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Understanding the Complex Structure of a Plant-Floral Visitor Network from Different Perspectives in Coastal Veracruz, Mexico

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Abstract

Our premise was to understand the basic structure of the flower-flower visitor community at La Mancha in Veracruz, Mexico. We used network analyses to study the structure of this community. In particular, to analyze, (1) if flower color and shape ("as a limited portion of the traditional floral syndromes definition") were linked to the arrival of certain floral visitors, (2) if visits to flowers were generalist, specific and/or modular; and (3) which plant species, if any, in the core of the network could affect the stability of floral visitors. In order to analyze the organization of the plant-floral visitor community, we prepared network graphics using Pajek, nestedness (as *NODF*) with Aninhado, and modularity with the *SA* algorithm. The network obtained was nested suggesting that generalist species (with the most associations) were interacting with specialists (with fewer associations). Furthermore, floral visitors (Hymenoptera, Diptera, Lepidoptera and Trochiilidae) did not exhibit a particular preference for a specific flower color or shape, each pollinator group visited most flowers/colors/shapes considered. The same was similar for all 14 resulting modules. As in other studies, we suggest that pollination leans to generalization rather than to specialization. We suggest that maybe seasonality/food resource could be the factors to analyze as the next step in floral visits which may be the answer to modularity in this seasonal ecosystem.

Introduction

Many interspecific interactions have been considered mutalisms, which in turn influence species' fitness and community organization (Thompson, 1999; Rico-Gray, 2001; Kothamasi et al., 2010). For instance, pollination and seed dispersal by animals, and ant-plant mutualisms, are key ecological processes in many biological communities (Vázquez et al., 2009). Animal pollination is the basis of many terrestrial communities, without it many flowering plants could not reproduce, and without plants, most herbivorous and carnivorous animals would disappear (Faegri & van der Pijl, 1979; Ollerton et al., 2011; Burkle et al., 2013; Tylianakis, 2013). It is then of the utmost importance to understand the basic structure of communities now that ecosystems are being massively destroyed. Floral or pollination syndromes are sets of floral traits adapted to attract a certain subset of available

pollinators (Richards, 1997), and have provided some of the strongest support for pollinator driven floral evolution (Danieli-Silva et al., 2012; Hirota et al., 2012). However, they could be misused, such that without previous observations a person could judge or ascertain which type of pollinator visits a certain plant species. Faegri & van der Pijl (1979) published a synthesis of this information, and thus established a paradigm in pollination ecology, although several doubts have arisen over its use (Waser et al., 1996; Hingston & McQuillan, 2000; Gómez, 2002; Olesen et al., 2007; Ollerton et al., 2009). For instance, some authors do not perform close observations of plant floral visitors in the field (Ollerton et al., 2009), or that such characteristics have been used to indicate that pollination tends to specialization (Valdivia & Hermann, 2006; but see Waser et al., 1996). Even though a highly criticized view (Waser et al., 1996), some authors assume that specialization is the rule and generalization an

exception (Kothamasi et al., 2010). Although different studies discuss the existence of pollination syndromes (Hingston & McQuillan, 2000; Fenster et al., 2004; Valdivia & Hermann, 2009; Danieli-Silva et al., 2012), only a few consider communities instead of populations (Ollerton et al., 2009).

Here we present a community based analysis of the plant-floral visitor system present at La Mancha, on the coast of the state of Veracruz, Mexico. This is a seasonal environment (e.g.; Rico-Gray, 1993) where not all flowering plants produce flowers at the same time but rather in a sequence. For instance, not all flower colors and/or shapes are present all the time, thus flower visitors should visit available flowers. For example, Which flowers do hummingbirds visit when no red-tubular flowers are available? What type of color and shape of flower are preferred by the different flower visitors? Do the use of 'traditional flower (pollination) syndromes' help to organize associations in the community under study? (see Methods: data analyses).

