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Drivers of compartmentalization in a Mediterranean pollination network

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We study compartmentalization in a Mediterranean pollination network using three different analytical approaches: unipartite modularity (UM), bipartite modularity (BM) and the group model (GM). Our objectives are to compare compartments obtained with these three approaches and to explore the role of several species attributes related to pollination syndromes, species phenology, abundance and connectivity in structuring compartmentalization. BM could not identify compartments in our network. By contrast, UM revealed four modules composed of plants and pollinators, and GM four groups of plants and five of pollinators. Phenology had a major influence on compartmentalization, and compartments (both UM and GM) had distinct phenophases. Compartments were also strongly characterized by species degree (number of connections) and betweenness centrality. These two attributes were highly related to each other and to phenophase duration. Differences among compartments in abundance were only apparent with GM. We attribute this to the fact that abundance is strongly correlated with Degree, and the GM algorithm is particularly powerful at discriminating species based on degree. On the other hand, the role of pollination syndrome-related features in compartmentalization mostly emerged with UM. Only UM compartments differed in corolla length and pollen production. Both UM and GM compartments differed in their pollinator spectra. We found inconsistent reciprocity between plant attributes and pollinator spectra, thus it is difficult to conclude compartments follow clear-cut syndromes. Also, both UM and GM identified a compartment composed of pollinators with long activity periods that acted as connectors, linking all compartments providing cohesiveness to the network.

The study of interactions using a network approach has provided valuable insights into the structure, dynamics and evolution of ecological communities. Notwithstanding some differences among communities, most ecological networks appear to share a number of structural features, of which compartmentalization is one of the most salient (Lewinsohn et al. 2006, Olesen et al. 2007, Allesina and Pascual 2009, Guimerà et al. 2010, Tylianakis et al. 2010). Compartments can be defined as groups of species that are more likely to interact among themselves than with the rest of the species in the network, or as groups of species with an interaction pattern in common. Although there is no empirical evidence linking compartmentalization with the persistence of network structure, the distribution of species across compartments and the connectivity pattern between compartments are believed to have important implications for the dynamics and stability of ecological communities (Tylianakis et al. 2010). For instance, compartmentalized webs are likely to be more robust, since perturbations are unlikely to spread quickly across compartments, although, at the same time, strong compartmentalization may result in a higher risk of

fragmentation (May 1972, Olesen et al. 2007, Guimerà et al. 2010, Thébaud and Fontaine 2010, Tylianakis et al. 2010, Stouffer and Bascompte 2011). For these reasons, it is important to explore different methods to describe compartmentalization and to understand its ecological and evolutionary drivers.

Compartmentalization has been extensively studied in food webs (May 1972, Pimm and Lawton 1980, Krause et al. 2003, Allesina and Pascual 2009, Guimerà et al. 2010), and more recently in pollination, ant-myrmecophyte and host-parasite networks (Dicks et al. 2002, Fonseca and Ganade 1996, Lewinsohn et al. 2006, Olesen et al. 2007, Allesina and Pascual 2009, Bosch et al. 2009, Dupont and Olesen 2009). However, although compartmentalization appears pervasive across ecological networks, its patterns and drivers are likely to differ between plant-pollinator and other types of interaction networks (Thébaud and Fontaine 2010, Tylianakis et al. 2010). Compartments have been related to body size and phylogenetic relatedness in food webs (Krause et al. 2003, Cattin et al. 2004, Rezende et al. 2009, Guimerà et al. 2010), with high levels of specialization

in ant–myrmecophyte networks (Fonseca and Ganade 1996, Lewinsohn et al. 2006), and as community level evidence for the occurrence of pollination syndromes in pollination networks (Dicks et al. 2002, Olesen et al. 2007, Dupont and Olesen 2009, Danieli-Silva et al. 2012). Pollination syndromes are groups of phenotypical traits that reflect coevolution among sets of plants and pollinators (Fægri and van der Pijl 1979, Fenster et al. 2004, Ollerton et al. 2009). For instance, according to pollination syndrome theory, flowers visited by butterflies tend to be large, usually pink, purple or blue-colored, have long narrow corollas, and produce nectar with low sugar concentration. Instead, bee-visited flowers tend to be either dish-shaped or zygomorphic, produce concentrated nectar and large quantities of pollen, and have yellow or blue corollas. In well-sampled communities where plant–pollinator interactions are structured according to various pollination syndromes, we would expect to detect compartments composed of plants sharing a number of phenotypical attributes, and being mostly visited by a given pollinator functional group. Other studies have shown a strong influence of phenology in the establishment of compartments (Bosch et al. 2009), which is likely to be particularly important in highly seasonal communities. Species with short phenophases (flowering/activity periods) will overlap in time with few partners and thus, other things being equal, are likely to be less connected than species with long phenophases (Olesen et al. 2008, Kallimanis et al. 2009, Martín González 2010). This is important because connectivity patterns (i.e. the number of interactions within and among modules) determine the role species play in compartmentalized networks. Highly connected species whose interactions are mostly within their compartment are termed ‘hubs’, whereas poorly connected species are termed ‘peripherals’, and species whose interactions are equally distributed among different compartments are termed ‘connectors’ (if these species have a low connectivity) or ‘network hubs’ (when they are highly connected; Guimerà and Amaral 2005a, b, Olesen et al. 2007). Connectors and network hubs can be identified using centrality measures, such as betweenness centrality, which measures the importance of a node as an intermediary in the spread of information across the network, whereas degree is useful to differentiate between hubs/network hubs from peripherals/connectors (Jordán et al. 2006, Martín González et al. 2010).

