sp networks Empirical	
	CN	PC	CN	PC	CN	PC
Insect pollinator nodes (<i>A</i>)	73	61	190	137	190	137
Pollen type nodes (<i>P</i>)	55	49	55	49	55	49
Total nodes (<i>A</i> + <i>P</i>)	128	110	245	186	245	186
Total interactions (<i>I</i>)	434	360	1342.79 \pm 6.0	882.74 \pm 5.88	681	506
Connectance (<i>C</i>)	0.11	0.12	0.13 \pm 0.001	0.13 \pm 0.001	0.07	0.08
Nestedness (<i>NODF</i>)	34.45*	38.65*	44.22 \pm 0.46*	43.78 \pm 0.42*	26.99*	29.67*

* $p < 0.001$. Significance value of NODF tested using the fixed row and column totals null model.

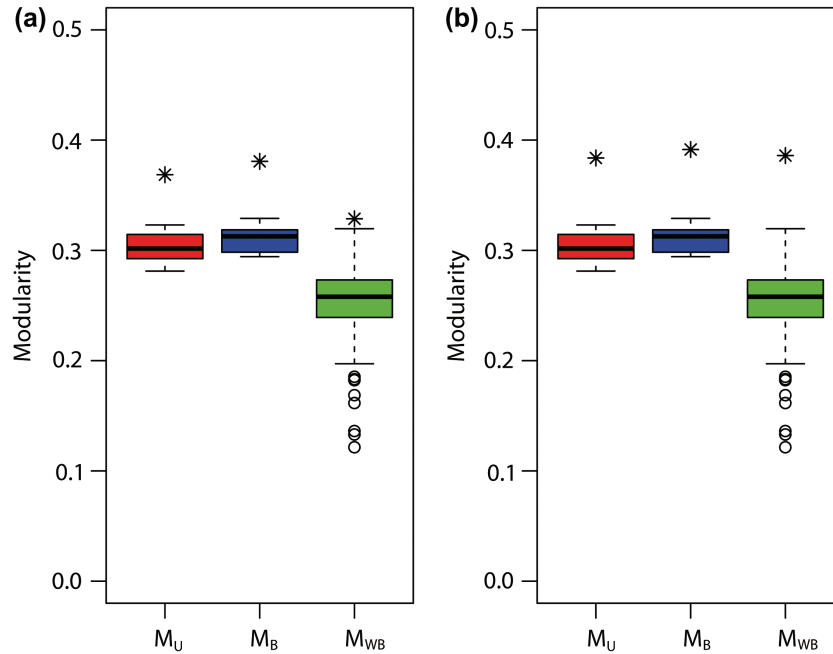


Figure 1. Modularity values of empirical i-sp networks obtained with three different metrics (M_U = unipartite modularity, M_B = bipartite modularity and M_{WB} = weighted bipartite modularity) compared to null i-sp networks without individual specialization (i.e. conspecific individuals act as generalized as their corresponding species). Box plots show the range of values obtained in 100 null i-sp networks whereas asterisks show the empirical modularity ((a): CN site and (b): PC site). Modularity in the empirical networks can be considered as significant when the asterisk falls outside the boxplot.

four insect individuals (Supplementary material Fig. A1b, Table 3). A nested pattern was found inside most modules (Table 3, Supplementary material Fig. A1). In more than half of the modules, insect individuals were structured around 1–3 plant pollen types, which acted as module hubs. Proportion of module and network hubs (always plant pollen types) was small in both networks (ca 2% of nodes). Most nodes (> 75%) acted as peripherals and the remaining as connectors (Supplementary material Fig. A2). The proportion

of connectors in CN site was high (28%) compared to PC (11%), and they were mainly hoverflies and small bees.

Interestingly, when downscaling networks to the level of individuals, individuals of the same species did not belong to the same module. Instead, species module membership changed throughout the flowering season (Fig. 2) and conspecific individuals were heterogeneously distributed among modules. In empirical i-sp networks, only two species, out of the 21 studied with ≥ 5 individuals captured,

Table 3. Composition and topological properties of modules detected in empirical i-sp networks at both study sites using the unipartite modularity metric.