For our community analysis we considered network metrics, such as nestedness, connectance, and niche overlap (Guimarães & Guimarães, 2006; Guimarães et al., 2006, 2007; Almeida-Neto et al., 2008; Dormann & Gruber, 2009; Díaz-Castelazo et al., 2010), a modularity analysis (SA algorithm) (Guimerà & Amaral, 2005a, b), a core-periphery analysis (UCINET) (Borgatti et al., 1999; Borgatti & Everett, 1999), and graphics (Pajek) (de Nooy et al., 2005). Although some of these metrics (e.g., nestedness, conecctance) may seem unrelated to a pollination/pollination syndrome analysis, they do serve to characterize the community under study. In particular we were interested to determine (1) if flower color and shape ("as a limited part of the traditional floral syndromes definition") were linked to the arrival of certain floral visitors, (2) if visits to flowers were generalistic, specific and/ or modular; and (3) which plant species, if any, in the core of the network could affect the stability of floral visitors.

Materials and Methods

Study site

Field work was carried out at Centro de Investigaciones Costeras La Mancha (CICOLMA), located on the coast of the state of Veracruz, Mexico (19º 36' N, 96º 22' W; elevation < 100 m). The climate is warm and sub-humid; a rainy season occurs between June and September, total annual precipitation is ca. 1500 mm and mean annual temperature is 22º-26ºC (Soto & García, 1989). The major vegetation types are tropical dry and deciduous forests (with *Bursera simaruba* (L.) Sarg., *Cedrela odorata* L., *Cnidoscolus herbaceus* (L.) I. M. Johnston*, Enterolobium cyclocarpum* (Jacq.) Griseb.), sand dune vegetation (with *Ipomoea pes-caprae* (L.) R. Br., *Canavalia rosea* (Sw.) DC., *Chamaecrista chamaecristoides* (Colladon) Greene, *Macroptilium atropurpureum* (Sessé et Mociño) Urban), mangrove forest (with *Rhizophora mangle* L., *Lagun-*

cularia racemosa L., *Avicennia germinans* L.), freshwater marsh (with *Typha domingensis* L.), and flooded deciduous forest (with *Annona glabra* L., *Pachira aquatica* Aubl. surrounding a freshwater lagoon) (Castillo-Campos & Medina, 2000; Moreno-Casasola, 2006).

To determine the associations among plants and their floral visitors (or potential pollinators), field work was done during five days per month between March 2007 and March 2008. We based sampling time in the size of the field station (64 ha) and the high variation within that area, which makes movements station relatively easy and fast. All observations were done walking along pre-established trails that covered the different vegetation associations present in the field station and surrounding area (Rico-Gray, 1993; Díaz-Castelazo et al., 2010, 2013), in periods of 15-20 min, between 08:00 and 16:00. We noted which plant species' were flowering at the time and which animals were visiting them. An observation was registered as an interaction when a visitor (insect or bird) was seen feeding off a flower in a way that its behavior allowed for body to touch floral reproductive structures (stigma, anthers). To minimize weather effects, observations were not done during rain or strong windy periods.

A limited number of plant samples were collected for identification at XAL herbarium of Instituto de Ecología, A.C. (INECOL) in Xalapa, Veracruz, Mexico, we also used published floras (for instance, Flora de Veracruz). Insect material was collected using nets and identified at INECOL using the IEXA collection. Hummingbirds were identified by sight only. As CICOLMA is a restricted area for collection, we based our identifications on voucher specimens already deposited either in XAL or IEXA. Furthermore, as this is a very seasonal environment, we considered that between-years comparisons may not be adequate since inter-year variations could render different results (Rico-Gray et al., 2012).

Data analysis

Data was organized using an Excel spreadsheet (Microsoft®). Network graphics were done using Pajek (de Nooy et al., 2005). Graphs helped to visualize the associations among nodes of two different (A, animals and P, plants) interactive (R) groups (Jordano et al., 2003, 2006), such that R = r A x P, where r = 0 when no interactions is present between animal species *i* and plant species *j*, or = 1 when an interaction is present. Adjacency Matrix 'R' will be composed by 'A + P' nodes or species and *k* interactions or links (Jordano et al., 2006).