Compartmentalization in pollination networks has been measured using ordination methods (Dicks et al. 2002) and more recently, using unipartite modularity (Olesen et al. 2007, Bosch et al. 2009, Dupont and Olesen 2009, Danieli-Silva et al. 2012). Unipartite modularity is a function that detects areas in the network with contrasting (high and low) connectivity, and divides networks into compartments (modules) composed of species that interact between themselves more frequently than expected by chance. Resulting compartments display a high within-compartment connectivity, while the connectivity between compartments is low (Newman and Girvan 2004, Guimerà and Amaral 2005a, b). The use of the modularity algorithm has several advantages over ordination methods: the number of compartments results from an unsupervised algorithm, and the significance of the resulting compartments can be assessed using randomizations (Newman and Girvan 2004, Guimerà

and Amaral 2005a, b, Olesen et al. 2007, Fortuna et al. 2010). Unipartite modularity has been widely applied to the analysis of food webs and other complex systems, such as social, metabolic, and technological networks, as well as species spatial distributions (Newman 2004, Guimerà and Amaral 2005a, b, Fortuna et al. 2010, Guimerà et al. 2010, Carstensen et al. 2012). Because modularity was not originally intended for bipartite networks, Guimerà and colleagues (2007) have proposed a bipartite version of modularity. In bipartite modularity, ‘events’ and ‘actors’ (in pollination networks, plants and pollinators) are grouped separately, and actors have a higher probability of being placed in the same compartment the more events they attend together (Guimerà et al. 2007). In pollination networks, pollinators with extensive overlap in their visitation patterns will be placed in the same compartment, as will plants sharing many pollinators. Along this line, Allesina and Pascual (2009) developed a different analytical approach, the group model (also known as ‘stochastic blockmodel’ in the social network literature), which also groups species according to the similarity of their interaction pattern. In the group model, a network is divided into compartments so that two species in the same group have similar interaction patterns with the other compartments (e.g. the species in the ‘blue’ compartment interact strongly with those in the ‘red’ compartment and weakly with the ‘yellow’ compartment). Although not intended specifically for bipartite networks, group model will separate plants and pollinators, as a plant and a pollinator do not share any interaction partners. Unipartite modularity and group model have yielded similar compartmentalization patterns in food webs (Guimerà et al. 2010), but, to our knowledge, neither bipartite modularity nor group model have yet been applied to the study of mutualistic networks.

In this study, we use unipartite modularity, bipartite modularity and the group model to explore compartmentalization in a Mediterranean pollination network. Irrespective of the approached used, species within a module or a group will have similar interaction patterns, and thus can be expected to share features related to their ability to interact. Thus, we analyze within-compartment homogeneity and between-compartment heterogeneity for a number of species attributes related to pollination syndromes, phenology, abundance and connectivity. Our first objective is to identify species biological (related to natural history) and ecological (related to abundance and interaction patterns) attributes driving compartmentalization. Given the high levels of seasonality and the lack of extreme morphologies observed in Mediterranean pollination communities (Herrera 1988, Petanidou and Ellis 1993, Bosch et al. 1997), we expect a greater role of phenology than morphology in determining compartmentalization. Our second objective is to compare the outcomes provided by the different approaches used to measure compartmentalization. Because of differences intrinsic to the modularity and group model approach to compartmentalization (detection of areas with contrasting connectivity vs detection of species with similar interaction patterns), and solution searching algorithms (simulated annealing vs genetic algorithm), we expect to find differences between the three methods. In particular, the three methods are likely to handle differently groups of species that have

different connectivity (specialist vs generalist) but share common partners.

Material and methods

Empirical data set

Fieldwork was conducted during the spring of 2006 in a 100×100 m plot in a Mediterranean scrubland in El Garraf Natural Park, northeastern Spain. We sampled plant–pollinator interactions two or three times every week from the beginning of March until the beginning of June (when bloom virtually ceased in coincidence with the summer drought). To assess floral abundance, we counted weekly all open flowers in six permanent transects (each 50×1 m) criss-crossing the study area. We identified 26 plant species, of which 19 plants accounted for $>99.7\%$ of the total number of flowers counted. We conducted pollinator surveys on these 19 species. On each sampling day, randomly-selected patches of species that were in bloom were observed several times throughout the day for 4-min intervals, during which we noted all insects actively visiting the flowers. Total field sampling time was 106 h, where we observed 4262 plant–pollinator contacts representing 432 specific plant–pollinator interactions. We identified 172 insect species visiting the flowers in our plot. A few specimens of most pollinator species observed were captured and placed individually in clean vials for pollen identification (methods described in Bosch et al. 2009). Pollen analysis revealed 393 interactions unrecorded during visual censuses, adding to a total of 825 interactions.

Detection of compartmentalization

Unipartite modularity (UM)

UM makes no distinction between node types. Nodes in module m have L_m connections within the module, and the total number of connections is L . d_m is the sum of the Degrees (i.e. number of connections) of all the nodes belonging to module m . Using this notation, UM can be written as the sum of the deviance from the expected number of within-module connections:

$$M = \sum_m \left(\frac{L_m}{L} - \left(\frac{d_m}{2L} \right)^2 \right)$$

The significance of UM is obtained by comparing observed value of modularity against the modularity values of random matrices (Olesen et al. 2007, Fortuna et al. 2010). We used two null models (NM2 and FLreal) to create random matrices. NM2 is the most commonly used null model in pollination networks. NM2 creates matrices of equal size and connectance as the original matrix, in which species interact neutrally based on their original connectivities (Bascompte et al. 2003, Vázquez and Aizen 2003). However, as our community is characterized by distinct and staggered blooming/activity periods, many species pairs cannot possibly interact due to non-overlapping phenophases (phenological forbidden links; Olesen et al. 2010). For this reason we also used FLreal, a null model similar to NM2 but

which accounts for the presence of forbidden links (in this case phenological forbidden links; Martín González 2010). FLreal creates matrices of equal size and connectance as the original matrix, in which species pairs with overlapping phenologies interact neutrally based on their original connectivities. We created 100 random matrices with each null model.

Bipartite modularity (BM)

To investigate modularity in bipartite networks, Guimerà et al. (2007) focus on one type of node at a time. For example, if the focus is on plants, each plant belongs to a module m . Two plants i and j have c_{ij} pollinators in common, while c_i and c_j are the number of pollinators of plant i and j respectively. With this notation in place, bipartite modularity is defined as

$$M = \sum_m \left(\alpha \sum_{i \neq j \in m} c_{ij} - \beta \sum_{i \neq j \in m} c_i c_j \right)$$

where α and β are suitable normalizing constants (Guimerà et al. 2007). Thus, modularity in bipartite networks expresses the cumulative deviation from what would be expected at random of the degree of overlap between pollinators (or plants). Other formulations of BM take into account both types of nodes at the same time (Barber 2007).