	CN i-sp network						PC i-sp network				
	Mod1	Mod2	Mod3	Mod4	Mod5	Mod6	Mod1	Mod2	Mod3	Mod4	Mod5
Total nodes	64	38	29	24	33	55	32	49	6	34	65
Plant pollen types	18	10	7	4	5	10	10	22	2	9	6
Insect individuals	46	28	22	20	28	45	22	27	4	25	59
No. insect species	26	20	17	14	17	25	16	18	4	21	34
Within-module links	121	41	41	38	44	102	47	83	5	50	147
Between-module links	115	32	91	97	86	165	83	69	13	78	105
Nestedness (<i>NODF</i>)	46.98*	18.72 ^{ns}	55.54*	42.86 ^{ns}	56.13*	51.65*	39.28*	38.35*	50.00 ^{ns}	46.57*	55.81*
Connectance (<i>C</i>)	0.15	0.15	0.27	0.48	0.31	0.23	0.21	0.14	0.62	0.22	0.42
Topological roles of nodes											
Network hub	1	0	1	2	1	2	1	1	0	1	0
Module hub	2	1	1	0	1	0	0	1	0	0	3
Connector	10	3	13	16	16	9	8	1	3	7	1
Peripheral	51	34	14	6	15	44	23	46	3	26	61
Phenological composition											
(1) May	17	31	0	0	0	0	1	4	0	0	0
(2) June	28	3	3	0	0	3	3	44	0	26	6
(3) July	19	2	21	19	7	45	26	1	4	8	42
(4) August	0	2	5	5	26	7	2	0	2	0	17