A nestedness analysis (*NODF* index - see Almeida-Netoel al., 2008) was done using Aninhado (Guimarães & Guimarães, 2006; www.guimaraes.bio.br). To determine if the degree of nestedness is higher than expected by chance alone, we compared the nestedness value of our network to 1,000 randomizations generated by null model II (Díaz-Castelazo et al., 2010). In this null model, the probability of an

interaction occurring is proportional to the level of generalization (mean number of interactions) of plant and animal species (Bascompte et al., 2003). This allowed us to assess whether the value of *NODF* observed in the empirical network was higher than expected for networks of equal size and with similar heterogeneity in interactions among species.

Niche overlap and connectance were analyzed using R-bipartite (Dormann & Gruber, 2009). Niche overlap was calculated using the mean similarity in interaction pattern between species *i* and *k* in both trophic levels (plants and plant-visitors*)* through

Connectance (C) is the proportion of possible interactions that are actually carried out within a network (Jordano, 1987; Olesen & Jordano, 2002).

Modularity index (*M*) was done using the *SA* algorithm (Guimerà et al., 2004; Guimerà & Amaral, 2005) to estimate the degree in which groups of species (animal and plants) interact more among each other than with other species in subgroups in the network. This analysis was based on a matrix using the following flower characteristics: flower symmetry (zygomorphic or actinomorphic), petals free or sympetalous, corolla tubular or not, and main flower color. The number of species sampled per flower color were: white 28 species, white/green 1, white/yellow 2, orange/yellow 2, yellow 19, pink 4, dark pink 1, lilac 9, lilac/white 1, beige 7, green/beige 1, green 3, red 5, burgundy 1, orange 1,purple 1, red/orange 1 specie. The above, of course, is a limited view of floral (pollination) syndromes, since (1) some of those characters may at times be correlated, and (2) it leaves out several traits that could be important, e.g., flower size, nectar characteristics or scent type.

The software used is based on a heuristic process in order to find an optimum solution for the modularity function. The *M* index vary from 0 (extreme generalization) to 1.0 (extreme number of compartments) and decreases when the fraction of links among modules increases in the total network. High values of *M* indicate that different animal and plant species form modules that are semi-independent from other modules (Rezende et al., 2009). To assess the significance of network modularity observed, we compared the obtained modularity value to 100 simulated networks generated by a null model (null model II) that have equal size and with similar heterogeneity in interactions among species as the original network. After the first run, three modules were chosen at random within them one pair of species was also chosen at random, since there were three modules, we then established three pairs of species A, B, and C (each having a plant and an animal). To assess that our results were accurate, the algorithm was repeated 15 times (heuristic process) and we 'followed' the pair of species checking for possible module changes during the other 14 randomizations (Rezende et al., 2009). The resulting *SA* modularity index *M* is a degree measure where a network is organized in modules with defined boundaries. Also, to test if links within modules were orga-

nized in a nested pattern, we performed nestedness (*NODF*) analyses for those modules with links among four or more species (nine out of 14 modules) (also see Dáttilo 2012; Dáttilo et al. 2013).