Group model (GM)

In group model all species are divided into groups (Allesina and Pascual 2009). The vector G identifies the group each species belongs to (partition of the nodes). The search for the ‘optimal’ G is based on the likelihood that a simple probabilistic model based on G will recover the empirical data (likelihood). The likelihood that the model, given a partition G , produces the empirical data is:

$$\mathcal{L}(A|G) = \prod_i \prod_j p_{G_i G_j}^{a_{ij}} (1 - p_{G_i G_j})^{1-a_{ij}}$$

where A is the adjacency matrix for the network and $p_{G_i G_j}$ is the probability that a species belonging to the same group as i connects to a species in the group of j . These probabilities can be set to their maximal likelihood estimates (Allesina and Pascual 2009). Because partitions involving a higher number of groups will typically yield higher likelihoods, the search for the ‘optimal’ G requires some form of model selection such as Akaike’s information criterion (Allesina and Pascual 2009, this study) or marginal likelihoods (Eklöf et al. 2011, Baskerville et al. 2011).

For convenience, we will use the word ‘compartment’ as a general term, ‘module’ for compartments obtained using the modularity function, and ‘group’ for compartments obtained with the group model.

Species attributes

For each species, we measured a number of features related to pollination syndromes, phenology, abundance and connectivity.

Pollination syndrome-related traits include floral attributes (corolla length, a measure of potential restriction to

pollinators; nectar production calculated as mg of sugar per flower; and pollen volume, calculated as mm³ per flower). These attributes were measured on 10–15 flowers of each species from different individuals scattered across the study plot. We also calculated pollinator spectra as the proportion of visits of the different pollinator groups to each plant species. Pollinators were divided into seven taxonomical functional groups: ants, bees, Coleoptera, Diptera, Lepidoptera, wasps and others (which included Heteroptera and Orthoptera; Faegri and van der Pijl 1979, Fenster et al. 2004).

Phenology-related features include beginning of bloom of plant species (calculated as the first week a plant species was recorded blooming in the flower transects), beginning of pollinator species activity period (calculated as the first week a pollinator species was recorded in the study plot or its close surroundings), duration of bloom of plant species (number of weeks a plant was recorded blooming in the flower transects) and duration of pollinator species activity period (determined using information from the interaction surveys supplemented with frequent records of pollinators observed in our plot or its close surroundings). We assume pollinator species were active during the entire time interval comprised between the first and last record dates, thus assuming overlap of generations for multivoltine species.

Flower abundance of each plant species was measured as the total number of flowers counted in the transects throughout the study. Pollinator abundance was estimated as the sum of weekly visitation frequencies obtained in plant–pollinator surveys (measured as individual interactions per observed flower), corrected by each plant species' weekly flower abundance.

Connectivity features include Degree (the number of interaction partners of a species, often used as a crude measure of generalization; Vázquez and Aizen 2003, Olesen et al. 2007, Martín González et al. 2010), and betweenness centrality (BC). BC of species *i* is defined as the fraction of shortest paths between all pairs of species in the network that pass through *i* (De Nooy et al. 2005). BC of a node *i* is calculated as

$$BC(i) = \sum_{ij} (g_{jk}(i)/g_{jk})$$

where g_{jk} is number of shortest paths linking any two species, and $g_{jk}(i)$ is the number of those shortest paths that pass through *i* (Wasserman and Faust 1994).

Association of species attributes and compartments

Because the distribution of most of the attributes was non-normal even after transformation, we analyzed between-compartment heterogeneity using one-way non-parametric ANOVA (Kruskal–Wallis test) with post hoc comparisons (Siegel and Castellan 1988) using SPSS17.0. Pollinator spectra of the various compartments was compared with a one-way non-parametric MANOVA (NPMANOVA) with Bonferroni post hoc corrections using PAST. As a measure of within-module homogeneity we use the inverse of the median absolute deviation ($MAD = \text{median}_i(|X_i - \text{median}_j(X_j)|)$), a robust estimator of dispersion highly insensitive to outliers.

Results

Detection of compartmentalization

Unipartite modularity (UM) resulted in four modules (Fig. 1), each composed of both plant and pollinator species (Table 1). Our network showed a UM of 0.265, which was significantly higher than UM in 100 random matrices obtained using NM2 (range = 0.195–0.216; $p < 0.001$) and 100 random matrices obtained with FLreal (range = 0.199–0.219; $p < 0.001$). The optimal group model partition (GM) resulted in nine groups (min $\Delta\text{AIC} = 24$; Fig. 1), of which four were composed exclusively of plant species, and the other five of pollinators (Table 1). Bipartite modularity could not divide our network into modules, and thus was not included in further analysis. To facilitate the comparison between the compartments obtained with UM and GM, we separated plants and pollinators in each UM module (henceforth Mpl and Mpo, respectively). Plant modules and groups were quite similar, but pollinator modules and groups were less coincidental (Table 1).

Association of species attributes and compartments

An influence of floral attributes on compartmentalization was only apparent when using UM (Table 2, Fig. 2). Mpl3 and Mpl4 plants had significantly longer corollas than Mpl1 and Mpl2 plants, and Mpl3 plants produced significantly less pollen than Mpl2 and Mpl4 plants. There were no differences in nectar production among modules (Table 2). In GM compartments only differences in corolla depth approached significance (Table 2). All pollinator functional groups were represented in more than one compartment, but compartments differed significantly in their pollinator spectra both when using UM and GM. Differences were mostly due to compartments Mpl4 and Gpl4, which were visited mostly by bees. After Bonferroni correction, the pollinator spectra of these compartments differed significantly from Mpl3 and Gpl2, respectively, which included plants visited by a wider spectrum of pollinator functional groups.

Phenology emerged as a strong determinant of compartmentalization in our community, and UM and GM yielded similar results for both plants and pollinators (Table 2). Plant compartments (Fig. 3) were quite distinct based on beginning of bloom, with an early-, two mid-, and one late-blooming compartments. On the other hand, plant compartments did not differ based on bloom duration (although results with GM approached significance, Table 2). Pollinator compartments (Fig. 4) were significantly distinct based on beginning and duration of activity period. GM identified a compartment (Gpo9) composed of species with long activity periods that was not apparent with UM.

Differences among compartments in species abundance were not significant with UM (Table 2). These differences were significant for pollinators and narrowly failed significance for plants with GM (Table 2, Fig. 4), which identified two groups with rare pollinators (Gpo6 and Gpo8), two with abundant pollinators (Gpo5 and Gpo7) and one with very abundant pollinators (Gpo9). It is important to

note that these differences in abundance closely resemble differences in duration of activity (Fig. 4).

