



RESEARCH ARTICLE - BEES

Topological Structure of Plant-bee Networks in Four Mexican Environments

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Abstract

We analyzed the topological structure (e.g., links per species, connectance, core-periphery analyses, specialization, nestedness, modularity) of plant-bee interactions of four areas in Mexico. We used qualitative data (binary networks). Mexico exhibits a complex geography and community variation that can affect bee networks. Network architecture is variable within large spatial scales, thus our results should vary according to site characteristics (La Mancha and Totula in Veracruz, Carrillo Puerto in Quintana Roo, and the Tehuacan-Cuicatlan valley, in Puebla), type of vegetation, endemism, altitude, size of area sampled. Network topology varied among sites, and the presence of nested or modular patterns was analyzed for robustness to simulated species extinctions. The lowest species richness was recorded for the Quintana Roo site (15 plant, 25 bee species), and the highest for the Tehuacan-Cuicatlan valley site (88 plant, 231 bee species). There was a tendency to have more connected networks when species richness was low and networks with greater species richness had a higher number of interactions. The distribution of interactions differed between environments but not due to network size and all were significantly nested. The robustness to cumulative extinctions showed a different pattern at each site; the most robust network was at Carrillo Puerto, which also was the site with less species. Sites with more endemic species (e.g. Tehuacan) had more specialized interactions, and were more susceptible to extinction.

Introduction

One of many goals in ecology is to understand how different mechanisms shape ecological interactions within natural communities (Loreau et al., 2001; Dyer et al., 2010). Using a network approach several studies have described complex, hyper-diverse communities (Bascompte et al., 2003; Lewinsohn et al., 2006; Hagen et al., 2012; Bascompte & Jordano, 2014). Most studies have primarily focused on mutualistic interactions between plants and animals (mainly pollinators and seed dispersers) (e.g. Vázquez & Aizen 2004; Olesen et al., 2008; Dupont et al., 2009; Donatti et al., 2011; Mello et al., 2011). Furthermore, in tropical regions, reproduction (pollination, fruit and seed dispersal) of more than 90% of shrubs and trees depends on animals (e.g., insects, birds, bats) (Bascompte & Jordano, 2008).

Traditionally, plant-pollinator systems have been studied as small groups of species (Stephens et al., 2009; Santos et al., 2012). However, modern network tools allow simultaneous analysis of species over different spatial and/or temporal scales (Stephens et al., 2009; Lange et al., 2013). Such analysis allows the study of complex systems and mega-diverse communities (Jordano et al., 2009; Hagen et al., 2012). Although several communities defy analysis based on few, incomplete samples, as the behavior of the system is often very different from the sum of its parts (Jordano et al., 2009). For instance, when most interactions are not reached by a study, the 'system' remains, essentially, unknown. Nonetheless, the conservation and management of the studied communities, as well as of pollination services, can receive useful information through these efforts (Burkle & Alarcón, 2011).



Understanding the ecological and evolutionary causes and consequences of spatial and/or temporal variation in plant/floral visitor systems is very important when formulating basic and applied questions on the structure and function of a community, evolution of floral characteristics (e.g. Hernández-Yáñez et al., 2013), and development of optimal conservation strategies (e.g. Burkle & Alarcon, 2011). Although landscape heterogeneity may augment the number of interactive species, these may not constantly share the same habitat (Jordano et al., 2009; Clemente et al., 2013). For instance, Olesen and Jordano (2002) analyzed plant-pollinator networks from different geographical areas and found that interaction patterns co-varied with factors such as latitude, altitude and habitat isolation (islands). Also, plant species are more generalized (i.e. have more interactions) at higher latitude and in lowland habitats. In oceanic islands, for instance, networks are often specialized (i.e. have less interactions), pollinators are scarce, and a low proportion of animals exists, relative to plant species, which may add to the idea of higher specificity in the tropics that at higher latitudes (Olesen & Jordano 2002). Based on high species numbers and the abundance of certain species, bees are probably the insect group best-adapted to floral biology and flower visits. This group is essential for pollination and sexual reproduction of most flowering plants (including many cultivars) (Roubik, 1992; Michener, 2000). The latter is very important in terms of securing future food supplies (Deguines et al., 2014).