Finally, analyses of species as core or peripheral components of the network were performed with UCINET for Windows 6.0 (Borgatti et al., 1999; Analytic Technologies Inc.; http://www.analytictech.com/downloaduc6.htm), which performs categorical core/periphery analysis for bipartite graphs (Borgatti et al., 1999; Borgatti & Everett, 1999). The core-periphery analysis is based on stochastic optimization processes, thus we performed 20 randomizations, obtaining the proportion of occurrences of a species within the core or the periphery for the entire set of randomizations. We obtained the flowering periods (months) for these species.
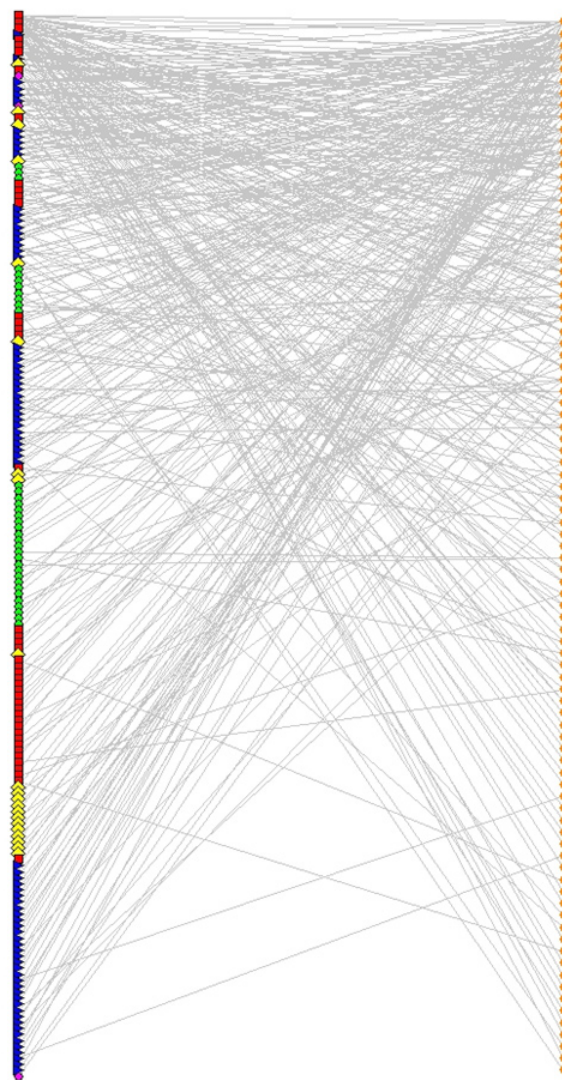

Figure 1. Bipartite graph of a plant-flower visitor interaction network at La Mancha, Veracruz, Mexico recorded from March 2007 to March 2008. Nodes on the left correspond to flower visitors, whereas nodes on the right to plant species. Lines ("links") connect interacting species. Color code: orange = plants, red = butterflies (Lepidoptera), yellow = wasps (Hymenoptera), pink = hummingbirds (Trochiilidae, green = flies (Diptera).

Results

We registered 392 interactions involving 89 plant species (there are more plant species in the station, for instance, wind-pollinated species) and 177 animal species [e.g., 29 flies (Diptera), 73 butterflies (Lepidoptera), 62 bees and wasps (Hymenoptera), and three hummingbirds (Trochilidae)] (Appendices 1 and 2). The interaction matrix consisted of 266 species (Fig. 1). The resulting network was significantly nested ($NODF = 3.99$, $p < 0.01$), and had a connectance of 0.02. Niche overlap was 0.05 for plant species, whereas 0.04 for floral visitors.

The modularity analysis produced 14 modules, grouped according to the pattern of interactions (Fig. 2). Five of these were not linked to other modules and contained less than four species, therefore were not used in nestedness analyses. This result shows that animal species were not associated to a given floral pattern within a module. Moreover, a module may consist of different flower shapes and colors. Similarly, animals within a module belong to different orders. The network was significantly modular (SA algorithm, $M = 0.636$, $P < 0.0001$, $n = 100$). The three pairs of species selected to follow within modules offered different results, pair 'A' was present in a module 100% of the program randomizations, pair 'B' was present in 27% of the randomizations, and pair 'C' was present in 80% of the randomizations. Different results were obtained