Differences among compartments in degree and BC were significant for both plants and pollinators, with UM and GM yielding similar results (Table 2). Plants from Mpl1, Mpl2, Gpl1 and Gpl2 had a higher degree and BC than plants from the other two plant compartments (Fig. 3). Pollinator compartments with high degree and BC coincided mostly with compartments with high abundance and duration of activity period. Mpo4 and Gpo9 had the highest degree and BC (Fig. 4).

We compared within-compartment homogeneity between UM and GM compartments by measuring the inverse of the median absolute deviation (MAD) of the different species attributes measured. The only attribute that differed significantly was pollinator degree ($t = 0.03$, $DF = 7$, $p = 0.03$), which was more homogeneous in groups

than in modules. Homogeneity in all other attributes did not differ between groups and modules (all $p > 0.13$).

Both UM and GM identified a connector compartment composed of pollinators (Mpo4 and Gpo9). Links out of these two compartments were more or less equally distributed among the various plant compartments, effectively connecting the entire network (Appendix 1). Pollinator species in these two compartments were characterized by long activity periods, high abundance, and high degree and BC (Fig. 4). Although plants have a higher BC than pollinators given their higher connectivity and consequently a more central position in the network, the majority of their interactions are restricted within their module or with few pollinator groups. The only exception to this is Mpl2, whose interactions are distributed more or less homogeneously across compartments (Mpl2) therefore acting as network hubs (Appendix 1).

Unipartite modularity

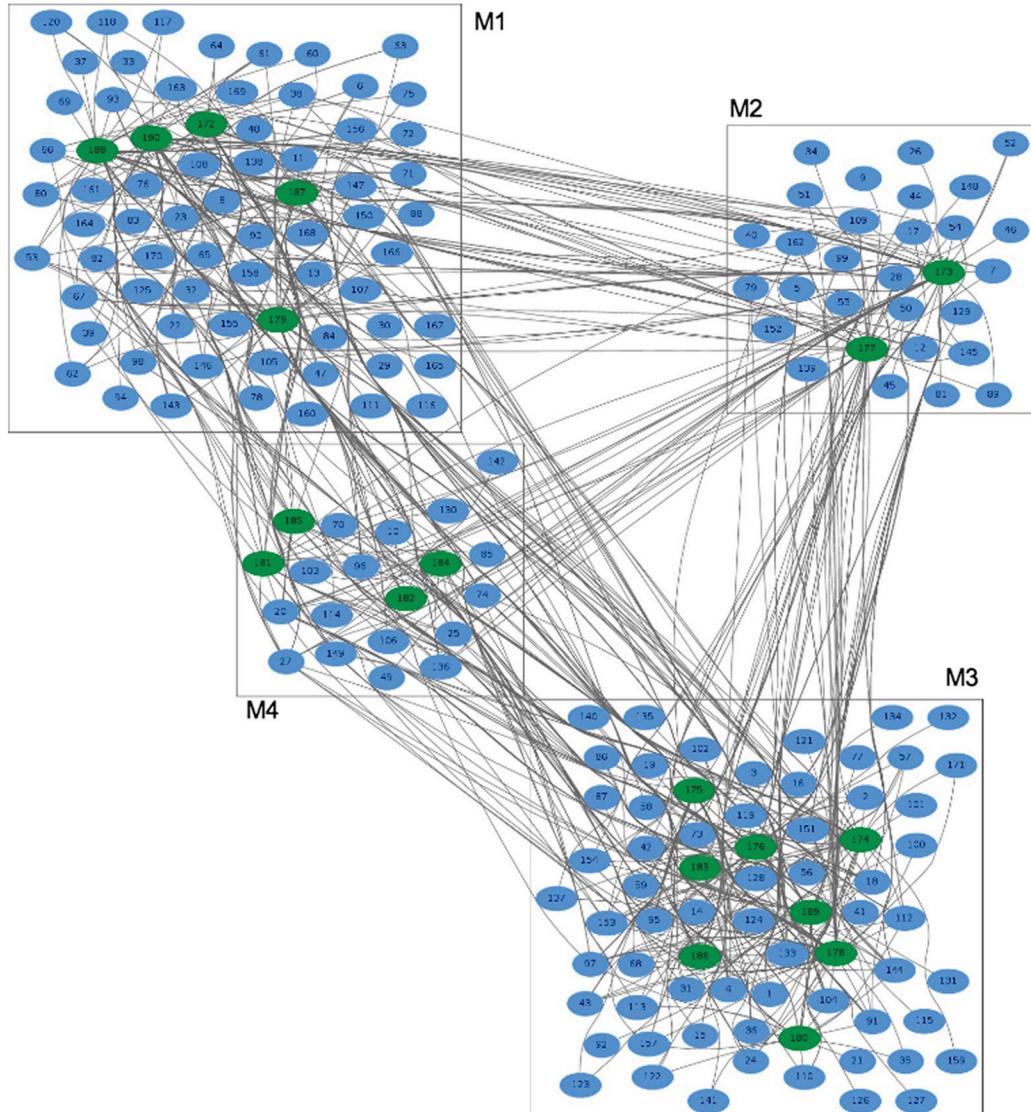


Figure 1. (Continued)