Specific studies (reviewed by Hagen et al., 2012) of plant-pollinator networks consider all floral visitors of different taxonomic groups (e.g. bees, flies, butterflies, beetles, wasps, birds, and bats), and have evaluated how different factors (biotic, abiotic) structure networks. However, despite the general growth of knowledge on network topology, little is known about how plant-floral visitor networks are structured and how they vary over space when only one taxonomic group is considered. Mexico exhibits a complex geography and community variation, both of which should affect plant-bee networks. Thus, network architecture (e.g. links per species, connectivity, core-periphery analyses, specialization, nestedness) is likely change within the country so that results should vary according to site characteristics (e.g. type of vegetation, endemism, altitude, size of area sampled). Here we describe the topological structure of plant-bee interactions in four distinct areas in Mexico. In particular, we searched for the presence of modular patterns and analyzed the pattern of secondary extinctions and stability of the networks in the range sampled.

Material and Methods

Study area and field work

Field work was accomplished in four Mexican sites: 1) Tehuacan-Cuicatlan valley, Puebla; 2) surroundings of Carrillo Puerto, Quintana Roo; 3) La Mancha, Veracruz; and 4) a traditional management coffee plantation in the montane forest in Totutla, Veracruz (Table 1). Due to the number of researchers involved, field work differed among sites, although entomological nets

were used throughout. The surveys in the Tehuacan and Totutla sites were guided by C. Vergara, the survey in Quintana Roo was guided by Villanueva and Roubick, and the survey at the La Mancha site was guided by N. Lara and V. Rico-Gray. The number of different areas per site was given by the vegetation changes (see Table 1). All accounts of visits by potential bee pollinators were determined by observations of bees on flowers and not from previous knowledge of the interactions.

In the Tehuacan-Cuicatlan valley the vegetation is a xerophytic shrubland (Rzedowski 1978), and Zavala-Hurtado (1982) described four vegetation types: shrubs with spines ('matorral espinoso'), tetechera, cardonal and izotal (*Yucca* spp.). Even though some of the vegetation types are in Spanish, the latter names are based on dominant plant species (see also Table 1). The biota of the valley is characterized by a high number of endemic species, the highest density known in Mexico (Méndez-Larios et al., 2004). Sampling was accomplished with monthly observations (3-5 days per visit) between July 1996 and June 1997. Five areas with similar plant composition were repeatedly surveyed (total area of site was 10,000 km²), which included the main vegetation associations and the border of agricultural fields. Plants with flowers were selected and bees were collected, killed and mounted the same day, and plants collected (see Vergara-Briceño, 1999). Bees and plant vouchers are deposited in the collection at Universidad de Las Americas.

In Carrillo Puerto, Quintana Roo field work was carried out in areas near the Carrillo Puerto-Valladolid highway and the road from Carrillo Puerto to Vigia Chico, which is within the Sian ka'an Biosphere Reserve, an area of a half million hectares (e.g. CIQRO, 1983). Five collecting sites were selected along a 48 km transect, which were visited every two months between June 2008 and September 2009. Bees were collected in each site within a 1 km radius, then killed, mounted and identified. Bees and plant vouchers are deposited in ECOSUR.

Two sites were sampled in the state of Veracruz: Centro de Investigaciones Costeras La Mancha (CICOLMA-La Mancha) and in the vicinity of Totutla.

At La Mancha, bees were collected monthly between March 2007 and March 2008 (five days per visit) along established trails that included different environmental types (see Rico-Gray, 1993). Bees and plants were collected, identified using the collections of Instituto de Ecología, A.C. (IEXA, XAL) and deposited in those collections.

The ranch "Finca El Mirador" is located in the vicinity of Totutla. Bees were collected every month in October-November 2005 and January through September 2006 in three sites within the ranch: El Desengaño, Loma Araucarias and Loma Ventura. A part of this site has been converted to an organic coffee plantation. Bees and plants were collected and plants were identified in XAL herbarium of Instituto de Ecología, A.C. and bees were identified by C. Vergara (UDLA-P), with the help of Terry Griswold (USDA Bee Laboratory, Logan UT, U.S.A.) and Michael Engel (Biodiversity Institute, University of Kansas, Lawrence, KS, U.S.A.). Plants and bees are deposited in C. Vergara's collection.