(heuristic program), and every time the program is run slight differences may be obtained, these results allow for a 69% of accuracy, considering that we used 21% out of the 14 modules. If we had "followed" a higher number of species our percentage of accuracy would have probably been greater. Five of the 14 modules contained nine core plant species (*Bahunia divaricata*, *Bidens pilosa*, *Randia laetevirens*, *Turnera ulmifolia*, *Lantana camara*, *Waltheria indica*, *Cynanchum* sp., *Tecoma stans*, *Piscidia piscipula*) (Table 1), and within each module they were highly linked to different animal species. Even though not simultaneously (rather one after the other), these nine species shared flowering during the 10 months of observations, offering permanent food resource. Bees were the most common animals within modules. Of which four species were present in the core of the network, *Apis mellifera, Lasioglossum* sp*., Trigona nigra* and *Euglossa viridissima*. When the nine modules were individually analyzed for nestedness, only one was significantly nested ($NODF = 20.92$, $p < 0.01$).

Discussion

Our results show a low degree of niche overlap (for both plants and visiting animal species in the network), high modularity (14 modules), low connectance, and significant nestedness. Within modules we found flowers of different
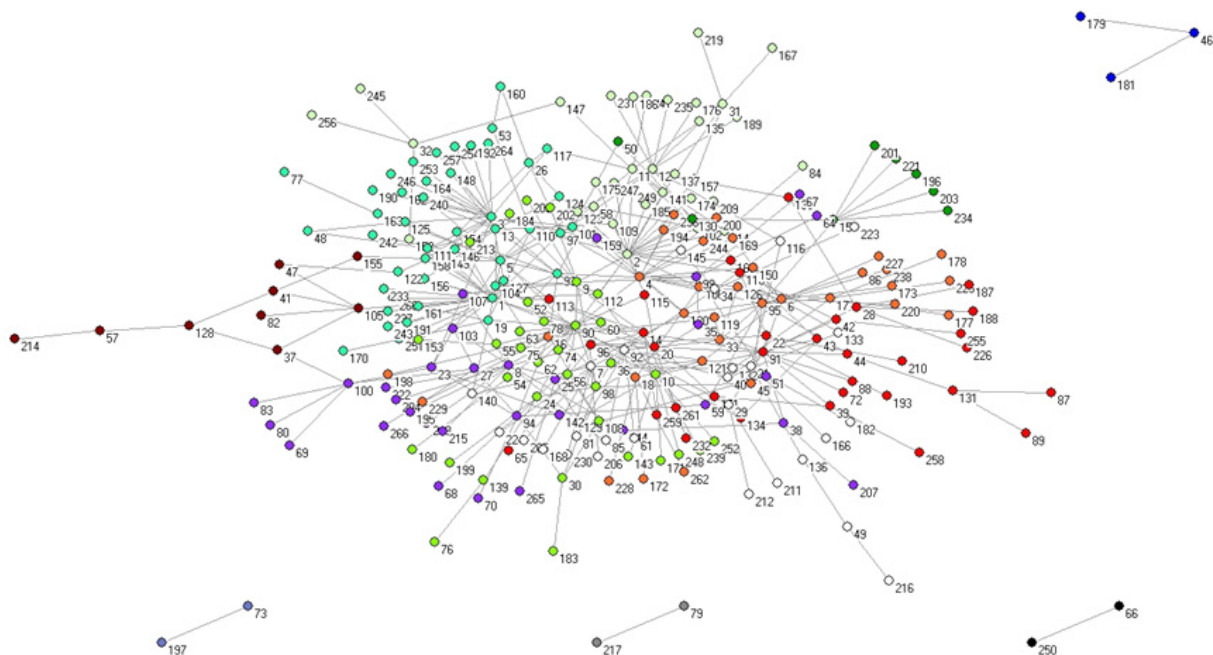

Figure 2. Network showing the modularity of a plant-flower visitor interaction network at La Mancha, Veracruz, Mexico. Each module has a different color (N= 14 modules/colors). Each circle represents one plant or visitor species and is colored according to the color of its module. Lines represent plant-visitor interactions. The majority of these modules are over-represented except for five of them that are formed only by two or three species. Moreover, no module was exclusively represented by a particular group of colors or shape of flowers or any guild of plant-visitor, indicating that floral visitors did not exhibited flower preference in this study.