* $p < 0.001$, ns = non-significant

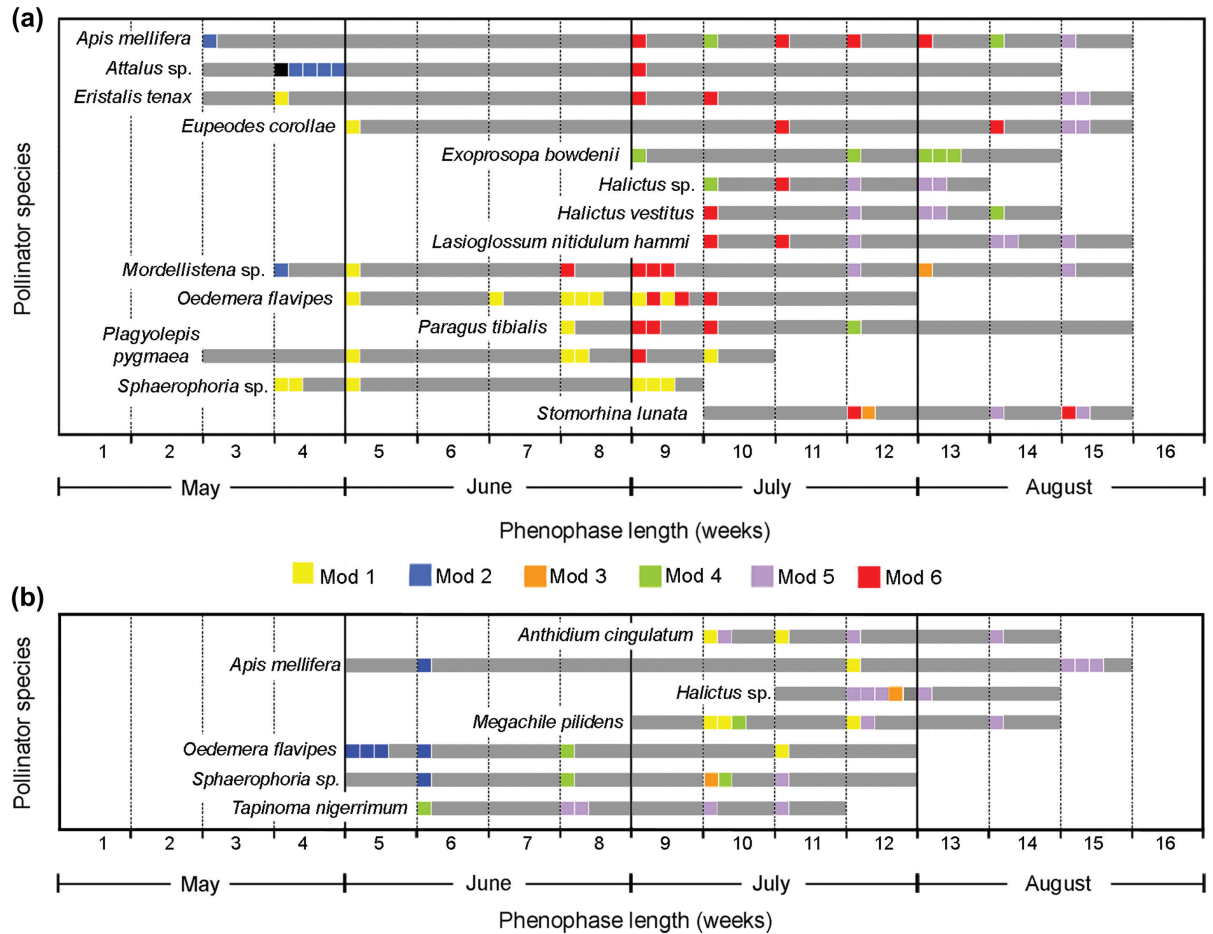


Figure 2. Grey bars represent active species phenophase duration estimated by field observations ((a): CN site, (b): PC site) and coloured squares indicate the time (sampling week) at which individuals were captured. Each square represents a single individual and the different colours show the module to which individuals belong. Squares representing captures of individuals within the same sampling week were coloured in the same order as individuals were captured. In most species conspecific individuals belong to different modules depending on the time of the season. Thus, species switch between modules, a behaviour that disappears at the sp–sp network level.

had all conspecifics grouped together within the same module (*Sphaerophoria* sp. in module 1 and *Exoprosopa bowdenii* in module 4 in the CN i–sp network). On average, a species belonged to 2.7 modules and the range was 1–5. Heterogeneity in module membership of conspecifics was 0.55 ± 0.27 at CN (mean $IQV \pm SD$; $n = 14$ species) and 0.63 ± 0.18 at PC ($n = 7$ species). A similar result was also obtained when M_B and M_{WB} metrics were used (M_B : $IQV_{CN\ site} = 0.59 \pm 0.14$; $IQV_{PC\ site} = 0.71 \pm 0.16$; M_{WB} : $IQV_{CN\ site} = 0.49 \pm 0.22$; $IQV_{PC\ site} = 0.61 \pm 0.19$). In null i–sp networks, as expected, individuals of the same species were always grouped inside the same modules, thus suggesting that individual specialization is a driver of module dispersion of conspecific individuals. However, the degree of heterogeneity in module membership among conspecifics was not proportionally related to the degree of individual specialization WTC/TNW ($R = -0.05$, $p = 0.75$). Species with longer phenophases or those for which more individuals were sampled were not more dispersed among modules than species with shorter phenophases or with relatively few samples (Spearman's $\rho = 0.411$, $p = 0.06$; Spearman's $\rho = -0.005$, $p = 0.97$, respectively), rejecting possible influence from these variables.

Biological factors and modularity

Results from the MRPP analysis showed that within-module pollen niche dissimilarity was significantly less than expected by random in both i–sp networks, although the deviation was small (CN: $\delta = 0.59$, $A = 0.24$, $p < 0.001$; PC: $\delta = 0.64$, $A = 0.17$, $p < 0.001$). Thus, affinity in pollen resources was higher between individuals from the same module (CN: $\overline{d_W} = 0.60$; PC: $\overline{d_W} = 0.62$) than between individuals from different modules (CN: $\overline{d_B} = 0.82$; PC: $\overline{d_B} = 0.84$) (Supplementary material Fig. A3).