Table 1. Characteristics per site (García 1981; INEGI 1988; Valiente Banuet 1998; Diaz-Castelazo 2004; Castillo-Campos et al. 2006; Deloya et al. 2007). Also, see the methods section ("study sites and field work").

Site	Altitude (m)	Climate	Temperature °C	Precipitation (mm)	Vegetation
La Mancha 19° 36' N–96° 22' W	20	Warm subhumid with dry period, wet in summer, and a cold front season in winter	24-26	1500	Dune pioneers, sand dune scrub, tropical dry and deciduous forests, mangrove and fresh water swamps
Carrillo Puerto 19° 42' - 19° 25' N 87° 52' – 88° 06' W	30	Warm subhumid with summer rain	25.8	1158	Subdeciduous tropical forest and secondary vegetation
Tehuacan-Cuicatlan 18° 14' – 18° 22' N 97° 26' – 93° 34' W	600-3000	Warm subhumid, summer rain, marked dry period during summer rain	21	400	Scrubs with spines, columnar cacti associations, and <i>Yucca</i> sp. associations
Totutla 19° 12' N–90° 53' W	1010	Temperate, humid with summer rain, hardly any thermic oscillation	20	1825	Rustic coffee plantation, montane forest

Network analyses

The manner in which networks were sampled, only allows us to build binary (qualitative) networks. We defined each sampling site as an adjacency matrix C , in which C_{ij} represents the number of interactions between bee species i and plant species j (Bascompte et al., 2003). We then calculated the following metrics derived from the network theory to describe the bee-plant networks in each of the four sites (Tehuacan-Cuicatlan valley, Quintana Roo, La Mancha, and Totutla): links per species, connectance, network specialization, nestedness, modularity, and robustness to species extinction. We used these metrics mainly because they provide a way to describe the organization of our networks in a way that allows direct comparison with previous studies on plant-pollinator networks and among our four sites.

We calculated the average degree for bees and plants using the arithmetic means of degrees (number of interactions in which each species was involved) of all species. We calculated the (C) connectance, defined as the fraction of registered interactions with respect to the total number of possible interactions: $C = I / (B \times P)$ where, I is the total number of interactions observed, B is the number of bees species, and P is the number of plant species (Jordano, 1987). We calculated the degree of specialization (H_2') for each network (Blüthgen et al., 2006). The index ranges from zero (extreme generalization) to one (extreme specialization). The index is derived from the Shannon index (H' is not dependent on sample size), rare species are not equally presented by the index and is robust to changes in sampling intensity and the number of interacting species in the network (Poole, 1974; Blüthgen et al., 2006). We used the package bipartite (Dormann et al., 2009) in "R" to perform network-specialization analysis.

We used the NODF metric (Nestedness metric based on Overlap and Decreasing Fill) (Almeida-Neto et al., 2008) to estimate nestedness in each network. To calculate nestedness we used ANINHADO 3.0 (Guimarães & Guimarães, 2006). Under perfect nestedness, generalist species interact with each other, while the specialist species interact with generalist species (Bascompte et al., 2003). We tested the significance of nestedness for each network through 1,000 simulated networks generated by the Null Model II (CE) (Bascompte et al., 2003), which allowed us to determine if the degree of nestedness was higher than those expected when compared to random patterns of interactions. In this null model, the probability that a bee-plant interaction occurs is proportional to the mean number of interactions of both species (Bascompte et al., 2003). Due to differences of sampling, and species richness, in our study sites, we also calculated nestedness controlling potential differences in richness and heterogeneity of interactions among our four sites by using a z-score, which normalizes the deviation from a mean value (Almeida-Neto et al., 2008).

We also tested whether there were groups of bee species that interacted more frequently with a particular group of plant species (Mello et al., 2011). We assessed modularity (M) within each network based on simulated annealing (SA) (Guimerà et al., 2004; Guimerà & Amaral 2005) using the

software MODULAR (Marquitti et al., 2013). The index ranges from zero to one, and high values of M indicate that different bees and plants species are grouped by modules that are semi-independent, within the network (Olesen et al., 2007). The significance of M also was estimated with Null Model II, described above. If a network was significantly modular, we also tested within each module for a nested pattern.