colors and shapes, as well as a variety of visiting animals. The results of the core-periphery analysis show four core bee species (social or solitary bees) having the most interactions or links, suggesting they are super-generalist species. Only one of the selected nine modules for nestedness analyses was indeed significantly nested. Nine plant species constituted the core of the networks (Table 1). Thus, visitors obtain floral resources from core plants (the most visited) in different seasons, suggesting that modules may not be built around syndromes but instead because visitors need food they search and forage throughout the year.

Table 1. Core of generalist plants species in the network and their flowering periods (based on XAL herbarium specimens). P_p = position of plant in the ordered matrix for nestedness.

Species / Months	P_p	J	D	N	O	S	A	Jl	Jn	My	Ap
Bahuinia divaricata L.	1									X	
Bidens pilosa L.	2			X	X						
Randia laetevirens Standl.	3								X		X
Turnera (ulmifolia L.) *velutina* Presl	4								X	X	
Lantana camara L.	5					X	X			X	
Waltheria indica L.	6				X			X	X		
Cynanchum sp.	12				X						
Tecoma stans (L.) Juss. ex Kunth	8	X	X	X	X						
Piscidia piscipula (L.) Sarg.	6	X									

Our results show low niche overlap for both groups (plants, animals), suggesting that each trophic level interacts with a different subset as its counterpart, which supports the high modularity result, and suggests that the same species' were the niche of one and the other. The local level of species richness affects both the individuals and their interactions. If tropical habitats are species saturated, high species density should increase competition among them, reduce niche overlap and cause that these species should be more specialized in the long-run (Olesen & Jordano, 2002). Although this may not be necessarily true due to flower color and shape, but it could be the result of competition for feeding resources (nectar, pollen). Furthermore, the latter does not mean that forbidden interactions do not exist or were dismissed, different phenotypes could result from adaptation, neutral evolution and/or phylogenetic constraints, and these can influence mutualistic interactions (Vázquez et al., 2009). The low overlap for flower visitors in our results (0.04) could also suggest the existence of competition, territoriality or very different feeding requirements. Whereas the low overlap in plant species (0.05) is possible since visits were differential and there was no simultaneous overload to certain flower characteristics, supporting network modularity.

That the network was significantly nested suggests that specialist species (those species with the least associations or links) were interacting with the generalists (those species with the most associations or links), and generalist species

were interacting among them, influenced by the existence of super-generalist species. This suggests generalization among animal species, also supported by the idea that abundance of certain species affects the network's nested pattern (Vázquez et al., 2009, Lange et al. 2013): mutualism in these species could be facultative. Moreover, a nested structure could also be generated by abundance, spatial distribution and/or similar ecological processes, which can be expressed along a variety of temporal and/or spatial scales (Lewinsohn & Prado, 2006). All these may suggest that nestedness is not always the result of a coevolutionary process (Kothamasi et al., 2010), as referred to many times in the past for flower-flower visitor interactions. Furthermore, bees have been considered as common in low-latitude regions (Olesen & Jordano, 2002) and indeed they were the most common visitor in our study site. Our results also suggest that bees were consistent in their visits throughout the day, which differs from the behavior of other animals (Baldock et al., 2011). Another consideration is the thin line between parasitism and the socalled facultative mutualists, which could easily cross it and become parasites if a floral visitor does not offer a reward to the plant, again exhibiting a tendency to generalization is some species (i.e., visit many species - have many links). Certain studies suggest extensive generalization as the rule (Waser et al., 1996) rather than the exception (Olesen & Jordano, 2002), which in turn may trigger an increase in biodiversity as a consequence of plants and flower visitors searching for generalization among their mutualistic counterparts (Kothamasi et al., 2010).