In addition, modularity in i–sp networks was also consistently associated to phenology (CN: Empirical $\chi^2 = 277.88$, mean permutations $\chi^2 = 15.18$, $DF = 15$, $p = 0.001$; PC: Empirical $\chi^2 = 136.82$, mean permutations $\chi^2 = 12.23$, $DF = 12$, $p = 0.001$). In most modules of the CN i–sp network we found a predominance of nodes from a certain month of the season (Fig. 3a): 1) module 2 was mainly composed of plants flowering in May and insect individuals from the beginning of the season, 2) module 1 contained 76% of all network plants and pollinator individuals from June, 3) plants and pollinators from July were found in several modules, but 39% of insect individuals and 47% of flowering

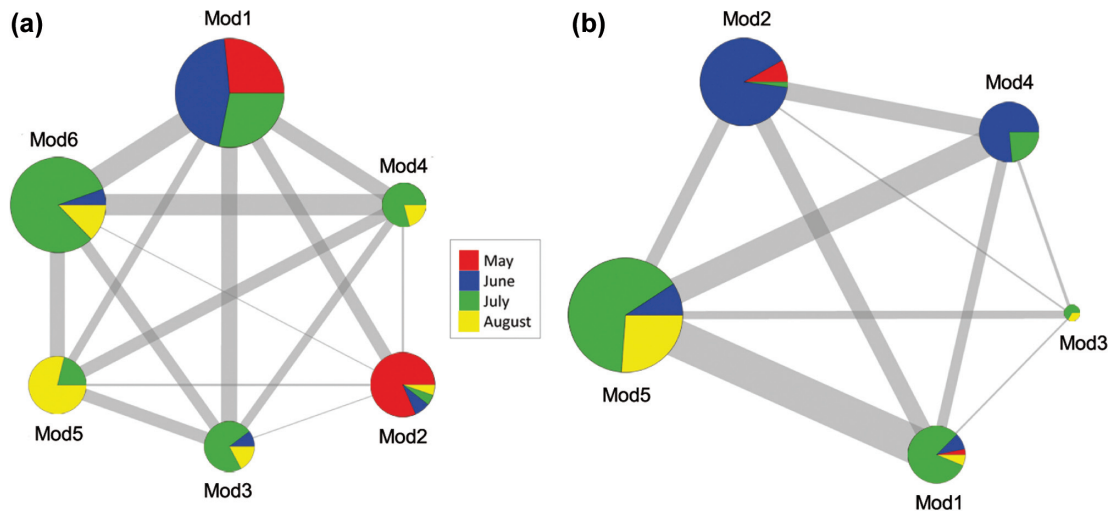


Figure 3. Representation of the two i-sp network graphs showing the change in phenological composition across modules in the two study communities: (a) CN, and (b) PC. Size of each pie chart is proportional to the number of nodes within each module and links connecting them are weighted by the number of between-module interactions. For insects, phenology (May, June, July, August) corresponds to the date the individual was captured whereas for plant pollen types it corresponds to the peak flowering date. A strong seasonality can be observed in each module.

plants from this month belonged to module 6, and 4) module 5 was made up of 57% of all plants and insect individuals from August. This seasonality in module composition was also detected in the PC i-sp network (Fig. 3b): 1) modules 2 and 4 included all plants with a flowering peak in June and 83% of pollinator individuals from this month, 2) module 1 contained mainly plants and insect individuals from July, and 3) module 5 was the largest module with 52% of total network nodes from July and 81% from August.

Association of node features with topological roles

Plant's and insect individual's topological roles in the network were determined by their biological features. Results from the multinomial and binary logistic models are reported in Supplementary material Table A2. For plant pollen types, longer flowering periods and higher pollen abundances significantly increased the probabilities of being a network or module hub (Supplementary material Fig. A4a–b). The model estimated a very high probability for plants with low pollen abundances to be peripherals in the interaction network, whereas plants with high pollen abundance had a higher likelihood of becoming module hubs. Moreover, only plants with very long flowering periods (14 weeks) were likely to become network hubs. For insect individuals, as expected, increases in linkage level increased the likelihood of being a connector. For instance, for a node with $L_i = 2$ the model predicted a probability of being a connector to 0.08%, whereas for a node with $L_i = 10$ it was 90%. This positive effect of linkage level was higher for individuals present at the end of the season, as shown by the significant positive interaction between individual linkage level and phenophase in the model (Supplementary material Table A2). The average probability of being a connector in May–June (early season) was 26% whereas in July–August (late season) it was 65% (Supplementary material Fig. A4c).

Discussion

Downscaling pollination networks to the individual level revealed a modularity pattern which can be hidden at the species level. Such modularity was associated to: 1) the heterogeneity and specialization in the partition of pollen resources among individuals, and 2) a dynamic switching of interactions within pollinator species during the season tracking plant flowering phenologies.