We calculated network robustness for each site, and to species extinction based on the cumulative random removal of species (*sensu* Burgos et al., 2007). We also used the robustness index (R) to estimate the area under the extinction curve (Burgos et al., 2007; Dáttilo, 2012). This index ranges from zero to one, and values of R close to one come from robust network curves, because their extinction curve decreases slowly (Burgos et al., 2007). When compared to other curves, a robustness index is not as sensitive to curve shape (Burgos et al., 2007).

The generalist core of species per network (G_c), and peripheral species, were categorized using core-periphery components (Dáttilo et al., 2013). When $G_c > 1$ the species are those with the greatest number of interactions when compared with other species in the same trophic level. They constitute the generalist species core. In contrast, when $G_c < 1$ the species exhibit a low number of interactions related to other species in the same trophic level, and form the periphery of the network (Dáttilo et al., 2013).

Results

Our results show that network topology among sites varied widely (Fig 1). The lowest species richness was recorded for the Quintana Roo site (15 plant and 25 bee species), and the highest was Tehuacan-Cuicatlan (88 plant and 231 bee species). The networks of La Mancha and Totutla had intermediate species richness (La Mancha: 65 plant and 43 bee species; Totutla: 56 plant and 156 bee species, Table 2). Networks with lower species richness were more connected: the Quintana Roo site exhibited $C = 0.26$ and Tehuacan-Cuicatlan $C = 0.03$ (Table 2). Greater species richness was linked to a higher number of interactions: Tehuacan-Cuicatlan, 764 bee-plant interactions; Totutla, 615 bee-plant interactions; La Mancha 134 bee-plant interactions; and the Quintana Roo site 98 bee-plant interactions. However, the distribution of interactions was different among the four environments, apparently unrelated to network size. Totutla exhibited the highest mean number of interactions per species (3.18), followed by the Quintana Roo site (2.45) and Tehuacan-Cuicatlan (2.39). The network from La Mancha had the least number of interactions per species (1.24) (Table 2).

The Totutla network had the lowest specialization value ($H_2' = 0.39$); the other specialization values were: the Quintana Roo site ($H_2' = 0.40$), La Mancha ($H_2' = 0.69$), and Tehuacan-Cuicatlan ($H_2' = 0.58$). Moreover, the four networks were significantly nested ($P < 0.05$) ($Z\text{-score}_{NODF}$ values: Quintana Roo site = 1.68, La Mancha = 5.74, Tehuacan-Cuicatlan = 15.28, and Totutla = 24.33). Additionally, the Tehuacan-Cuicatlan network exhibited significant modularity ($M = 0.469$) ($P = 0.02$), with only four of the resulting eight modules significantly nested (Table 2).

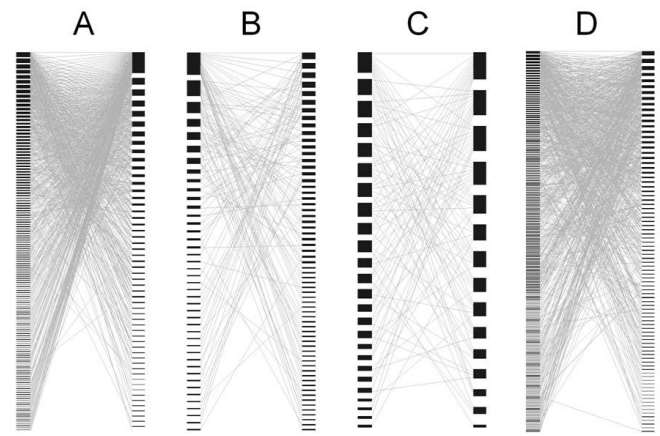


Fig 1. Ecological network involving bees (right) and plants (left) sampled in four different sites of Mexico: (A) Totutla, Veracruz (B) La Mancha, Veracruz (C) Carrillo Puerto, Quintana Roo and (D) Tehuacan-Cuicatlan valley, Puebla. Each node or rectangle represents one plant or bee species, and lines represent bee-plant interactions. Rectangle size represents the number of interactions of a certain species, for instance, a larger rectangle is equal to more interactions by that species.