Group model

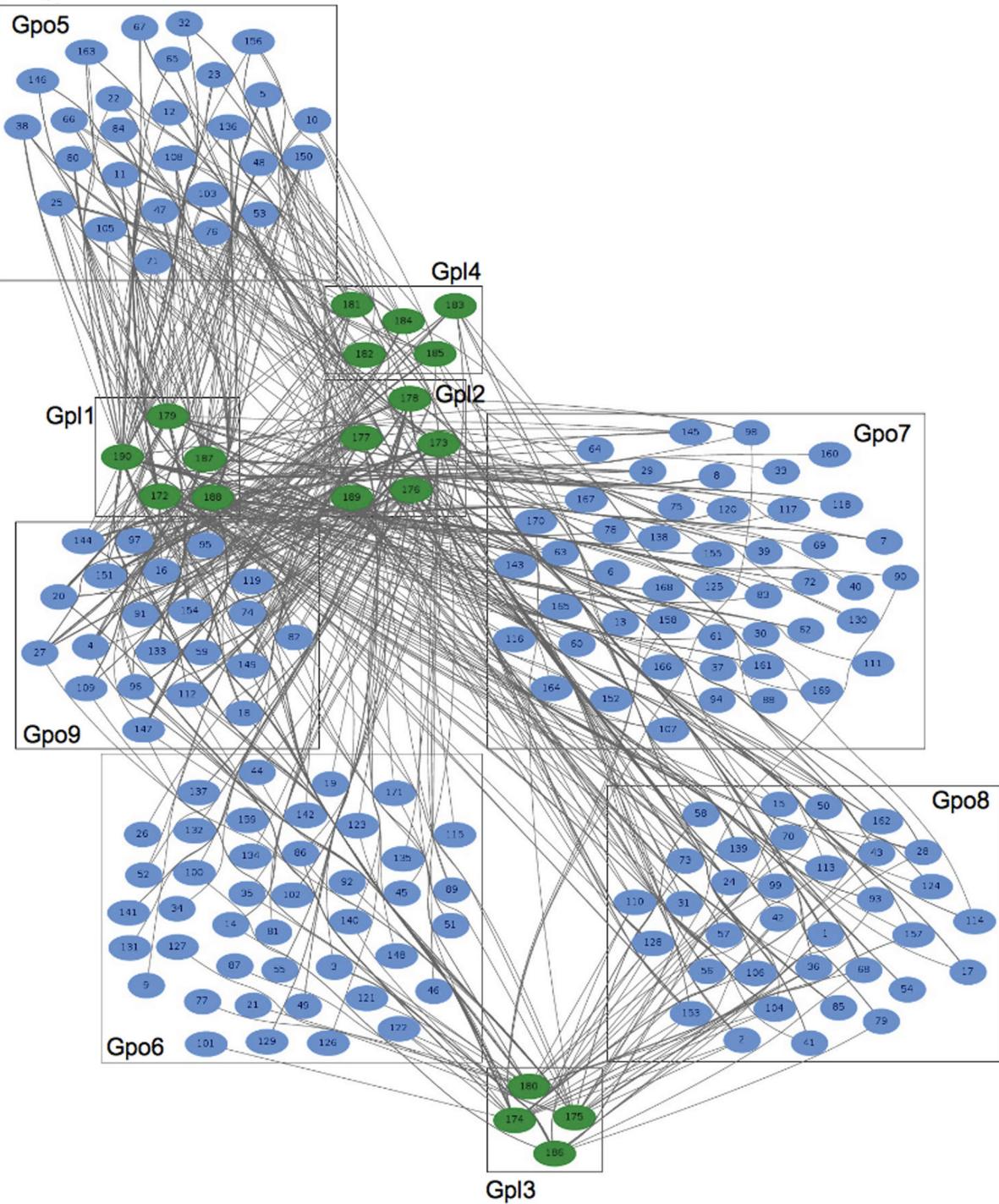


Figure 1. Compartmentalization in the Garraf pollination network using (a) unipartite modularity, and (b) group model. Nodes represent species, pollinators in blue, plants in green. Lines between nodes represent links between species. Compartments are contained within boxes.

Discussion

Bipartite modularity could not divide our pollination network into modules, likely a consequence of the high connectivity among compartments. In bipartite modularity, compartments are determined based on proportions of unique versus shared partners of plants or of pollinators.

However, the Garraf network is highly connected (connectance 25% compared to 4–9% in similar-sized matrices reviewed by Jordano et al. 2006), strongly nested ($N_T = 0.77$, NODF = 44.9; both significant at $p < 0.001$; Guimarães and Guimarães 2006, Almeida-Neto et al. 2007), and as shown by both unipartite modularity and group model, includes a series of pollinator species with

Table 1. Number of species shared by the various unipartite modularity and group model compartments.

Unipartite modularity	Group model				
	Gpl1 (5 species)	Gpl2 (5 species)	Gpl3 (4 species)	Gpl4 (5 species)	
Plants					
Mpl1 (5 species)	5	—	—	—	
Mpl2 (2 species)	—	2	—	—	
Mpl3 (8 species)	—	3	4	1	
Mpl4 (4 species)	—	—	—	4	
	Gpo5 (27 species)	Gpo6 (47 species)	Gpo7 (34 species)	Gpo8 (42 species)	Gpo9 (21 species)
Pollinators					
Mpo1 (67 species)	21	42	—	1	2
Mpo2 (28 species)	2	4	13	8	1
Mpo3 (60 species)	—	—	27	21	13
Mpo4 (16 species)	4	1	2	4	6

long activity periods, that connect effectively the various compartments (Bosch et al. 2009). By sequentially interacting with different species with short phenophases that would otherwise not share partners, connector species lower the ratio of unique versus shared partners, hindering the detection of compartments by bipartite modularity. Unipartite modularity, on the other hand, was able to define compartments in spite of the high connectance of our system because it uses a less restrictive criterion which focuses on areas of the network with contrasting link densities. An alternative approach to bipartite modularity (besides group model) would be to project the network into two unipartite subnetworks (one composed of plants and the other of pollinators, in which two pollinators are linked if they share visitation with at least one plant species, and vice versa for plants). Then, compartmentalization could be analyzed for both subnetworks using unipartite modularity. However, this approach would result in loss of information, such as the size of the original compartments, and the number of partners shared (in unweighted projections; Guimerà et al. 2007).

Unipartite modularity and group model differentiated compartments in our pollination network. UM divided our network into four modules. In a meta-analysis exploring unipartite modularity in pollination networks by Olesen and colleagues (2007) networks of similar number of species to ours (five networks of size 182–209 species) presented a higher number of modules (6–11). Group model differentiated four plant and five pollinator groups in our pollination network. Food webs analyzed with GM show similar numbers of groups to our study (6–13) despite being composed of a lower number of species (25–85 species; Allesina and Pascual 2009). For plants, modules and groups in our network showed similar species composition, but less so for pollinators.

When characterized using species attributes, modules and groups in our network showed strong similarities, but also some important differences. With both approaches, phenology differed significantly among compartments. Our community is characterized by staggered phenophases, shorter than the overall flowering period of the community (Martín González 2010), a pattern typical of

Table 2. Results of the non-parametric ANOVA and non-parametric MANOVA (for pollinator spectra) tests among compartments of various plant and pollinator attributes related to pollination syndromes, phenology, abundance and connectivity.