Results showed that when conspecific individuals are aggregated into species in the process of constructing species-based pollination networks, a misleading or incomplete picture of overall network patterns can be obtained because the existing inter-individual variation in flower foraging behaviours is not considered. For instance, in our study, empirical i-sp networks were less connected and nested than expected from the null models because generalized pollinator species were, in fact, composed of specialized and idiosyncratic conspecific individuals (Tur et al. 2014). Particularly, and in contrast to the results of Dupont and Olesen (2012) showing that a modular pattern was stable to changes in temporal scale, we found that modularity was not consistent across the two hierarchical scales of organization (i.e. species and individuals), regardless of the metric used to measure it. When downscaling, i-sp networks turned more modular than expected with our null model. The explanation for this is the strong specialization and heterogeneity in resource partitioning within species in empirical networks (Tur et al. 2014), as modularity tends to increase with higher specialization of interactions (Prado and Lewinsohn 2004, Lewinsohn et al. 2006). Therefore, our results suggest that individual specialization plays an important role in the magnitude of emergent modularity in i-sp networks. Further studies are needed to assess how consistent a modular pattern in pollination networks at the scale of individuals is. Exploring community structure at this level offers

the opportunity to link network topology to the mechanisms underlying variation among conspecific individuals, such as differences in phenotypical traits, foraging preferences, sex, physiological condition or social status (Araújo et al. 2011, Dall et al. 2012), and thus ultimately differential natural selection regimes and evolution.

Resource partitioning and niche organization have been suggested as drivers of network modularity in previous studies at the species level (Prado and Lewinsohn 2004, Guimerà et al. 2010). Indeed, resource partitioning proved to be a driver of floral diversification in models (Rodríguez-Gironés and Santamaría 2010). However, resource partitioning operates at the individual scale, as foragers compare the available resources and make the choice providing the maximum energy intake (MacArthur and Pianka 1966). Studies focusing on diet variation within a single species found a modular network structure reflecting differences in how individuals rank preferred resources (Araújo et al. 2008, Tinker et al. 2012). Variation in how flower-visitor individuals forage through space can also determine the modular pattern of a network (Dupont et al. 2014). Here, modules in i-sp networks matched groups of individuals, which shared a common pool of pollen resources regardless of their species identities, i.e. individuals of the same species were not necessarily grouped into the same module. This means that, contrary to the traditional view in static species-based pollination networks, a species does not belong unambiguously to a single module, but, one may say, more or less to a module. For instance, a hoverfly individual of *Eristalis tenax* had a higher pollen resource affinity with a bee individual of *Osmia latrellei* than with another conspecific hoverfly individual. The identified modules were composed of functionally different pollinators (e.g. small bees, large bees, beesflies, hoverflies, flies) with overlapping pollen niches, so the view of modules as a set of species with convergent morphological traits (Olesen et al. 2007, Danieli-Silva et al. 2012) or taxonomical relatedness (Rezende et al. 2009) might not necessarily be the main rule at the individual level.

Conspecific individuals were distributed into different modules due to the heterogeneity in the use of pollen resources within species (Tur et al. 2014). By belonging to several modules a species might reduce intraspecific competition, as competition between modules can be lower than within modules (Rezende et al. 2009), although we did not test this hypothesis here. However, the degree of heterogeneity in module membership for each species was not proportionally related to a quantitative measure of the degree of individual specialization. This suggests that other factors might be important for the assignment of individuals to a particular module, such as species sociability traits, voltinism or other life history traits. Incorporating this kind of information in future studies as well as data on intraspecific trait variation will provide a better understanding on how interactions are distributed among individuals.