The robustness to cumulative extinctions showed a different pattern at each site. The most robust network was the Quintana Roo site, where plants exhibited a robustness of $R = 0.86$ and bees $R = 0.65$. The bees at La Mancha were the most vulnerable ($R = 0.25$), while plants ($R = 0.49$) exhibited a similar value that for Tehuacan-Cuicatlan. The Totutla

Table 2. Network descriptors for bee-plant networks studied in four sites of Mexico.

Network descriptor	Tehuacan-Cuicatlan valley	La Mancha	Carrillo Puerto	Totutla
Plant richness	88	65	15	56
Bee richness	231	43	25	156
Connectance	0.03	0.04	0.26	0.08
Network specialization (H_2')	0.58	0.69	0.40	0.39
Links per species	2.39	1.24	2.45	3.18
No. of interactions	764	134	98	616
Nestedness ($NODF$)	11.76*	14.62*	38.39*	48.38*
Nestedness ($Z\text{-Score}_{NODF}$)	15.28	5.74	1.68	24.33
Modularity	0.46*	0.61	0.31	0.34
Robustness to cumulative plant extinctions (R)	0.32	0.49	0.86	0.49
Robustness to cumulative bee extinctions (R)	0.49	0.25	0.65	0.26
No. of species in the generalist core (% of total)	15 (17.04%)	10 (15.38%)	4 (26.66%)	6 (10.71%)
No. of species in the generalist core (% of total)	24 (10.38%)	5 (11.62%)	4 (12%)	16 (10.25%)

* represents $P\text{-values} < 0.05$

network exhibited very similar values to those of La Mancha (bees $R=0.26$, plants $R=0.49$). Finally, the plants in Tehuacan-Cuicatlan were most vulnerable to species extinctions ($R=0.32$), while bees exhibited higher robustness to species loss ($R=0.49$) (Table 2).

The Quintana Roo site network exhibited the most robust species core (26.66% of total plant species in the network), while only three bee species (12% the total, see Appendix) were included in the network core. Compared to the other three sites, the number of plant species in the core of the Totutla network was the smallest (10.71%) ($n=6$ species, see Appendix), with a similar result for core bee species (10.25%) ($n=16$ species) (Figure 2). The La Mancha plant species core was the second smallest (15.38%), however, more species were included ($n=10$ species, see Appendix), the La Mancha bee core exhibited an intermediate value (11.62%) ($n=5$ species, see Appendix). Core bees for Tehuacan-Cuicatlan were fewer (10.38%), although composed by 24 species (see Appendix). The plant core exhibited intermediate size (17.04%) and was composed by 15 species (see Appendix). Overlap is meaningless among core species (plants, bees): 1 plant species between sites 1 and 2, and 1 plant species between sites 2 and 3; 1 bee species between sites 1 and 4, and 2 bee species between sites 1 and 2.