		Unipartite		Group model	
		χ^2	p	χ^2	p
Pollination syndromes					
	corolla length	9.98	0.019	7.66	0.054
	nectar production	2.27	0.518	1.99	0.576
	pollen production	9.82	0.020	1.20	0.753
	F			F	
	pollinator spectra		3.16	<0.001	2.48
					0.003
Phenology					
plants	beginning of blooming period	10.12	0.017	10.37	0.016
	duration of blooming period	4.51	0.211	7.34	0.062
pollinators	beginning of activity period	67.47	<0.001	98.92	<0.001
	duration of activity period	7.90	0.048	84.03	<0.001
Abundance					
plants		4.28	0.232	7.18	0.066
pollinators		2.61	0.456	46.50	<0.001
Connectivity					
plants	degree	11.81	0.008	14.74	0.002
	betweenness centrality	9.07	0.028	12.75	0.005
pollinators	degree	10.59	0.014	139.22	<0.001
	betweenness centrality	10.29	0.016	135.53	<0.001

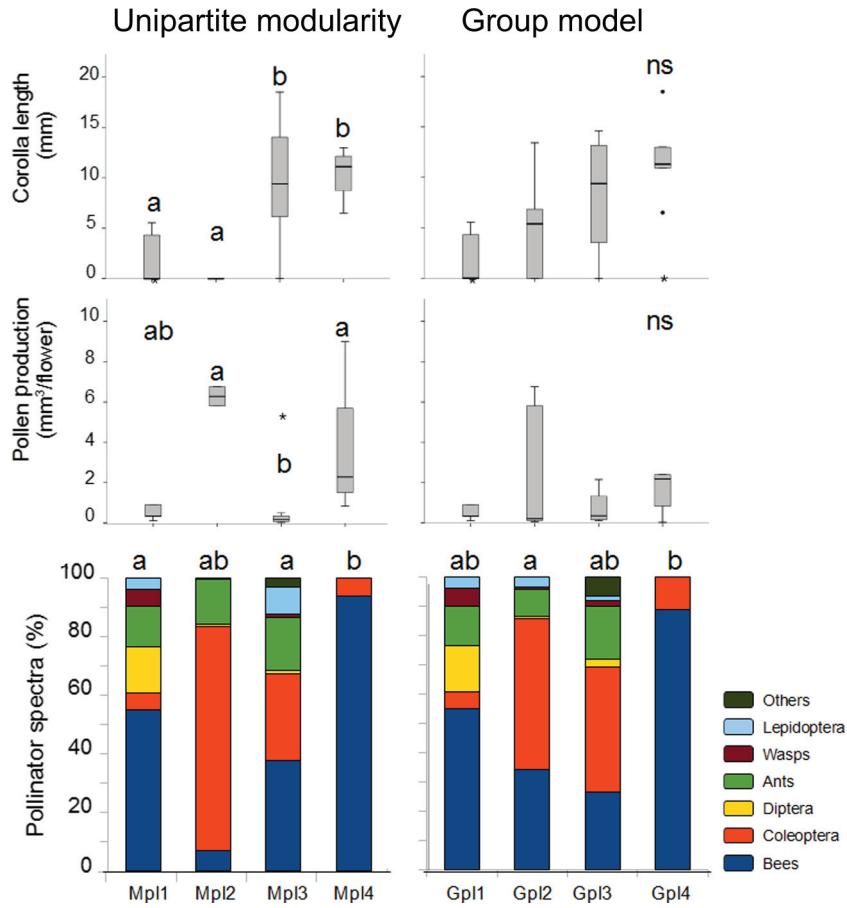


Figure 2. Box plots of corolla length, pollen production and pollinator spectra in compartments obtained with unipartite modularity and group model. Boxes in box plots indicate the 75th, 50th and 25th percentiles, and whiskers indicate the highest and lowest values within 1.5 times the interquartile range. Outliers (1.5–3 times the interquartile range) are represented by circles, and extreme values (>3 times the interquartile range) are represented by asterisks. Pollinator spectra are shown as the median value of the number of visits by each pollinator functional group to plant species in each compartment. Different letters indicate significant differences in post hoc comparisons. ns: non-significant.

Mediterranean plant–pollinator communities (Herrera 1988, Arroyo 1990, Bosch et al. 1997). For this reason, an important fraction of potential interactions cannot occur due to lack of temporal overlap of species pairs (Basilio et al. 2006, Kaiser-Bunbury et al. 2009, Fründ et al. 2010, Olesen et al. 2010), thus restricting species connectivity patterns and contributing to the observed compartmentalization.

Both UM and GM compartments could also be characterized according to their degree (a crude measure of specialization). Differences between compartments in species degree can be partly attributed to the positive correlation between degree and duration of blooming/activity periods (plants: $r = 0.52$; $p < 0.01$; pollinators: $r = 0.78$; $p > 0.01$), a relationship reported also in other communities (Olesen et al. 2008, Kallimanis et al. 2009). Species with longer phenophases have a higher frequency of interaction and a higher probability of interacting with many partners. Degree appeared as a strong determinant of compartmentalization, with stronger differences between compartments and significantly higher within-compartment homogeneity in groups than in modules. This is because, as opposed to the UM algorithm, the GM algorithm places species in the same group when they share a high number of common species

regardless of whether these belong to one or more groups (Newman and Girvan 2004, Guimerà and Amaral 2005a, b, Allesina and Pascual 2009, Guimerà et al. 2010). For instance, the modularity function places specialist pollinators in the same module as their main host plants but, when networks are highly nested, these plants are also visited by highly connected pollinators (Bascompte et al. 2003, 2006). Thus, in modules, specialists and generalists are placed together, hence showing a higher heterogeneity in species degree. By contrast, in GM specialists and generalists are grouped separately because, although they may have some common partners, generalists interact with many other species, thus showing a different interaction pattern. Thus, at least in highly nested bipartite networks, the GM algorithm will result in more distinct compartments than unipartite modularity.