Phenology was one of the main drivers of modularity in the i-sp networks, implying that time means more than taxonomy. In most modules we detected predominance of plant pollen types and insect individuals present at a particular month of the season. Modularity in pollination networks has been associated to phenology in previous studies (Bosch et al. 2009, Martín González et al. 2012). However, in our

study, phenological compartmentalization was evident only when downscaling networks from species to individuals. At the individual level, a temporal dynamics hidden at species level appeared, revealing the existence of module turnover in the network. Modules changed through time during the flowering season, so as the season advanced new modules are formed and old ones dissolve. In fact, as the season progressed, pollinator species switched from one module to the next, a behaviour detectable only at the individual scale. Changes in species module membership through time might be a consequence of adjustment of foraging choices in response to changes in flower abundances, availability of resources and/or density of foragers throughout time (Goulson 1999). Therefore, a continuous interaction rewiring process is occurring at the species level which is driven by the dynamics of the adaptive foraging behaviour of individuals to resource fluctuations. These species switches in resource choice can enhance the stability of networks and community persistence (Kondoh 2003, Kaiser-Bunbury et al. 2010, Valdovinos et al. 2013).

Relatively few studies until now have attempted to correlate species traits with species roles (Donatti et al. 2011, Schleuning et al. 2014, Dupont et al. 2014). However, such knowledge might be relevant for the conservation of species interaction networks (Tylianakis et al. 2010). In our i-sp modular networks, phenology was an important determinant of network structure, and thus flowering period length of plant pollen types and phenophase of individual insect species turned out to be important attributes determining a node's topological role. Similar to other pollination networks (Dupont and Olesen 2009, 2012), the modules of individuals assembled around 1–3 plant pollen types, which were the module or network hubs. These plant hubs were species with long flowering periods (7–10 weeks) and also with high abundances in the study area, such as *Hypericum balearicum*, *Santolina chamaecyparissus*, *Teucrium* spp., *Bellium bellidioides*, *Micromeria filiformis*, *Euphorbia characias* and several Asteraceae species. As modules detected in networks were related to a temporal dynamics, these network hubs become key species not only because of their importance to the cohesiveness of the entire network at a given point in time, but also because of their role acting as temporal couplers (Rasmussen et al. 2013). In contrast, no insect species acted as hubs, which seems to be an almost general trend in pollination networks (Dupont and Olesen 2009), also when sampling is not plant-centered like here. In particular, we note that even within a single pollinator species, individuals played different roles, thus not all individuals of a population are equivalent from a network structural point of view. This implies that the potential impacts of a disturbance might be different depending on whether affected individuals are connectors or peripherals. The loss of connector individuals, for example, might cause the isolation of modules (Olesen et al. 2007, Guimerà et al. 2010). Thus, our findings highlight the importance of considering intraspecific variation in foraging behaviours also for topological roles, although further studies are needed to determine which individual traits, in particular, define whether an individual acts as connector, peripheral or hub (Dupont et al. 2014).

The downscaling approach improve our understanding of the structure and dynamics of species-based networks,

as it assists in unravelling ecological processes which actually take place at the scale of individuals but act as potential network pattern drivers. This is, for instance, the case of individual foraging behaviour, which is known to be an important driver of network structure in food-webs (Beckerman et al. 2006, Petchey et al. 2008) as it ultimately determines which interactions are realized and which are not. In addition, the module turnover identified at the individual scale highlights the importance of studying networks from a temporal viewpoint, not only across years or seasons, but also in series of smaller temporal windows (Rasmussen et al. 2013) or at different organizational scales. Finally, network downscaling may facilitate bridging ecology and evolution through its focus upon determinants of individual fitness.

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Data accessibility: quantitative pollen-transport network data: DRYAD entry doi: 10.5061/dryad.63fp5 (Tur and Traveset 2013). R script and data for all analysis included in this paper: <<http://dx.doi.org/10.6084/m9.figshare.1190856>>.

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Supplementary material (available as Appendix oik.01668 at www.Oikosjournal.org/readers/appendix). Appendix 1. Comparison of module identification by different measures. Appendix 2. Measure of the degree of individual specialization. Appendix 3. Biological features studied to characterize network nodes and their topological roles. Figure A1. Modular pollen-transport interaction matrices for both study sites. Figure A2. c-z plot for i–sp networks at both study sites. Figure A3. Pollen resource affinity within- and between modules in i–sp networks. Figure A4. Plots of estimated effects of plant pollen abundance, flowering length, linkage level and phenophase on the topological role of nodes. Table A1. Congruence between modules obtained for empirical i–sp networks using different modularity metrics. Table A2. Results from multinomial and binary logistic models.