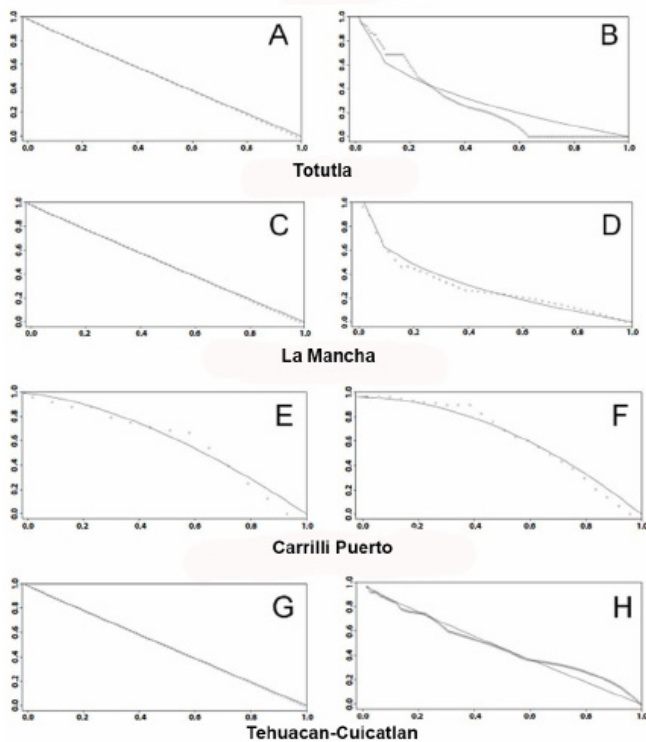


Fig 2. Robustness to cumulative species removal of plants and bees in (A-B) Totutla, Veracruz (C-D) La Mancha, Veracruz (E-F) Carrillito Puerto, Quintana Roo and (G-H) Tehuacan-Cuicatlan valley, Puebla. The images on the left (A-C-E-G) simulate the extinction of plant species, and the images on the right (B-D-F-H) simulate the extinction of bee species. The x-axis axis represents the proportion of primary extinctions of a trophic level, and the y-axis represents the proportion of species in the other trophic level still alive.

Discussion

We found that in the four areas bees exhibit a nested pattern of foraging, independent of variation in local and landscape environmental factors or species composition. Plant-pollinator networks have been evaluated in different types of habitats around the world, and in most cases they exhibit a highly nested pattern (Olesen & Jordano, 2002; Bascompte et al., 2003; Jordano et al., 2003). Despite differences in habitat structure among areas, we observed that our networks were significantly nested, suggesting that different populations of plants and bees interact in a similar way independent of variations in local and landscape environmental factors, and are highly stable as predicted by previous studies (Bascompte et al., 2003; Vázquez et al., 2009; Hagen et al., 2012). Biologically, the nested pattern decreases interspecific competition within mutualistic networks and increases species coexistence, generating a stable pattern of plant-animal interactions (Bastolla et al., 2009). Based on this perspective, we show that our nested networks have great stability to simulated species loss when compared with structurally different networks (e.g. highly compartmentalized) (Mello et al., 2011; Dáttilo, 2012; Clemente et al., 2013).

However, when we evaluated network robustness to simulated species extinction, we observed that areas with greater specialization (e.g. Tehuacan-Cuicatlan valley and La Mancha) tend to be less robust. This probably occurred because environments with a high number of specialist interactions tend to have lower functional redundancy, and therefore, when a species is extinct in a trophic level only a few species from another trophic level can “dampen” the system (Mouchet et al., 2010; Joner et al., 2011). Due to the high specialization of bee-plant networks in the Tehuacan-Cuicatlan valley and La Mancha generated by different mechanisms, it is expected that these areas are functionally less redundant and resilient to disturbances (e.g. Sánchez-Galván et al., 2012). This was confirmed when species were removed from these networks, the extinction curves declined faster compared with other networks, because deletion of one species necessarily causes the deletion of other partner species. Our results demonstrate that environments with many specialized interactions are highly susceptible to loss of species and this pattern should occur in other systems of ecological networks with a high degree of specialization (wasp-plant and ant-myrmecophyte) (Dáttilo et al., 2012; Clemente et al., 2013).

It has been noted that as species richness increases in the community, the number of registered interactions also increases; however, connectance decreases exponentially (Jordano, 1987; Blüthgen, 2010). Our results corroborate these studies, since the most species-rich networks (Tehuacan-Cuicatlan and La Mancha) were the least connected networks. Our results suggest that this occurred because bees and plants within these networks had fewer interactions per species, when compared with the other study sites. This result indicates that most interactions in less connected networks tend to be pairwise (Fonseca & Ganade,

1996), which could generate a high degree of specialization within such networks, as found in our networks. Why were the Tehuacan-Cuicatlan and La Mancha networks the most specialized? We believe that different mechanisms could be responsible for the high degree of specialization found in these areas. In La Mancha, sampling was conducted in locations with different environmental complexities, and therefore, so that certain groups of plants and bees could be habitat specialists (i.e. collected in few sites) and cause more specialized interaction profiles (McPeck, 1996; Warren et al., 2001). The high degree of specialization in Tehuacan-Cuicatlan possibly occurred due to the extreme endemism that occurs in the area. For instance, areas with large numbers of endemic species tend to have more specialists and rare interactions (Olesen et al., 2002; Hansen et al., 2002), which is due to the great geographical isolation over evolutionary time and may lead to specialized processes among species (Thompson, 2005). Interestingly, when data on floristic richness and endemism is compared with that of other natural areas in Mexico, it becomes evident that Tehuacan-Cuicatlan is highest for endemic species (Méndez-Larios et al., 2004). Therefore, based on the differences between Tehuacan-Cuicatlan and La Mancha, it is important to consider that structural characteristics of the vegetation and endemism may be important factors shaping the ecological interactions involving bees and plants.