Furthermore, generalization could result from competition among flower visitors. When these are removed or displaced by competitors from preferred flower species, they have the option of returning after visits to alternative plants in bloom, thus the latter species benefit from displaced visitors (Kothamasi et al., 2010), contributing to community coexistence and diversity. For instance, large pollination networks have modules whereas small networks do not, such that connectance could be the basis, modularity a complement of nestedness, and generalist species the glue between modules (Bascompte & Jordano, 2007). If connectance increases, the generalist core of species also increases and instead of a few species being the glue between modules these should disappear (Bascompte & Jordano, 2007). These authors, using data from different geographical areas and mostly collected in only one season and in different habitats, found that the biological contents of those modules tend to correspond to certain floral syndromes (Bascompte & Jordano, 2007). Our data, however, was obtained from only one seasonal tropical community, exhibiting a long dry period (ca. 6-7 months), intermixed in a winter with cool strong northern winds (cold fronts or 'nortes'), a short wet season (4-5 months), and many coexisting species. Furthermore, these analyses differ in purpose, Olesen and collaborators (2007) were searching in different networks for the presence of modules, and not to understand why these modules were present.

If interactions were highly generalist then why have modules? Our results suggest that species within modules

may not comply with the 'established rules' of floral syndromes, and other factors prevail. For instance, (1) competition, where some individuals are temporally displaced towards other flowers; (2) time of day (when observations were done), since plants vary throughout the day in the quantities of nectar and/or pollen offered (Baldock et al., 2011); (3) plants could have nectar guides, suggesting special attractiveness for bees (Free, 1970), or (4) have the correct phenology (available for any visitor). Any structure forming compartments results from constraints of hosts and their visiting fauna (Lewinsonh & Prado, 2006). Phenology is a very important constraint, since there is no way an interaction can exist if the two organisms do not have similar phenologies (Jordano et al., 2003). Not all links among flowers and visiting animals happen at the same time, and the impact of some of these interactions critically depend on time, which, on the other hand, allows for visits by other animals (even within a single day), e.g. shared-pollinators (Baldock et al., 2011). Lewinsohn and Prado (2006) suggest the existence of mixed networks, i.e. nested compartments, although a nested network with compartments is not possible (Lewinsohn & Prado, 2006). Our results suggest, however, a nested network with compartments, which may be possible if we consider the effect of temporal variation in the community (seasonality). Moreover, the above studies were done under a variety of environmental conditions, which could be the answer to differences in results.

The low connectance value obtained for our network supports the modularity analyses, indicating that not all possible interactions or links were enabled in the community. In pollination networks in general, connectance increases while network size decreases (Olesen & Jordano, 2002). What happens then with modularity? Each analyzed module was very cohesive, whereas the opposite was obtained between modules. Suggesting that species within a module were strongly interacting, while they were weakly interacting with species in other modules (Jordano et al., 2006); this could explain the high modularity of the network. Another explanation for the high modularity and nestedness values could be the super-generalist status of bee species in the network, also a common feature in modules. Such 'specialization' suggested by our results could very well be the result of a phenological spatio-temporal synchronization of plants in modules, which is also supported by a lack of nestedness in practically all modules. There really was no specialization within modules, which could simply suggest the possible existence of preferences for quality and/or quantity of flower nectar, competition or phenology. In general, modularity could be explained by a combination of seasonality (phenology) and resource quality.

Beyond constraints elicited by plants and directing us to flower syndromes (Bascompte, 2009), we suggest the importance of analyzing the temporal scale, which is probably the sole way to acknowledge what visitors do when preferred flowers are not available. When we review the flowering times of different species in the core of the network, they do not flower simultaneously rather they are distributed throughout the year. Thus visitors can obtain floral resources from core plants (the most visited) in different seasons, suggesting that modules may be built around syndromes because visitors need food dearly throughout the year. The latter suggests that pollination leans to generalization rather than to specialization.

Acknowledgments

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