Both modules and groups differed strongly in BC. Highly connected species usually have a central role in pollination networks (Martín González et al. 2010), our community shows a particularly high correlation between degree and BC (plants: $r = 0.94$; pollinators: $r = 0.93$; both $p < 0.001$). This high correlation is indicative of high connectivity among compartments (Martín González et al. 2010). This

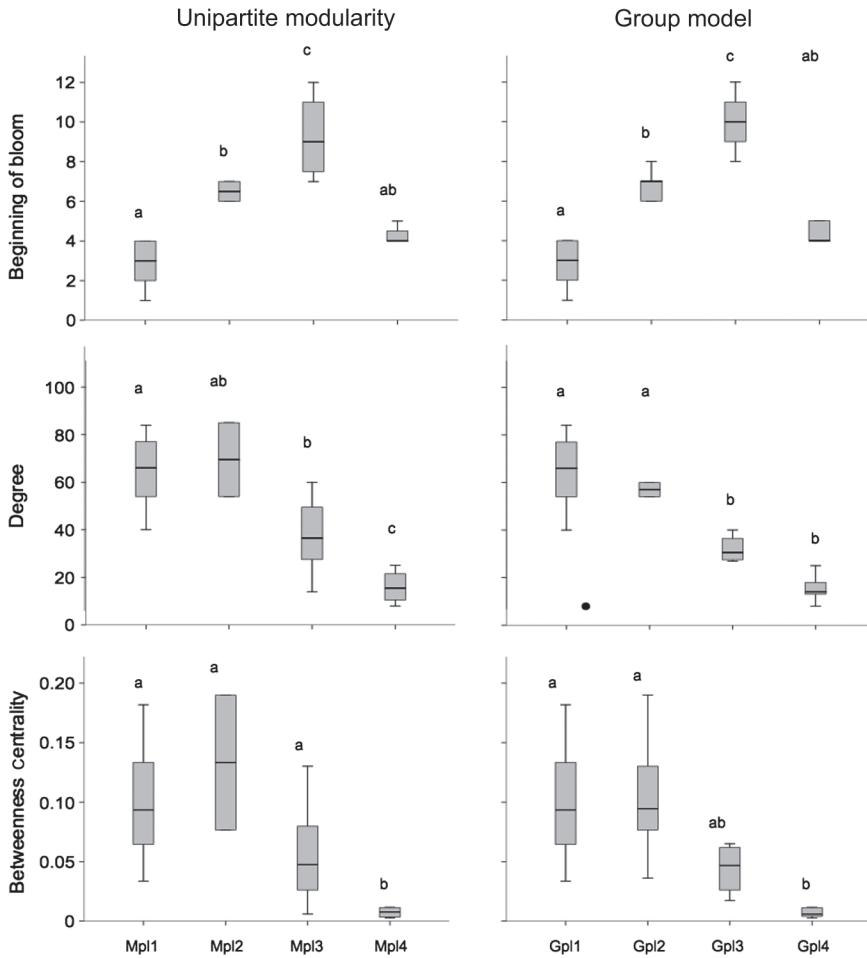


Figure 3. Box plots of beginning of bloom, degree and betweenness centrality in plant compartments obtained with unipartite modularity and group model. Boxes in box plots indicate the 75th, 50th and 25th percentiles, and whiskers indicate the highest and lowest values within 1.5 times the interquartile range. Outliers (1.5–3 times the interquartile range) are represented by circles, and extreme values (>3 times the interquartile range) are represented by asterisks. Different letters indicate significant differences in post hoc comparisons. ns: non-significant.

result is again related to species phenology because connector species were pollinators (mostly bees) with activity periods covering most of the season. No plants had such a connecting role (despite their, on average, higher degree and BC) due to their shorter blooming periods. Thus, in our community, pollinators provide cohesiveness to the network by interacting with successively blooming plants and ‘glueing’ the community together.

Whereas modules and groups were highly coincidental based on phenological and connectivity attributes, they showed important differences when characterized in terms of abundance and pollination syndrome-related features. Differences in species abundance were apparent in groups (highly significant for pollinators, narrowly non-significant for plants), but not in modules. This difference is again consequence of the different properties of the compartment-searching algorithms. Generalist species tend to be highly abundant whereas specialists are usually rare species, with a significant relationship between species degree and abundance (plants: $r = 0.53$; pollinators: $r = 0.34$; both $p < 0.01$). This relationship has also been reported in other networks, and is thought to be a consequence of the higher

frequency of interaction of abundant species (Vázquez and Aizen 2003, Vázquez et al. 2009). As stated previously, in nested networks specialist/rare species interact with subsets of the interaction partners of more generalist/abundant species. By focusing on shared interaction partners, UM places abundant and rare species within the same module (Guimerà and Amaral 2005a, b, Olesen et al. 2007), thus masking differences in abundance among modules.

The validity and universality of pollination syndromes has been strongly questioned based on the high levels of generalization observed in plant–pollinator interactions (Waser et al. 1996), and to the fact that most pollination systems do not conform to established syndromes (Ollerton et al. 2009). However, previous studies examining compartmentalization in pollination networks (using ordination methods, Dicks et al. 2002; or UM, Olesen et al. 2008, Dupont and Olesen 2009, Danieli-Silva et al. 2012), emphasize the resemblance between compartments and pollination syndromes. In our network, syndrome-related features appear as important determinants of compartmentalization, particularly when using UM. Corolla length and pollen production, but not nectar production, differed