Several studies have demonstrated that pollination networks can be highly modular (Olesen et al., 2007; Ramos-Jiliberto et al., 2010; Hernández-Yáñez et al., 2013). These structures only refer to the presence of groups of species (plants, animals) that interact more intimately with other species in their group rather than with other species in the network (Olesen et al., 2007). However, these studies have evaluated networks considering different taxonomic groups together. Here we only considered bees, and we should expect a scarce presence of modules, because having only one type of organism a certain historical evolution is shared. In fact, the presence of a modular pattern depends on several factors, from evolutionary to spatial and temporal (Olesen et al., 2007; Mello et al., 2011). Our results only show a modular pattern for the plant-bee network collected in Tehuacan-Cuicatlan valley. It is possible that through evolutionary time, the high endemism found in this area contributed to the convergence of traits in phylogenetically related bee groups, which currently may visit a group of common plants.

Finally, part of the Totutla forest has been converted to an organic coffee plantation, altering the interactions naturally found there (Steffan-Dewenter et al., 2001; Tylianakis et al., 2007). Our results suggest that the abundance of *Bidens pilosa* (Compositae, Asteraceae), a common secondary plant species, could be explained due to the type of management used.

In summary, our results show that structural characteristics of the environments over space are extremely important factors that shape interactions involving plants and bees. Moreover, we found that areas with endemic species tend to have more specialized interactions, and that the nature of this characteristic can also influence the patterns of interactions

among organisms and the susceptibility to extinction of species. Therefore, our results reinforce the role of environmental variation in species maintenance and biodiversity in hyper-diverse systems.

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Appendix

Species (plants, bees) in the core of the networks per sampled site

La Mancha, Veracruz

Plants

Bauhinia divaricata
Bidens pilosa
Randia laetevirens
Turnera diffusa
Lantana camara
Waltheria indica
Palafoxia lindenii
Hyptis suaveolens
Tecoma stans
Piscidia piscipula

Bees

Apis mellifera
Lasioglossum sp1
Trigona nigra
Ceratina sp1
Euglossa viridissima

Carrillo Puerto, Quintana Roo

Plants

Gymnopodium floribundum
Cassia fistula
Croton campechianus
Parthenium hysterophorus

Bees

Centris sp.
Augochlora sp.
Trigona fulviventris

Totutla, Veracruz

Plants

Bidens pilosa
Elephantopus molis
Smallanthus maculatus
Sida rhombifolia
Marsypianthes chamaedrys
Cyperaceae sp1
Ceratina sp1
Trigona fulviventris
Lasioglossum sp8
Augochlora aurifera
Ceratina nautlana
Melissodes tepaneca
Lasioglossum costale
Trigona corvina
Trigona nigerrima

Bees

Augochloropsis sp1
Ceratina sp2
Bombus medius
Lasioglossum sp1
Paratetrapedia apicalis
Apis mellifera

Tehuacan-Cuicatlan valley, Puebla

Plants

Salvia polystachya
Ipomoea pauciflora
Sanvitalia fruticosa
Echinocactus platyacanthus
Hechtia podantha
Gymnosperma glutinosum
Tecoma stans
Wigandia urens
Flaveria pringlei
Prosopis laevigata
Viguiera dentata
Verbesina neotenoriensis
Beaucarnea gracilis
Macroptilium atropurpureum
Nissolia microptera
Exomalopsis pueblana
Agapostemon sp1
Lasioglossum sp13
Centris transversa
Ceratina sp3
Ceratina nautlana
Lasioglossum sp18
Megachile otomita
Melissodes tepaneca

Bees

Plebeia frontalis
Agapostemon cockerelli
Melissodes gilensis crenata
Augochlora neglectula
Lasioglossum sp16
Centris atripes
Lasioglossum sp6
Halictus ligatus
Paraugochloropsis vesta
Ashmeadiella zapotitlana
Macrotera azteca
Megachile zapoteca
Paraugochloropsis metallica
Anthidium maculifrons
Anthophora californica