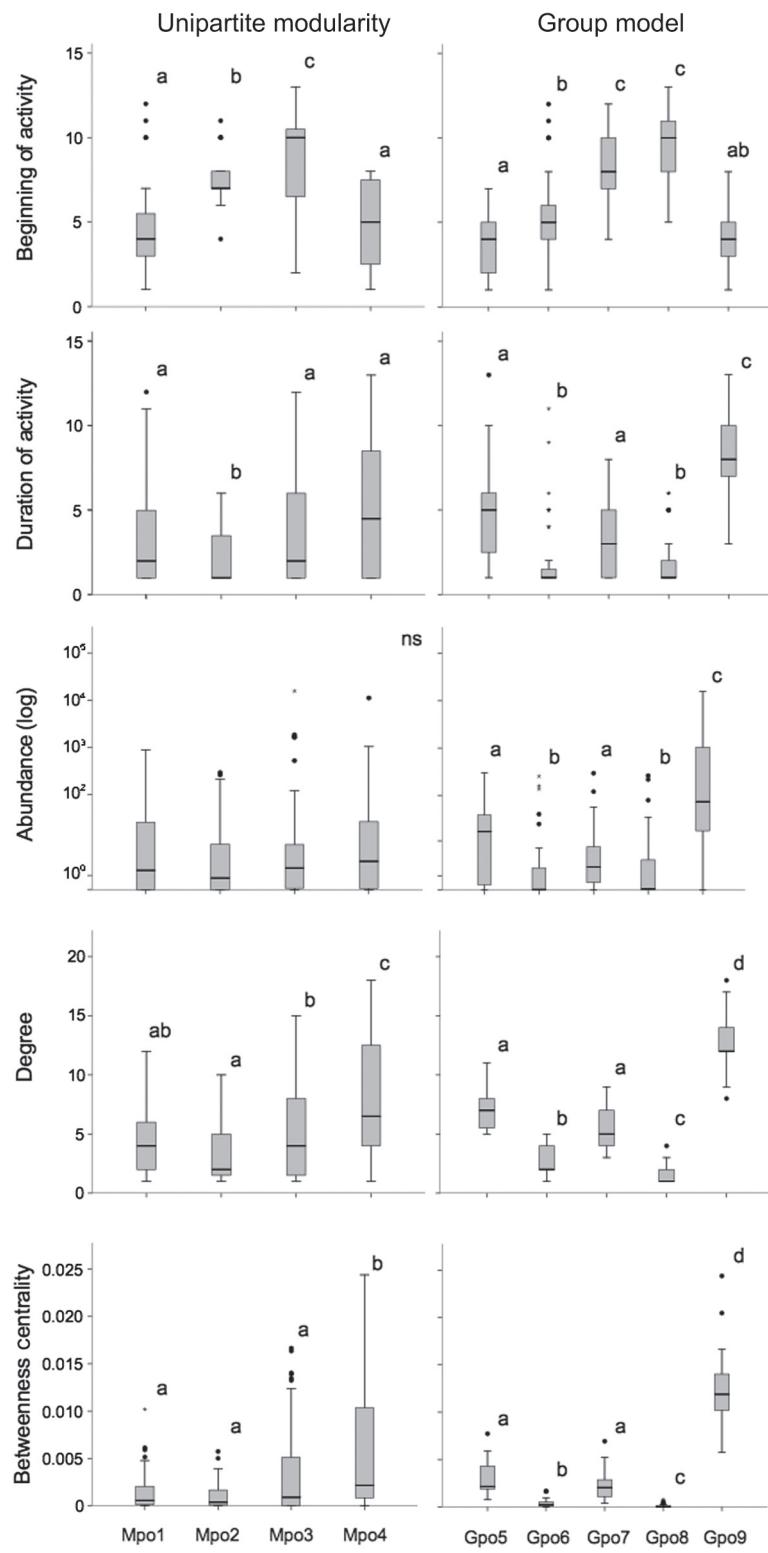


Figure 4. Box plots of beginning of activity, duration of activity period, abundance, degree and betweenness centrality in pollinator compartments obtained with unipartite modularity and group model. Boxes in box plots indicate the 75th, 50th and 25th percentiles, and whiskers indicate the highest and lowest values within 1.5 times the interquartile range. Outliers (1.5–3 times the interquartile range) are represented by circles, and extreme values (> 3 times the interquartile range) are represented by asterisks. Different letters indicate significant differences in post hoc comparisons. ns: non-significant.

among modules. However, the reciprocity between plant features and pollinator visitation was not consistent in all compartments. For instance, short corollas were coupled with a high visitation by beetles in Mpl2, but beetles performed almost no visits to Mpl1 plants, which also had short corollas. Similarly, high pollen production was coupled with high visitation by bees in Mpl2 and beetles in Mpl4 (two pollinator groups with high pollen requirements; Proctor et al. 1996), but although Mpl3 had a significantly lower production of pollen, the visitation by bees and beetles was still high. Differences in pollinator spectra were significant in both modules and compartments, and in both cases a phenological pattern could be discerned, with the early-season compartment interacting mostly with bees and dipterans, an important irruption of beetles in the intermediate and late-season compartments, and a preponderance of bees in the connector module (Mpl4, Gpl4). This pattern of pollinator seasonality appears to be common to other Mediterranean communities (Herrera 1988, Bosch et al. 1997).

To our knowledge, this is the first time the group model is used to analyze the structure of a pollination network. Interestingly, compartments obtained with GM were very similar to those obtained with UM for plants, but not so much for pollinators. In spite of these differences, both approaches agree in highlighting phenology, and two related species attributes (degree and betweenness centrality) as factors strongly associated with compartmentalization. Although phenology has been previously proposed as an important determinant of species interaction pattern (Olesen et al. 2008, Kallimanis et al. 2009), previous pollination network studies (Olesen et al. 2007, Dupont and Olesen 2009, Danieli-Silva et al. 2012; but see Bosch et al. 2009) did not identify phenology as a major driver of compartmentalization. We expect phenology to be particularly important in strongly seasonal communities composed of species with short phenophases. Other factors influencing compartmentalization (abundance and floral attributes) are only apparent when using one of the two approaches. These discrepancies are noteworthy because the use of one algorithm or the other may condition results obtained in future studies investigating compartmentalization in bipartite networks. For example, GM may define clearer compartments in highly nested networks. We thus encourage the use of multiple compartmentalization detection algorithms. Of special relevance to network cohesiveness is the fact that both GM and UM found differences in connectivity among compartments, and identified a connector compartment composed of bee pollinators. Differences in connectivity imply that compartments differ in their importance for the flow of information across the network and in their contribution to network resilience. In general, disturbances within a compartment are unlikely to spread across the network (Guimerà and Amaral 2005a, b, Olesen et al. 2007, Tylianakis et al. 2010, Stouffer and Bascompte 2011), but in our network disturbances in the connector compartment are likely to spread rapidly to other compartments, which would then become more isolated, thus increasing the risk of fragmentation. How compartments relate to each other is, therefore, essential to understand network robustness.

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Appendix 1

Distribution of interactions among compartments, both for plant and pollinator species. Percent interactions is the proportion of interactions of plant compartments with each pollinator compartment (upper panels) and of pollinator compartments with each plant compartment (lower panels).

